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Maximal Caudal Autotomy in *Podarcis hispanica* (Lacertidae): The Caudofemoralis Muscle Is Not Sundered

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In recent years, the pattern of maximal caudal autotomy in lizards has come under consideration, with attention being focused on how nonsegmental muscles in the tail base, specifically the m. caudofemoralis longus and the m. retractor penis magnus, may limit autotomy where they cross autotomy planes or, alternatively, how they may be ruptured if maximal autotomy is practiced. In this paper, we demonstrate that in the lacertid lizard *Podarcis hispanica* a number of autotomic vertebrae are spanned by the m. caudofemoralis longus, that maximal caudal autotomy does occur, and that the caudofemoralis muscle dissociates from its vertebral attachments but is not torn in the process. Anatomical and histological data reveal that this muscle has a specialized structure and relationship with surrounding muscles, skeletal elements, and connective tissues that result in minimal damage upon maximal autotomy. Furthermore, upon caudal regeneration, the m. caudofemoralis longus reestablishes contact with the newly formed cartilaginous axial skeleton of the tail.

CAUDAL autotomy in lizards has long been of interest in the contexts of community ecology (Jaksic and Busack, 1984; Brandl and Volkl, 1988), evolution in general (Arnold, 1984; Zani, 1996), and morphology (Hoffstetter and Gasc, 1969; Raynaud et al., 1975) of both shedding and regeneration. Autotomy has also been studied from functional ecology (Brown et al., 1995; Fox et al., 1998), functional evolution (Arnold, 1994; Barbadillo and Bauwens, 1997), and mechanistic (Bellairs and Bryant, 1985; Russell and Bauer, 1992) perspectives. Much of this has been reviewed by Arnold (1988). Within and between major clades of lizards, the ability to autotomize the tail varies both in an absolute sense and also in the context of the proportion of the tail that can be shed (Arnold, 1994; Zani, 1996). In 1992, Russell and Bauer advanced the hypothesis that the extent of the m. caudofemoralis in the base of the tail imposed a constraint on the proportion of the original tail that could be shed and subsequently regenerated. This hypothesis was founded upon the observation that the m. caudofemoralis longus is an unsegmented muscle that ''invades'' (Romer, 1942) the tail base during ontogeny to capture a series of caudal vertebrae. In contrast, the caudal muscles typically shed as a result of autotomy are segmental, with well-demarcated boundaries between them that are associated with the intravertebral fracture planes and, thus, are separated from each other along well-defined zones of weakness (Bellairs and Bryant, 1985). Essentially the caudal segments bridged by the m. caudofemoralis longus were hypothesized not to be free to shed because that muscle possesses no autotomy mechanism (Russell and Bauer, 1992).

This was discussed by Arnold (1994) who examined the question of whether the spread of the m. caudofemoralis longus along the tail is a causal agency in the suppression of autotomy. Employing a phylogenetic method in which the extent of the m. caudofemoralis longus and the persistence or loss of autotomy were mapped onto a well-corroborated cladogram of the major groups of lizards, he concluded that no clear signal of correlation was evident. In contrast, Zani (1996) examined this hypothesis in a phylogenetic context and concluded that the evolution of the length of the m. caudofemoralis longus is directly correlated with the reduction of caudal autotomy in certain groups of lizards.

Although the outcome of these debates is still to be fully resolved, a particular side issue of some significance has arisen. Russell and Bauer (1992) advocated that the most proximal point of autotomy, when present, must lie distal to the distalmost extent of the m. caudofemoralis longus, because the latter is nonsegmental and would need to be physically ruptured if it was to be involved in the autotomy process. Zani (1996) accepted this as part of his working hypothesis and stated that the m. caudofemoralis longus is not involved in caudal autotomy. His overall conclusions were that the average point of caudal autotomy occurs distal to the average posteriormost point of origin of the m. caudofemoralis longus.

However, Arnold (1994) had already unearthed the paradox to be considered here. Although Zani (1996) dealt with average positions, Arnold (1994) examined actual anatomical relationships. He noted that there is a close, if imperfect, correlation between the furthest posterior extent of the m. caudofemoralis longus and the most anterior of the autotomy planes and that in some species this muscle spreads somewhat beyond the first autotomy plane. He implied that such an overlap need not necessarily inhibit those autotomy planes bridged by the m. caudofemoralis longus by stating of this muscle that ''its efficiency should not be greatly reduced if tail breakage were to occur at this point because the muscle has multiple origins on many vertebrae'' (p. 522). He indicated that the m. retractor penis magnus may be more significant in establishing the anteriormost point of autotomy (in males at least) as it has only a single point of origin.

