The Gross Anatomy of the Original and Regenerated Tail in the Green Anole (*Anolis carolinensis*)

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ABSTRACT

This study investigates the gross anatomy of the original and the regenerated tail in the green anole (*Anolis carolinensis*). Dissections were conducted on 24 original and 13 regenerated tails. While the extrinsic muscles of the original tail in *A. carolinensis* are similar to those in other known *Anolis* lizard species, the extent of the origins of *m. caudofemoralis longus* and *m. caudofemoralis brevis* is more restricted. These differences may underlie variation in locomotor performance among anole ecomorphs. The intrinsic muscles of the original tail are also described, confirming previous findings and documenting new details, including muscle origins and insertions and the range of intraspecific variation. A comparison of the intrinsic muscles of the original tail and the regenerated tail muscles reveals key differences, such as the lack of interdigitating muscle segments and intramuscular septa in the regenerated tail. These findings, along with the replacement of interlocking vertebrae with a stiff, cartilaginous rod, suggest that important functional differences exist between the original and regenerated tail. In particular, the regenerated tail is predicted to be less capable of coordinated, fine movements. Studies of the physical properties and range of motion of the original and regenerated tail are required to test this hypothesis. This atlas of tail anatomy in *A. carolinensis* represents a key resource for developmental and genetic studies of tail regeneration in lizards, as well as studies of anole evolution and biomechanics. Anat Rec, 295:1596–1608, 2012.   ©2012 Wiley Periodicals, Inc.

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Many lizard taxa exhibit the remarkable ability to regenerate their tails and spinal cords and, as such, represent the group most closely related to mammals that possesses this facility. While the process of tail regeneration in lizards has been documented in some detail (Hughes and New, 1959; Bryant and Bellairs, 1967; Cox, 1969a,b; Simpson, 1964, 1968, 1970; Bellairs and Bryant, 1985; Duffy et al., 1990; Alibardi et al., 1993; Simpson and Duffy, 1994; Alibardi, 1993, 1994a,b,c, 1995a,b; Alibardi and Toni, 2005; Alibardi, 2010), the anatomy of the regenerated tail has not been fully characterized. Moreover, the anatomy of the original tail has only been described for a few lizard species.
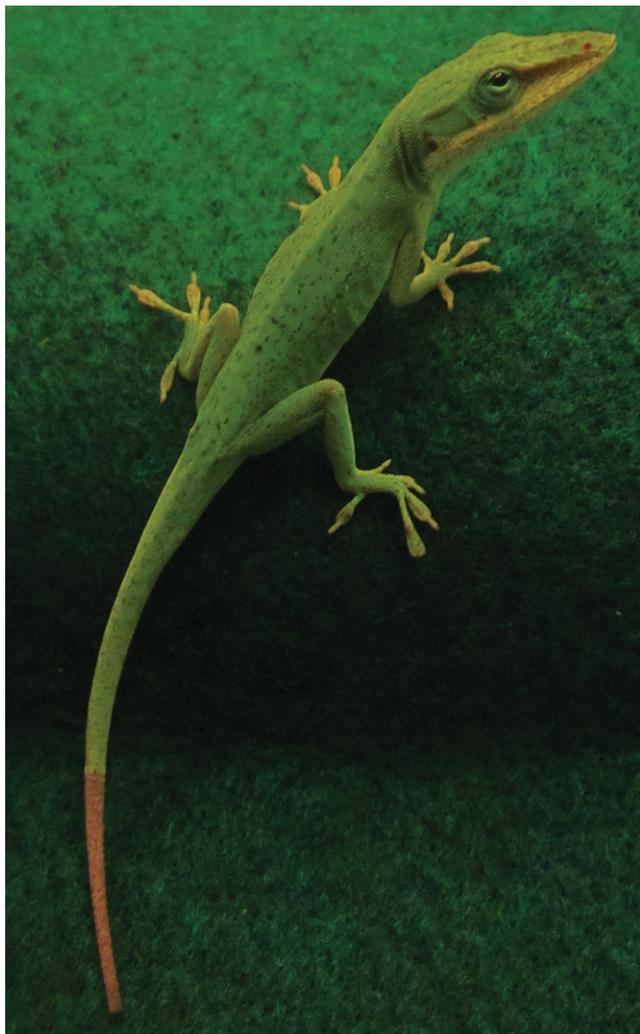
Fig. 1. Male *A. carolinensis* specimen with a regenerated tail. The brown, distal portion of the tail is the regenerated segment. Photograph courtesy of Inbar Maayan.

This study examines the anatomy of the original and regenerated tail in the green anole (*Anolis carolinensis*) (Fig. 1). *A. carolinensis* was chosen as a model for understanding tail anatomy and regeneration in lizards for three main reasons. First, it is a suitable taxon for developing and maintaining captive breeding populations, and colonies of healthy animals can be developed and maintained relatively easily (Lovern et al., 2004). Second, the process of tail autotomy, whereby the tail is shed to evade predators, as well as the process of tail regeneration are relatively well understood in *A. carolinensis* compared with many other lizard species with this ability (Simpson, 1968; Cox, 1969a,b). Finally, the genome of *A. carolinensis* has been sequenced (Alföldi et al., 2011), making it an excellent model for understanding the genetic regulation of tail regeneration and underscoring the need for detailed anatomical investigations of the original and the regenerated tail in this species. Members of this research team are currently carrying out studies of the genetics underlying tail

regeneration, including characterization of the *A. carolinensis* transcriptome (Eckalbar et al., 2012).

A. carolinensis is an arboreal lizard native to the southeastern United States and some Caribbean islands. The presence of *A. carolinensis* on the mainland is due to a Pliocene invasion from the West Indies (Buth et al., 1980; Glor et al., 2005; Nicholson et al., 2005; see also Auffenberg and Milstead, 1965; Williams, 1969). *A. carolinensis* is one of roughly 375 species included in the genus *Anolis* (Losos, 2009), and comparative studies within the genus have been widely used to examine niche partitioning and other evolutionary questions. Anole lizards diversified as a result of multiple adaptive radiations, and species from the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico) have been classified into "ecomorphs" or groups that share aspects of morphology, microhabitat use, and behavior that have evolved convergently on each of the four islands (Rand and Williams, 1969; Williams, 1972, 1983; Losos and Sinervo, 1989; Losos, 1990a,b,c, 1992; Irschick and Losos, 1998; Losos et al., 1998).

Much of the distinction among the anole ecomorphs is related to limb size and resultant effects on locomotion (Williams, 1983; Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos, 1992; Losos and Irschick, 1996; Irschick and Losos, 1998, 1999; Losos et al., 1998; Vanhooydoonck et al., 2006a,b; Herrel et al., 2008; Losos, 2009). In addition to the considerable effect that limb morphology has on locomotor performance, the tail (in both its original and regenerated forms) is important in balance and stabilization during locomotion (Ballinger, 1973; Ballinger et al., 1979; Punzo, 1982; Daniels, 1985; Brown et al., 1995; Martin and Avery, 1998; Chapple et al., 2004; Lin et al., 2006; Gillis et al., 2009). The lizard tail may also function in predator defense and evasion, sexual displays, and fat storage (Vitt et al., 1977). All of these functions may be affected by autotomy and subsequent regeneration of the tail (Congdon et al., 1974; Vitt et al., 1977; Dial and Fitzpatrick, 1981; Fox and Rostker, 1982; Schall et al., 1989; Arnold, 1990; Martín and Salvador, 1992, 1993; Fox and McCoy, 2000; Fitch, 2003; Clause and Capaldi, 2006). To fully understand how the original and regenerated tails function (as well as to determine what functional differences, if any, exist between the original and regenerated tails), the anatomy of the tail in its original and regenerated forms must be documented.