Such observations were effectively empirically tested by Barbadillo et al. (1995). These investigators examined four species of lacertid lizard and considered the position of maximal autotomy in males and females. Their working hypothesis was that morphological structures in the tail may constrain the capacity of autotomy and that the m. caudofemoralis longus and the m. retractor penis magnus were the most likely agencies, with the latter exercising the greatest constraint so as to prevent damage to the hemipenial mechanism. They predicted sexual dimorphism within species in terms of maximal autotomy, because females are not constrained by the hemipenial musculature in this context.

By examining the distribution of autotomous and nonautotomous vertebrae within the tail and their association with the m. caudofemoralis longus and the hemipenial muscles, Barbadillo et al. (1995) found that sexual dimorphism was most pronounced for the position of the first autotomous vertebra, with an average posterior displacement of two vertebrae in males. They also found that the m. caudofemoralis longus of both sexes of all four species clearly originated from the autotomous portion of the tail, apparently spanning as many as three or four vertebrae with fracture planes [see table I in Arnold (1994) for taxa in which such compromise may occur—two species of tropidurid, one lacertid and one scincid].

Observations by Barbadillo et al. (1995) indicated that, in about one-third of all cases of naturally occurring tail breaks, the entire autotomic part of the tail was involved. This led them to the conclusion that in such instances the m. caudofemoralis longus must be physically damaged, with the postulation that, because it is nonsegmental, it is torn in the process and its function disrupted.

In light of this conclusion, there is potential for major damage to an important locomotor muscle if autotomy is maximally expressed. This stands in sharp contrast to the situation in the rest of the tail, in which intersegmental boundaries are structured in such a way as to promote ease of breakage. This minimizes the trauma and exposure of mesodermally derived tissues (a potential source of major problems for the immune system). Thus, we investigate the morphology of this bridging zone and examine the nature and extent of damage at the time of maximal autotomy.

MATERIALS AND METHODS

Barbadillo et al. (1995:table I) summarized their findings for the positions of the caudal vertebrae bearing the first incomplete and complete fracture planes and the distalmost point of origin of the m. caudofemoralis longus and m. retractor penis magnus for all four species examined by them. Of these four species, *Podarcis hispanica* is indicated as having the largest region of overlap of vertebrae bearing complete fracture planes and the nonsegmental m. caudofemoralis longus. Thus, we chose *P. hispanica* as the primary taxon for examination of the anatomical relationships in this bridging region of the tail base.

Examination and dissection of the cleared-and-stained ($n = 14$) and alcohol-preserved ($n = 12$) specimens employed by Barbadillo et al. (1995) were undertaken. The former specimens allowed us to check statements made about the position of fracture planes. The latter specimens allowed us to determine the extent of the m. caudofemoralis longus by dissection of individuals with both original and regenerated tails. Radiology was employed to determine the relative positions of the m. caudofemoralis longus and the caudal vertebrae to the cloaca, which was used as a landmark. Following dissection of the m. caudofemoralis longus, an entomological pin was inserted into the tail at the point of its distalmost origin, and another such pin was placed transversely at the level of the cloaca (Blob, 1998). Specimens were then radiographed using a Hewlett-Packard Faxitron model 4380N radiology unit and Polaroid® black-and-white positive/negative film.

Subsequent to radiology the tail bases of five of these specimens (two males with original tails, one male with a maximally autotomized and regenerated tail, one female with an original tail, and one female with a maximally autotomized and regenerated tail) were excised, cleared, dehydrated, embedded in paraffin wax, and sectioned in the frontal plane at 8–10 μm.

The resulting slides were stained with Milligan's trichrome (Humason, 1979) to reveal histological details of the relationships of the tissues in the tail base and their overall morphology. Radiographs and histological sections of the same specimens of *P. hispanica* could thus be aligned for correlation of detail and position.

Two female specimens of *Lacerta vivipara* (one with an original and the other with a regenerated tail) were sectioned in the same way but with the bases of the hind limbs and the pelvic region still intact. Because of the limited number of *P. hispanica* specimens available for sectioning, this provided a more complete anatomical map of this region for reference purposes.

RESULTS

Basic anatomy.—Anatomical relationships gleaned from radiographed specimens are summarized in Table 1. From these, and the data provided by Barbadillo et al. (1995:table I), it is evident that the m. caudofemoralis longus traverses vertebrae that bear complete fracture planes. In males, one to three such vertebrae are involved and, in females, one or two (Fig. 1A–B) in specimens that we examined. We encountered no individuals in this investigation in which four such vertebrae are involved (as noted by Barbadillo et al., 1995), but recognize that *P. hispanica* is morphologically a highly variable species and that in some individuals the m. caudofemoralis longus may traverse as many as four autotomic vertebrae. In either case, same basic principles apply.

Examination of specimens with autotomized but unregenerated tails (Fig. 1C–D) reveals that the m. caudofemoralis longus does not tear to permit maximal autotomy but, instead, detaches from the shed vertebrae to remain intact and is left extending from the stump of the tail (Fig. 1C). This observation requires explanation in the context of the nature of the attachment of the m. caudofemoralis longus to the vertebrae with complete fracture planes, its mode of release and its fate and morphology in the regenerated tail. To elucidate these aspects, we present the results of the histological investigation.

Original tails: a baseline from radiographs and histology.—Because of sexual differences in the base of the tail, the myology in this region is different between males and females. In the ventral part of the tail base, females have a more laterally positioned m. caudofemoralis longus than do males. This is because of the absence of the hemipenes and the m. retractor penis magnus in females. In males, the m. caudofemoralis longus is limited in this region to a narrow medial strip lying between the hemipenial apparati.

In both males and females, the ventral portion of the m. caudofemoralis longus originates from the haemal spines and the vertical skeletogenous septum that runs longitudinally between them (Fig. 2A). This septum consists of a continuous membrane of collagenous connective tissue that runs between the haemal spines, and envelops them. Distally, the fibers of the m. caudofemoralis longus originate more acutely (in a more parallel manner) from the septum than they do proximally. The vertical skeletogenous septum thickens slightly between the last two haemal spines associated with nonautotomic vertebrae and then thins out noticeably in the autotomic portion of the tail. In this region, it also becomes less taut, its path being more irregular in histologically prepared material.

More dorsally, the m. caudofemoralis longus originates from the haemal arches, the centra of the vertebrae, then from the anterior faces of the transverse processes, and finally from the sides of the centra again, as noted by Raynaud et al. (1975) in *Lacerta viridis*. Origin is always from a surrounding septal membrane and never directly from the bone or periosteum (Fig. 2B).

In males, the m. retractor penis magnus occurs lateral to the m. caudofemoralis longus. It is bound completely by a membrane of collagenous connective tissue (Fig. 2C). This membrane, on its medial surface, also covers the lateral surface of the m. caudofemoralis longus. The m. retractor penis magnus has one main point of origin, from the vertical skeletogenous septum. This site of origin is at least partially shared by the distalmost fibres of the m. caudofemoralis longus.

The dorsal lobe of the m. caudofemoralis longus, like the ventral lobe, is bound by a continuation of the vertical skeletogenous septum on its medial surface and by the connective tissue membranes of more lateral muscles on the outer surface. The main difference between the ventral and dorsal lobes is that the latter is bordered by the outer segmental muscles of the tail (Fig. 2D), whereas the former is bordered by the m. retractor penis magnus. The posterior extremity of the dorsal lobe of the m. caudofemoralis longus does not abut any other muscle.

Maximal autotomy (radiographs).—When the tail is maximally autotomized, the ends of the m. caudofemoralis longus, in both sexes, and the m. retractor penis magnus in males, are ex-

TABLE 1. ANATOMICAL FEATURES OF THE TAIL BASE OF *Podarcis hispanica*. Registered specimen numbers refer to the collections of the Biology Department of the Autonomous University of Madrid. Numbers in parentheses are medians of *P. hispanica* as recorded by Barbadillo et al. (1995) (M/F).

	Specimen											
Registered number	H77	H81	H85	H86	H74	H76	H91	H94	H75	H79	H83	H95
Sex	M	M	M	M	M	M	M	M	F	F	F	F
Original, autotomized or regenerate tail	Orig	Orig	Autot	Autot	Regen	Regen	Regen	Regen	Orig	Autot	Autot	Regen
Position of cloaca in relation to caudal vertebrae	1–2	2–3	1–2	1	2	1–2	2	1–2	2	1–2	2	1–2
No. of caudals without fracture planes (5/4)	5	6	5	5	5	6	5	5	4	4	4	5
No. of caudals with incomplete fracture planes (1/1)	1	2	1	1	1	1	1	1	1	1	1	1
First caudal with a complete fracture plane (7/6)	7	9	7	7	7	8	7	7	6	6	6	6
Distalmost caudal from which m. caudofemoralis longus originates (11/8)	9	10	NA	NA	NA	NA	NA	NA	8	NA	NA	NA
Vertebra at which tail break occurred	NA	NA	7	7	7	8	7	7	NA	6	7	7