The goal of this study is to describe the musculature, osteology, and chondrology of the original and the regenerated tail in *A. carolinensis*. This study serves as a complement to the histological analysis of the tail in this species (Fisher et al., in press). Together, gross anatomical and histological studies of *A. carolinensis* will provide a framework for examining potential functional differences between the original and regenerated tail. More generally, the present study provides a detailed anatomical atlas that will ultimately inform studies of the comparative morphology and locomotor performance of anoles as well as the genetic control of tail regeneration in *A. carolinensis*.

CAUDAL OSTEOLOGY

Among lizard species, the osteology of the tail varies dramatically in terms of the total number of vertebrae,

changes in the size and shape of the transverse processes and neural spines along the length of the tail, and the presence or absence of fracture planes [i.e., the plane at which autotomy occurs; Etheridge (1967)]. Many authors (e.g., Holder, 1960; Mufti and Hafiz, 1972; Bellairs and Bryant, 1985; Russell and Bauer, 1992) have referred to the more proximal caudal vertebrae that lack fracture planes as "pygal vertebrae" and the more distal caudal vertebrae that possess fracture planes as "postpygal vertebrae." However, many lizard taxa lack fracture planes in their caudal vertebrae altogether, making this classification difficult to apply in these cases (Etheridge, 1967; Bellairs and Bryant, 1985). Furthermore, in some species (including *A. carolinensis*) the most distal of the transverse process-bearing vertebrae may possess fracture planes and should technically be called postpygal vertebrae, despite the fact that they more closely resemble the more proximal, non-fracture plane-bearing vertebrae in overall morphology (Cox, 1969a). Due to these problems, the terms "pygal" and "postpygal" will not be used in this study. Instead, the more proximal, transverse process-bearing vertebrae will be referred to collectively as the "TP vertebrae," whereas the more distal, nontransverse process-bearing vertebrae will be referred to collectively as "NTP vertebrae."

While the caudal osteology of lizard species is highly variable, Etheridge (1967) defined six general types of lizard caudal vertebral sequences. These types were based on the number and type of transverse processes and the presence and location of fracture planes. Based on the categories proposed by Etheridge (1967), Bellairs and Bryant (1985) included *A. carolinensis* in a group that is characteristic of many autotomizing and nonautotomizing species in the genus *Anolis*. Species in this group possess a short series of caudal vertebrae with a single pair of transverse processes (TP vertebrae) followed by a series of NTP vertebrae (Fig. 2). The distalmost vertebra in the TP series is the only one in that series that may bear a fracture plane, and the NTP vertebrae may or may not possess fracture planes (Bellairs and Bryant, 1985). In *A. carolinensis* specifically, only the 9th to 18th caudal vertebrae may possess fracture planes (Cox, 1969a). However, autotomy in *A. carolinensis* can occur in any vertebra distal to the one bearing the first fracture plane (Cox, 1969a). Interestingly, zones of cartilage or connective tissue do not demarcate the fracture planes in *A. carolinensis*, as seen in other lizard taxa (Cox, 1969a; Hoffstetter and Gasc, 1969).

EXTRINSIC TAIL MUSCLES

The tail muscles that have attachments outside the tail (the "extrinsic tail muscles") have not been fully characterized in *A. carolinensis*. Existing descriptions relate solely to the muscles associated with the hemipenes in males (Ruiz and Wade, 2002; Wade, 2005). However, some of the extrinsic tail muscles in other species in the genus, including *A. garmani* (Russell and Bauer, 1992) and *A. sagrei* and *A. valencienni* (Herrel et al., 2008) have been described. In addition, a number of studies have documented these muscles in the confamilial genus *Iguana* [i.e., *I. iguana* (Haines, 1935; Olson, 1936; Bellairs and Bryant, 1985; Russell and Bauer, 1992; Tsuihiji, 2005, 2007) and *I. tuberculata* (Mivart, 1867)]. However, it should be noted that not all of these

accounts agree (see Terminology below). The anatomy of the extrinsic tail muscles in more distantly related lizard taxa has also been described (Sanders, 1874; Romer, 1922; Ali, 1947; John, 1971; Zaaf et al., 1990).

Based on these studies, the anatomy of the extrinsic tail muscles is relatively conserved in lizards. However, important variation has been noted in the extent of the origin of *m. caudofemoralis longus* on the caudal vertebrae (Russell and Bauer, 1992). This muscle, which is the primary extensor of the hip joint in lizards (Snyder, 1952, 1954; Gatesy, 1990), originates on the caudal vertebrae and inserts onto the femur. Because it is a nonsegmental muscle, autotomy cannot occur in the vertebrae associated with the origin of *m. caudofemoralis longus*. In fact, in a study of a diverse sample of lizard taxa, Russell and Bauer (1992) demonstrated that the extent of the origin of this muscle corresponds closely to the location of the first fracture plane-bearing vertebra.

INTRINSIC TAIL MUSCLES

Compared with the extrinsic muscles of the tail, the muscles that attach exclusively to bones and septa within the tail (the "intrinsic tail muscles") have been documented in very few taxa. The most detailed study of the anatomy of the intrinsic tail muscles in *A. carolinensis* was performed by Cox (1969a). The intrinsic muscles have also been described in the confamilial *I. tuberculata* (Mivart, 1867). Lizards in the more distantly related suborder Scleroglossa have also been analyzed, including species in the families Chameleonidae [*Chameleon zeylanicus* (Ali, 1947); *Furcifer pardalis* (Zippel et al., 1990)], Gekkonidae [*Sphaerodactylus* sp. (Hughes and New, 1959); *Hemidactylus flaviviridis* (Mufti and Hafiz, 1972)], and Scincidae [*Corucia zebrata* (Zippel et al., 1990)]. In addition, Bellairs and Bryant (1985) provided a detailed account of the intrinsic muscles in lizards. However, these authors did not provide specific taxonomic details (i.e., the names of the taxa in which the described anatomy had been observed); therefore this account is best treated as a general baseline from which individual lizard species may diverge to varying degrees.

Cox (1969a) noted that the tail musculature in *A. carolinensis* is composed of a number of myomeric segments that are separated by horizontal intramuscular septa into epaxial (dorsal) and hypaxial (ventral) muscles. The muscles are further divided into left and right sides by ventral and dorsal septa, resulting in quadrants. In addition, the myosepta between adjacent myomeres are folded such that the muscles in each quadrant resemble a "W" shape (Cox, 1969a). According to Cox (1969a), each myomere extends across the length of three vertebrae, and each extension of the "W" fits into the adjacent myomere like nonregularly stacked cones. Furthermore, Cox (1969a) reported that, when autotomy occurs, 10 muscle slips extend from the proximal end of the autotomized portion of the tail, while 10 corresponding cavities are left in the intact tail stump, and eight muscle slips extend distally from the stump (Cox, 1969a).

REGENERATED TAIL

The muscles and cartilage in the regenerated tail have not been systematically studied in most lizard species [see reviews by Bellairs and Bryant (1985) and
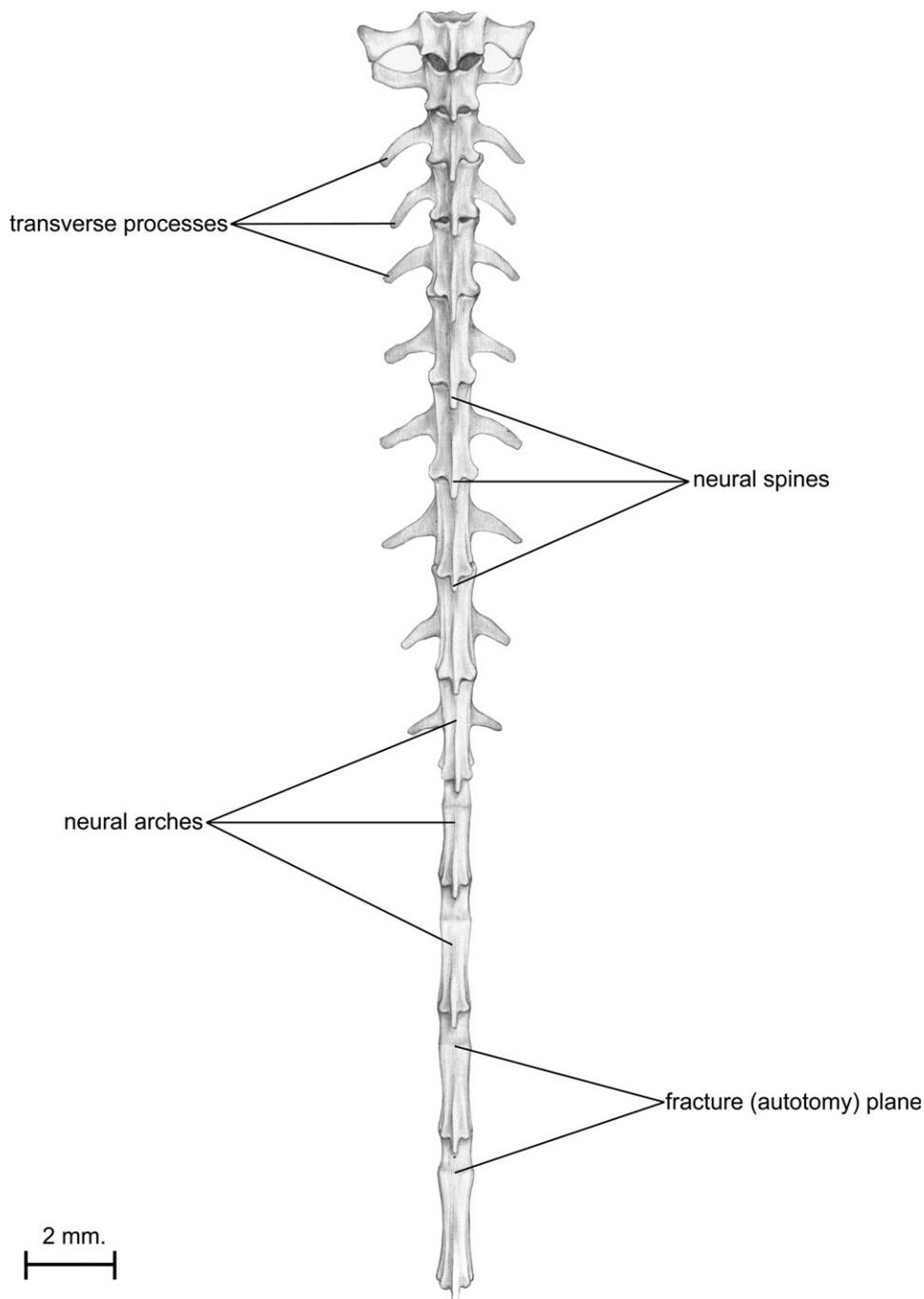
Fig. 2. Caudal osteology of *A. carolinensis*. Ca1 is located at the top, with more distal caudal vertebrae located at the bottom. Illustration by Yue Yuan.

Alibardi (2010)]. The most conspicuous difference between the original and the regenerated tail in lizards is that, in the regenerated tail, the caudal vertebrae are replaced by a cartilaginous tube that may become calcified or ossified (Cox, 1969a; Bellairs and Bryant, 1985; Alibardi, 2010). The regenerated muscles have been characterized as less regular and lacking any attachment to the caudal vertebrae proximal to the fracture point (Bellairs and Bryant, 1985). The regenerated

muscles begin as a series of new myomeres (Hughes and New, 1959; Simpson, 1968; Cox, 1969a) and thin connective tissue inscriptions separate adjacent muscle segments (Bellairs and Bryant, 1985). Unlike the intrinsic muscles in the original tail, the regenerated tail lacks well-defined septa and, therefore, also lacks clearly defined quadrants (Bellairs and Bryant, 1985). Instead, the regenerated tail muscles are separated into a number of longitudinal myomeres (Bellairs and Bryant,

TABLE 1. Muscle names used in the present study and previous studies

Muscle names used in present study	Alternative muscle names
M. caudofemoralis longus (John, 1971; Zaaf et al., 1990; Russell and Bauer, 1992; Organ, 2006; Herrel et al., 2008; Sheffield et al., 2011)	*M. caudifemoralis* (Romer, 1922; Arnold, 1984; Ruiz and Wade, 2002); *M. caudofemoralis* (Haines, 1935); *Femoro-caudal* (Mivart, 1867)
M. caudofemoralis brevis (Haines, 1935; John, 1971; Zaaf et al., 1990; Herrel et al., 2008)	
M. iliocaudalis (Romer, 1922; John, 1971; Ruiz and Wade, 2002; Herrel et al., 2008; Arbour, 2009)	*Supracaudal* (Mivart, 1867)
M. coccygeus inferior (Herrel et al., 2008)	*M. ischiocaudalis* (John, 1971; Ruiz and Wade, 2002); *Pars ischiocaudalis of ilio-ischiocaudalis* (Arnold, 1984)
M. ischiocaudalis (Romer, 1922; Ruiz and Wade, 2002)	*Pars iliocaudalis of ilio-ischiocaudalis* (Arnold, 1984)
M. extensor caudae medialis (Olson, 1936)	*M. levator caudae internus* (Gregory and Camp, 1918)
M. extensor caudae lateralis (Romer, 1922; Olson, 1936)	*M. levator caudae externus* (Gregory and Camp, 1918); *M. ischiocaudalis* (Herrel et al., 2008)

1985). Specifically, Bellairs and Bryant (1985) report that up to 14 such myomeres are present in a transverse section of the regenerated tail of Lacertidae, but no mention is made of the species upon which this observation is based.

TERMINOLOGY

In the descriptions below, caudal vertebrae are referred to with the prefix "Ca" (i.e., the sixth caudal vertebra is denoted as "Ca6"). The muscle names in this study derive from a consensus of the literature on lizard hindlimb and tail anatomy (Table 1). In general, the muscle names follow those used by Romer (1922) and Olson (1936). It should be noted that a large degree of confusion exists in the literature on lizard tail myology. Specifically, there is a general lack of agreement among authors regarding which of the muscles in the transversospinalis group contribute to the dorsal extrinsic muscles of the tail. This lack of consensus is due in large part to a lack of clarification about the homology and names of the muscles in the transeversospinalis group (Tsuihiji, 2005). In this study, the conventions outlined in Tsuihiji (2005) for naming the muscles in this group were used, and the contributions of these muscles to the dorsal extrinsic muscles of the tail are described.

MATERIALS AND METHODS

Adult *A. carolinensis* lizards were obtained from The Sullivan Company (Nashville, TN) and Marcus Cantos Reptiles (Fort Myers, FL). All animals were maintained according to the guidelines of the Institutional Animal Care and Use Committee at Arizona State University. Lizards were housed in incubators (Percival Manufacturing Co., Boone, IA) at 70% humidity, with 14 hr of daylight at 28°C and 10 hr of darkness at 22°C. Anoles were fed crickets once every 2 days, with weekly Rep-cal calcium and Vitamin D supplementation (Repcal Research Labs, Los Gatos, CA). Water was provided by daily mist-spraying of artificial plant surfaces.

Lizards were euthanized by intracoelomic sodium pentobarbital injection (final concentration of 120 µg/g), fresh frozen, and then subsequently defrosted in water and fixed in 70% ethanol for 72 hr. Specimens were then stored in water and dissected within 1 week of being fixed. All dissections were performed using a Nikon SMZ800 stereo dissecting microscope and digital photo-graphs were taken at all stages of the dissections using a Nikon Coolpix E995 digital camera with a Coolpix MDC relay lens. Thirty-seven lizards were dissected. The anatomy of the original tail was examined in 24 specimens (12 males and 12 females); these specimens were intact apart from three of the male specimens, which consisted of detached tails only. The regenerated tail was examined in 13 specimens (seven males, six females); these specimens were also intact apart from three of the male specimens, which consisted of detached tails only. All of the regenerated tails were completely regenerated (>100 days postautotomy). The mean snout-vent length was 60.30 ± 3.97 mm for males (N = 9) and 50.85 ± 3.12 mm for females (N = 8). Mean mass was 5.72 ± 1.30 g in males (N = 7) and 3.09 ± 0.89 g in females (N = 7).

Six skeletal preparations (one male, five females) were performed to provide material for investigating the morphology of the caudal vertebrae (e.g., neural spines, fracture planes). The protocol used for skeletal preparation was based on protocols described in Kaufmann (1992), Hanken and Wasserug (1981), and Taylor and van Dyke (1985). However, the following modifications were made: (1) Specimens were placed in acetone 2 days before staining; (2) the concentration of Alcian blue stain was changed to 0.2% Alcian blue in 70% ethanol and 30% glacial acetic acid; (3) an additional clearing step was added using 1% aqueous potassium hydroxide for 12 to 48 hr [whenever clearing was not complete after this step, an additional clearing step was added using 2% aqueous potassium hydroxide for 12–48 hr (or until clearing was complete)]; and (4) the length of the last clearing step was changed to 1 week in each of four downgraded concentrations of glycerol and potassium hydroxide (i.e., 0% glycerol, 25% glycerol, 75% glycerol, and 100% glycerol). In addition to the skeletal preparations, five intact specimens with nonautotomized tails (two males, three females) were dissected to perform counts of caudal vertebrae. These specimens were euthanized, frozen, and fixed in the same way as described above.

RESULTS
Caudal Osteology

In the intact *A. carolinensis* skeletons examined for this study, the total number of caudal vertebrae varied between 39 and 41 in males (N = 2) and between 37 and 43 in females (N = 3). The proximal most 8 to 13 vertebrae are characterized by long and slender transverse

processes (TP vertebrae; Fig. 2). The transverse processes of Ca1-2 or 3 are proximolaterally oriented; however, these transition to a more lateral orientation in the distal vertebrae in this sequence. In addition, distal to Ca2-3, the transverse processes gradually decrease in size. The TP vertebrae also possess slender neural spines. In Ca1-2 or 3, the spines originate from the middle of the centra; however, the spines shift to the distal half of the centra in the rest of this sequence. Chevron bones are also present in the TP vertebrae, with the exception of Ca1-2 or 3. Located on the ventral aspect of the centra, the chevron bones form hemal arches that transmit the caudal vasculature. Fracture planes were not observed in the TP vertebrae (contra Cox, 1969a). Distal to the series of TP vertebrae is a longer series of 24–35 NTP vertebrae (Fig. 2). The NTP vertebrae become smaller and longer (relative to their dorsal–ventral dimension) distally. In the specimens examined for this study, fracture planes were observed in only the proximal most five to seven vertebrae in this sequence. When present, the fracture planes lie approximately one-quarter of the way from the proximal end of the centrum. Along the entire caudal spine, the prezygapophyses are oriented dorsally, whereas the postzygapophyses are oriented ventrally.

Extrinsic Tail Muscles

M. spinalis caudalis. This muscle originates via thin tendons from the proximal and dorsal aspects of the neural spines and inserts via fleshy fibers onto the lateral aspect of the base of the neural arch (Fig. 3A,B). It is composed of numerous, separable musculotendinous units that run proximomedially to distolaterally and extend three to four vertebral levels. The *m. spinalis caudalis* terminates at the level of Ca5 or 6 and represents a continuation of *m. spinalis dorsi* into the tail, sharing the same origin and insertion points, albeit on the caudal, rather than the lumbar and thoracic vertebrae (see Tsuihiji, 2005). These muscles are distinguished arbitrarily at the level of Ca1. The *m. spinalis caudalis* is hypothesized to be a stabilizer of the vertebral column.

M. extensor caudae medialis. This muscle originates via thin tendons from the distal and dorsal aspects of the neural spines (Fig. 3A). The tendons course proximomedially to distolaterally and give rise to fleshy fibers that insert onto the lateral aspect of the neural arches of each of the vertebrae it crosses. The *m. extensor caudae medialis* is a continuation of *m. semispinalis dorsi* into the tail (see Tsuihiji, 2005), and these muscles are distinguished arbitrarily at the level of Ca1. At the level of Ca5, the fibers of *m. extensor caudae medialis* join those of *m. extensor caudae lateralis*. The two muscles are fused but distinct until Ca8 at which point they merge completely to give rise to the dorsal intrinsic muscles (see below). In most specimens, *m. extensor caudae medialis* was organized into chevron-shaped units by tendons on its superficial surface. However, the tendons contributing to the chevron-shaped units were less developed in some specimens and absent in a few of the smaller female specimens that were examined. This chevron-shaped arrangement is also seen in the dorsal intrinsic muscles, where two adjacent chevrons fuse to form a "W"-shaped segment (see below). The *m. extensor caudae*
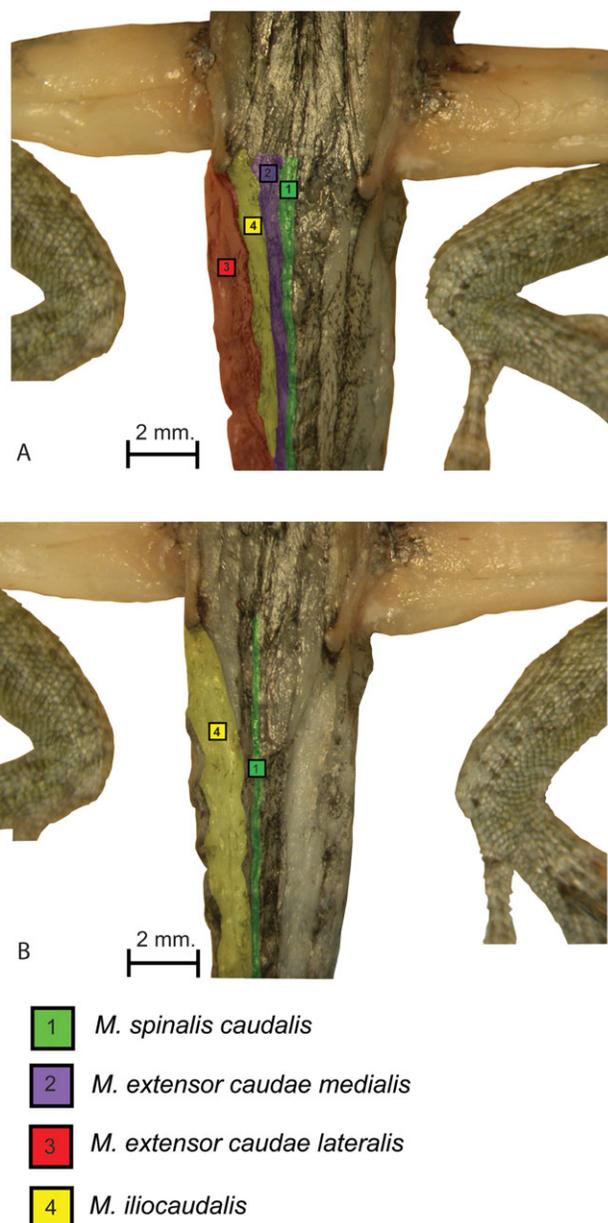

Fig. 3. Dorsal views of the extrinsic muscles of the original tail in *A. carolinensis*, including a superficial (**A**) and deep (**B**) dissection. In A, the specimen has been skinned, but all of the musculature is intact. In B, the *mm. extensor caudae lateralis* and *medialis* have been removed.

medialis is hypothesized to be a tail extensor when it contracts bilaterally and a lateral flexor of the tail when it contracts unilaterally.

M. extensor caudae lateralis. This muscle originates via a robust tendon from a tuberosity on the cranial aspect of the iliac crest and via fleshy fibers from the caudoventral aspect of the pelvis, the lateral aspects of the transverse processes of Ca2-8 or 9, and the horizontal intramuscular septum (Fig. 3A). Proximal to Ca6, *m. extensor caudae lateralis* inserts onto the dorsal fascia of the tail via fleshy fibers. At the level of Ca5, its

fibers join those of *m. extensor caudae medialis*. The two muscles are fused but distinct until Ca8, when they merge to give rise to the dorsal intrinsic muscles (see below). In most specimens, *m. extensor caudae lateralis* was organized into chevron-shaped units by tendons on its superficial surface. However, the tendons contributing to the chevron-shaped units were less developed in some specimens and absent in a few of the smaller female specimens that were examined. This chevron-shaped arrangement is also seen in the dorsal intrinsic muscles, where two adjacent chevrons fuse to form a "W"-shaped segment (see below). The *m. extensor caudae lateralis* is hypothesized to be a tail extensor when it contracts bilaterally and a lateral flexor of the tail when it contracts unilaterally.

M. iliocaudalis. This muscle lies deep to the *m. extensor caudae medialis* and originates via fleshy fibers from the iliac crest (Fig. 3A,B). It inserts via fleshy fibers onto the horizontal intramuscular septum as well as the chevron bones and dorsal aspect of the transverse processes of Ca3-6 or 7. The fibers of *m. iliocaudalis* are noticeably bipennate. Near its origin, *m. iliocaudalis* is directly adjacent to the distalmost fibers of *m. longissimus dorsi*. These fibers are closely adhered to each other, but a fascial plane is present, and the two muscles are easily separated. The *m. iliocaudalis* is hypothesized to be a tail flexor when it contracts bilaterally and a lateral flexor of the tail when it contracts unilaterally.

M. transversus penis/M. transversus perinei. In males, *m. transversus penis* overlies the hemipenis through its entire course and overlies *m. retractor penis magnus* more distally (Fig. 4A). In females, *m. transversus perinei* overlies the soft tissue related to the cloaca, where the hemipenes are located in males. In both sexes, the muscle attaches via fleshy fibers to *m. ischiocaudalis* laterally and *m. cocygeus inferior* medially. Fibers from *m. transversus penis* also surround the hemipenis dorsally (i.e., between the hemipenis and the underlying *m. caudofemoralis longus*). In some male specimens, transverse fibers of *m. transversus penis* partially covered the fibers of *m. cocygeus inferior*. The distalmost extent of this muscle corresponds with the point at which *m. cocygeus inferior* and *m. ischiocaudalis* join (i.e., Ca3-4 in females; Ca4-5 in males). Although the function of this muscle is difficult to discern, previous researchers have argued that, in males, this muscle everts the hemipenis through the vent of the cloaca (Arnold, 1984).

M. retractor penis magnus. This tube-like muscle attaches to the distal tip of the hemipenis and inserts onto the transverse processes of Ca8, in conjunction with the origins of the left and right *m. caudofemoralis longus* (Fig. 4B). Like that of *m. transversus penis*, the function of *m. retractor penis magnus* is difficult to deduce. However, this muscle likely acts to help retract the hemipenis into the cloaca after copulation (Arnold, 1984).

M. caudofemoralis longus. This muscle originates via fleshy fibers from the bases of the chevron bones and the ventral aspects of the transverse processes of Ca3-8 (Fig. 4A–E). It is composed of two heads (ventral and dorsal) that are fused for most of their length and give rise to a common tendon. The common tendon divides to give rise to: (1) a broad and stout tendon that inserts onto the cranial aspect of the proximal one-fifth of the femur, and (2) a thin tendon that inserts onto the knee joint capsule, between the proximal aspects of the two bellies of *m. gastrocnemius* and the right and left femoral condyles. The *m. caudofemoralis longus* is hypothesized to be a hip extensor when the tail is fixed and a tail flexor (with bilateral contraction) and a lateral flexor of the tail (with unilateral contraction) when the hindlimb is fixed.

M. caudofemoralis brevis. This muscle originates from the ventral aspects of the centra of Ca1-3 and inserts via mixed fleshy and tendinous fibers onto the dorsolateral aspect of the ischium, ilioischiadic ligament, and proximal femur (Fig. 4C–E). The origins on the ischium and ilioischiadic ligament were more tendinous in the males than in the females examined. In both sexes, the insertion onto the femur is via a thin, fleshy slip. The muscle belly of *m. caudofemoralis brevis* lies deep to *m. caudofemoralis longus*. However, its tendon wraps around *m. caudofemoralis longus* laterally to insert onto the pelvis, femur, and ilioischiadic ligament. Thus, this muscle forms a sling around *m. caudofemoralis longus*, and it is unlikely to have a strong ability to act on the tail or hip joint. Instead, contraction of this muscle is hypothesized to draw the proximal portion of *m. caudofemoralis longus* medially, changing the angle of that muscle's action so that it is parallel with the long axis of the tail. This action would reduce the moment arm of *m. caudofemoralis longus* (Herrel et al., 2008).

M. ischiocaudalis. This muscle mostly originates via fleshy fibers from the ventrolateral aspect of the ilium and the ventral aspect of the transverse processes of Ca1-8 (note: the origin from Ca1 is tendinous) (Fig. 4A–E). The fibers of *m. ischiocaudalis* join those of *m. cocygeus inferior* in the ventral midline at the level of Ca3-4 (in females) and Ca5-6 (in males). The muscles remain distinct for three vertebral levels, after which point, they merge completely to give rise to the ventral intrinsic muscles (see below). In most specimens, *m. ischiocaudalis* was organized into chevron-shaped units by tendons on its superficial surface. However, the tendons contributing to the chevron-shaped units were less developed in some specimens and absent in a few of the smaller female specimens in the sample. This chevron-shaped arrangement is also seen in the ventral intrinsic muscles, where two adjacent chevrons fuse to form a "W"-shaped segment (see below). The *m. ischiocaudalis* is hypothesized to be a tail flexor when it contracts bilaterally and a lateral flexor of the tail when it contracts unilaterally.

M. cocygeus inferior. This muscle originates via a stout tendon from the caudodorsal aspect of the ischium, inserts partially onto the ventral tips of the chevron bones from Ca2-Ca8, and then continues distally to give rise to the ventral intrinsic muscles (see below) (Fig. 4A–E). The fibers of *m. cocygeus inferior* join those of *m. ischiocaudalis* in the ventral midline at the level of Ca3-4 (in females) and Ca5-6 (in males). The muscles remain distinct for the next three vertebral levels and subsequently fuse completely to form the ventral intrinsic muscles (see below). In most specimens, *m. cocygeus*
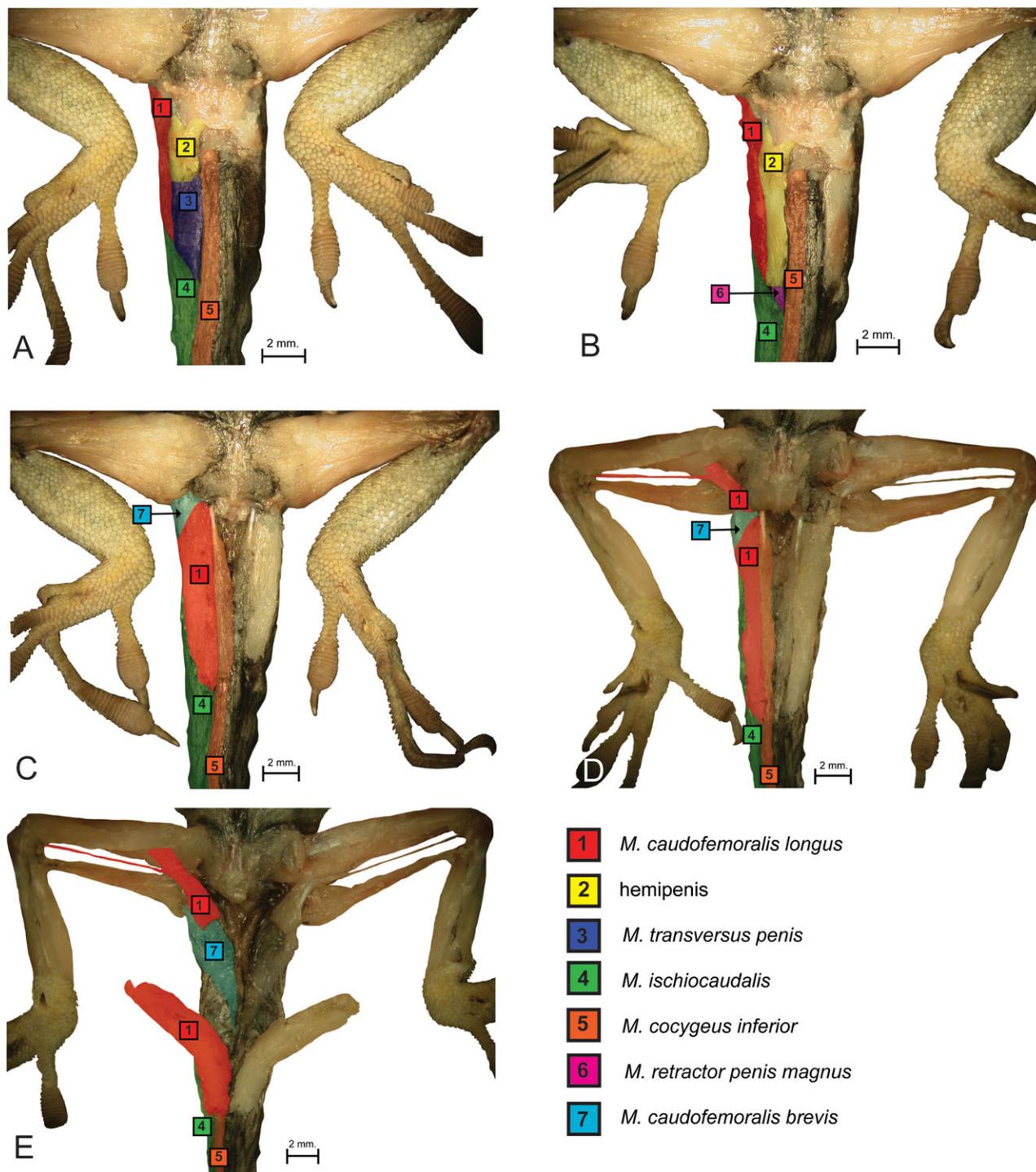
Fig. 4. Ventral views of the extrinsic muscles of the original tail in *A. carolinensis*. Dissections are shown from most superficial (**A**) to deepest (**E**). In A, the specimen has been skinned, but all of the musculature is intact. In B, *m. transversus penis* has been removed. In C, the hemipenes have been removed. In D, *m. ischiocaudalis* has been resected, and the insertion of *m. caudofemoralis longus* has been revealed by removing the *mm. puboischiotibialis*, *flexor tibialis externus*, and *ilioischiofibularis*. In E, *m. caudofemoralis longus* has been bisected.

inferior was organized into chevron-shaped units by tendons on its superficial surface. However, the tendons contributing to the chevron-shaped units were less developed in some specimens and absent in a few of the smaller female specimens in the sample. This chevron-shaped arrangement is also seen in the ventral intrinsic muscles,

where two adjacent chevrons fuse to form a "W"-shaped segment (see below). The *m. cocygeus inferior* is hypothesized to be a tail flexor when it contracts bilaterally and a lateral flexor of the tail when it contracts unilaterally.

Intrinsic Tail Muscles

The intrinsic muscles of the original tail are divided into quadrants by four intramuscular septa, including two horizontal, one dorsal, and one ventral septum. The horizontal intramuscular septa are connected to each vertebra on the transverse processes (if present) or on the lateral aspect of the centrum (Fig. 5A,B). The dorsal intramuscular septum connects to the neural spines in the vertebrae that possess them and onto the dorsal midline of the centra in the vertebrae lacking spines (Fig. 5A). The ventral intramuscular septum is connected to the ventral midline of the centra and chevron bones (Fig. 5B).

The intrinsic muscles of the tail begin at Ca6, as *m. cocygeus inferior* and *m. ischiocaudalis* merge (ventrally) and *m. extensor caudae medialis* and *m. extensor caudae lateralis* merge (dorsally) to form "W"-shaped segments, or myomeres. *M. cocygeus inferior* and *m. ischiocaudalis* contribute equally to the most proximal "W" in each of the ventral quadrants. However, *m. extensor caudae medialis* has a larger contribution than *m. extensor caudae lateralis* to the proximal "W" in each of the dorsal quadrants. All of the intrinsic muscles of the tail are covered superficially with a tendinous aponeurosis and fascial myosepta exist between each "W"-shaped segment.

The "W"-shaped segments interdigitate to form a series of nested cones, with each "W" spanning three vertebral levels (Fig. 6A,B). When the tail was mechanically autotomized at a fracture plane during dissection, the configuration of the "W"s were more evident, and 10 muscle slips could be seen extending from the proximal end of the autotomized portion of the tail (Fig. 6C) with corresponding cavities in the intact portion of the tail. In addition, eight muscle slips were observed extending distally from the intact portion of the tail. The "W"s necessarily get narrower distally (due to the elongation of the vertebrae; Fig. 2), but otherwise the configuration remains constant (i.e., they span the same number of vertebral levels and have the same attachments). The proximal half of each "W" has no bony attachment, leaving the proximal half of a NTP vertebra free of muscular attachments (Fig. 5A). However, the distal half of each "W" is attached via fleshy fibers to the distal half of a single caudal vertebra (distal to the fracture plane) (Fig. 5A). In addition, laterally and at the dorsal and ventral midlines, the "W"s attach to the bone indirectly via the intramuscular septa, rather than via fleshy fibers (Fig. 5A,B).

Regenerated Tail

A sharp border exists between the regenerated and the original muscles, and this junction coincides with an abrupt change in the skin, demarcating the location of the fracture plane where the autotomy occurred (Fig. 1). Whereas the skin of the original tail is green (brighter green in males and greenish-brown in females), the skin on the regenerated tail is a solid brown color (Fig. 1).
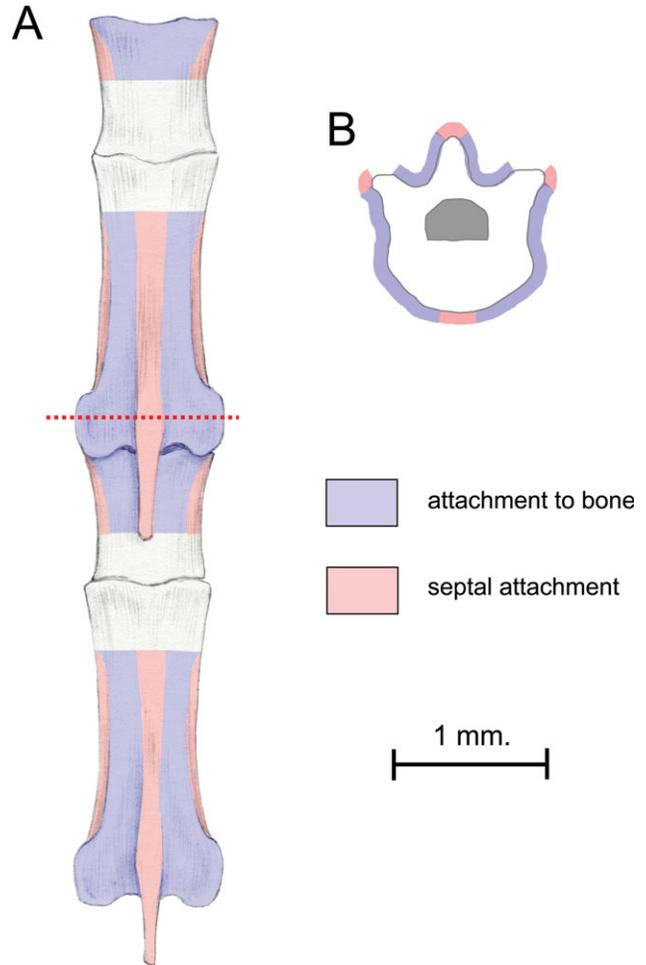

Fig. 5. **A**. Dorsal view of a series of NTP vertebrae with the attachments of the intrinsic muscles in *A. carolinensis* illustrated. The top of the illustration is proximal; the bottom is distal. Illustration by Yue Yuan. **B**. Cross-section of a NTP vertebra with the attachments of the intrinsic muscles in *A. carolinensis* illustrated. In A and B, the red areas indicate where the dorsal, ventral, and horizontal septa attach to the vertebrae, thus providing an indirect attachment for muscles, while the blue areas indicate where the intrinsic muscles attach directly onto the vertebrae.

However, other than differences in color and scale pattern, the external appearance of the original and regenerated tail appears to be very similar (i.e., there is no change in the width or circumference of the tail).

No bony tissue is present in the regenerated tail in *A. carolinensis*. Instead, the regenerated tail contains a cartilaginous tube to which the regenerated muscles are attached. The cartilaginous tube is a relatively stiff structure and, in gross dissection, the junction between the last intact vertebra and the cartilaginous tube appears seamless (i.e., neither a joint nor a joint capsule are evident). Based on our dissections, it was clear that the regenerated muscles are connected directly (and seem to originate from) the original segmental muscles. However, regularly spaced, "W"-shaped segments are not present in the regenerated tail. Instead, the regenerated muscle forms a series of longitudinal myomeres that span the entire length of the regenerated tail (Fig. 6D).
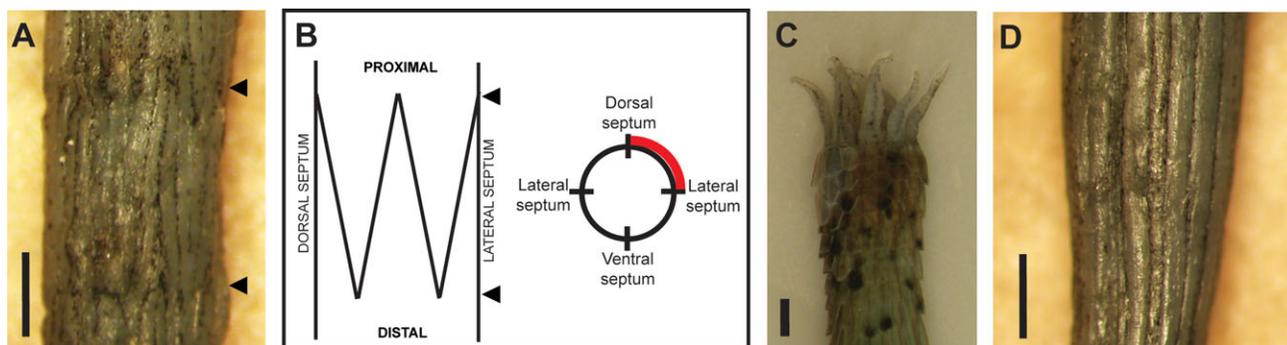
Fig. 6. Intrinsic muscles of the original tail compared with the regenerated tail muscles in *A. carolinensis*. **A**. Dorsal view of a segment of an original tail, approximately halfway between the sacrum and the distal tip of the tail. **B**. Schematic of the "W"-shaped myomeres found in each quadrant. **C**. Photograph of an autotomized tail segment, illustrating the muscle slips that extend from the proximal end. **D**. Dorsal view of a segment of a regenerated tail, approximately halfway between the sacrum and the distal tip of the tail. All scale bars are 1 mm.

The regenerated muscles (Fig. 6D) are pale compared with the original segmented muscles (Fig. 6A), which appear darker due to the presence of pigment cells. Consisting of 12 to 14 tube-shaped myomeres, the regenerated muscles are arranged radially around the cartilaginous tube. The myomeres vary in circumference and individual myomeres may also vary in width at different points along their length. Intramuscular septa are absent and the myomeres appear to be irregularly organized around the cartilaginous tube. The muscles are attached to the cartilaginous tube along their entire length. As the muscle fibers course distally, they become somewhat narrower and consequently cover less of the tube, leaving a small bare spot at the distalmost end of the tube.

DISCUSSION
Comparative Myology and Locomotor Performance in Anole Ecomorphs

The extrinsic tail muscles in *A. carolinensis* appear to be very similar to those in other known *Anolis* lizard species; however, the origins of *mm. caudofemoralis longus* and *brevis* are distinct. The *mm. caudofemoralis longus* and *brevis* are typically the primary extensors of the hip joint in lizards, contributing most of the force required for achieving limb retraction (Synder, 1952, 1954). However, in anoles, the morphology of *m. caudofemoralis brevis* suggests a primary role in altering the moment arm of *m. caudofemoralis longus* (Herrel et al., 2008). The morphology of these muscles in *A. carolinensis* corresponds closely to that observed in *A. sagrei* and *A. valencienni* (Herrel et al., 2008). However, the origin of *m. caudofemoralis longus* spans fewer vertebral levels in *A. carolinensis* (Ca3-8) compared with *A. sagrei* (Ca2-8) and *A. valencienni* (Ca2-9). Similarly, the origin of *m. caudofemoralis brevis* also spans fewer vertebral levels in *A. carolinensis* (Ca1-3 compared with Ca1-4 in *A. sagrei* and *A. valencienni*; Herrel et al., 2008). These findings indicate that *A. carolinensis* may be capable of more fine control of hip extension and lateral flexion and flexion of the tail compared with *A. sagrei* and *A. valencienni*.

Consideration of the behavioral ecology and overall morphology of these species may help elucidate the observed myological differences. *A. sagrei* occupies a trunk-ground niche and is characterized by a long tail and limbs and fast running speeds (Losos, 2009). In contrast, *A. valencienni* and *A. carolinensis* are arboreal species with short limbs. *A. valencienni*, a twig anole, has a short tail and moves slowly, while the long-tailed *A. carolinensis* is a faster-moving trunk-crown anole (Irschick and Losos, 1998; Toro et al., 2004; Vanhooydoonck et al., 2006a,b; Losos, 2009). One could hypothesize that fine control of tail and hip movements would be more highly selected for in *A. carolinensis*, an arboreal species navigating narrow supports at higher speeds than *A. valencienni*. In order to further test this hypothesis, more data are needed for additional anole species in these and other ecomorph categories. However, these findings suggest that myological features (e.g., extent of origins and insertions) may help elucidate variation in locomotor behavior (e.g., jumping and sprinting ability; Losos and Sinervo, 1989; Irschick and Losos, 1998; Macrini and Irschick, 1998) that is not explained by variation in hindlimb length or other variables.

Functional Differences Between the Original and Regenerated Tail

The arrangement of the intrinsic muscles of the original tail and the regenerated tail muscles observed here closely match previous descriptions of *A. carolinensis* (Cox, 1969a). However, in the present study, we have been able to more precisely describe the origins and insertions (Fig. 5A,B). We are also able to discuss the range of intraspecific variation and sex differences for the first time, as previous studies lacked data on the number or sex of the specimens analyzed (Cox, 1969a). Very little variation was observed in the origins and insertions of the extrinsic muscles studied, although the point of fusion of *m. cocygeus inferior* and *m. ischiocaudalis* did vary according to sex. In addition, apart from differences in overall size, the intrinsic tail muscles in male and female *A. carolinensis* appear to be similar. However, in the regenerated tails, 12 to 14 longitudinal myomeres were observed, with variation among the

specimens in the sample. Bellairs and Bryant (1985) reported that up to 14 myomeres are also present in some lacertids.

The findings of this study also underscore differences between the original and regenerated tail musculature in *A. carolinensis*. Specifically, these results suggest that there may be major functional differences between the original and regenerated tail. Chief among the factors underlying this difference is the fact that a single cartilaginous tube replaces the interlocking vertebrae of the original tail. While the flexibility of the cartilaginous tube would facilitate gross bending movements, the lack of joints along the length of the tail suggests that the regenerated tail is much less capable of fine movements compared with the original tail. The lack of regularly spaced, interdigitated muscular segments also limits the potential range of motion of the regenerated tail. Coordinated contraction of certain groups of myomeres in the regenerated tail may produce gross movements (e.g., extension, flexion, or lateral flexion), but fine movements of specific sections of the regenerated tail would not be supported.

Although the anatomy of the regenerated tail suggests that it would be less capable of coordinated, fine movements compared with the original tail, relatively few experimental data are available to corroborate this argument. Studies of a wide range of lizard taxa indicate that, by and large, tail loss has a detrimental effect on locomotor performance, including running speed (Pond, 1978; Ballinger et al., 1979; Punzo, 1982; Formanowicz et al., 1990; Martin and Avery, 1998; Downes and Shine, 2001; Chapple and Swain, 2002; Lin and Ji, 2005), stride length (Martin and Avery, 1998), stability (Ballinger, 1973; Daniels, 1985; Brown et al., 1995), and control of body position during jumping (Bonvini, 2007; Gillis et al., 2009). However, it should be noted that in some terrestrial species, tail loss is not associated with a loss in running speed (Daniels, 1983, 1985; Huey et al., 1990; Brown et al., 1995; Lin and Ji, 2005). Moreover, all these studies have compared experimental groups of animals whose tails have been recently autotomized and have not regenerated with groups of animals who possess intact original and regenerated tails. The few studies that have tested for differences between original and regenerated tails have failed to find significant differences in sprint speed (Brown et al., 1995; Downes and Shine, 2001; Chapple and Swain, 2002) or climbing ability (Downes and Shine, 2001; Chapple and Swain, 2002). Further studies on the physical properties and range of motion of the original and regenerated tail are required in order to determine if the anatomical differences observed in this study do in fact result in functional differences.

In conclusion, the present study indicates that the extrinsic tail muscles in *A. carolinensis* are very similar to those in other known *Anolis* lizard species. However, the extent of the origins of the *mm. caudofemoralis longus* and *brevis* differs, and these differences are relevant for comparative studies of locomotor performance in the genus *Anolis*. The descriptions of the intrinsic tail muscles provided here confirm the findings of Cox (1969a) and important new details about these muscles (e.g., specific sites of origin and insertion, intraspecific variation) have been presented. The comparative anatomy of the original versus the regenerated tail suggests that important functional differences exist. In particular, the regenerated tail is predicted to be less capable of coordinated, fine movements. In concert with the findings from the histological study of the tail in *A. carolinensis* (Fisher et al., in press), this study provides a detailed anatomical atlas of the tail for use in developmental and genetic studies of tail regeneration in lizards, as well as in studies of anole evolution and biomechanics.

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