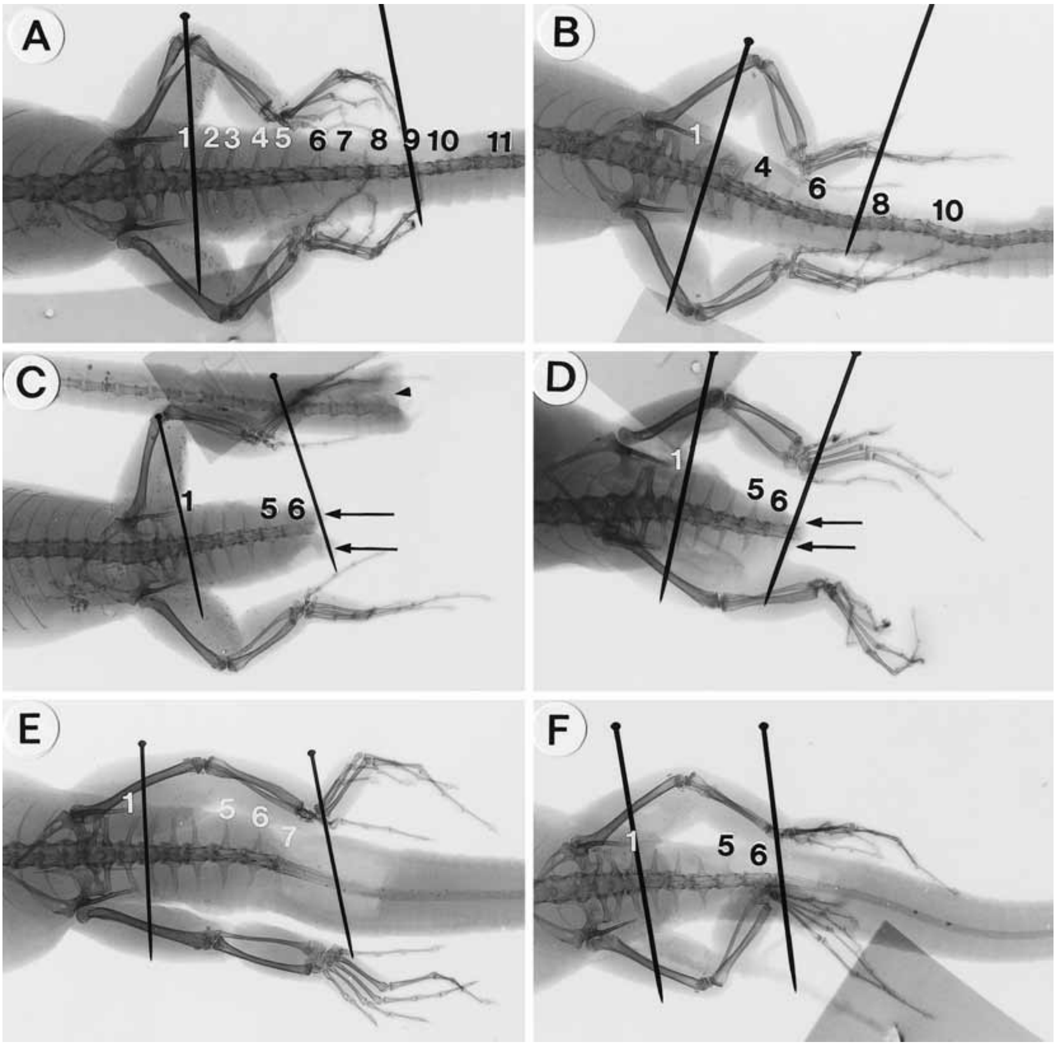

Fig. 1. Autotomy planes and the extent of the m. caudofemoralis longus in *Podarcis hispanica*. In all cases, the more anteriorly placed of the two pins is inserted at the level of the cloaca, and the more posteriorly placed one indicates the distalmost point of origin of the m. caudofemoralis longus. (A) The original tail of a male (H77; see Table 1) showing the nonautotomic caudal vertebrae (1–5), one vertebra with an incomplete fracture plane (6), and a series of autotomic vertebrae (7–11). Note that the distalmost point of origin of the m. caudofemoralis longus occurs on the proximal half of vertebra 9, indicating an overlap of 2.5 autotomic vertebrae by this muscle. (B) The original tail of a female (H75). The numbering convention is as for (A), above. Note that the distalmost point of origin of the m. caudofemoralis longus coincides with the proximal part of vertebra 8. (C) A male (H86) showing maximal autotomy without regeneration. Vertebral numbers as in (A). The conelike projections of the exposed m. caudofemoralis longus are evident (arrows). They are somewhat retracted, but the cavity from which one of these has been withdrawn is evident on the detached tail (arrowhead). (D) A female (H83) showing maximal caudal autotomy and conelike projections (arrowhead) of the m. caudofemoralis longus. Vertebral numbers as in (A). (E) The regenerated tail of a male (H91) that had experienced maximal autotomy. Vertebral numbers as in (A). The pin marking the distalmost origin of the m. caudofemoralis longus intersects the cartilaginous rod of the regenerated tail an appreciable distance beyond the remaining vertebrae. (F) The regenerated tail of a female (H95) that had experienced maximal autotomy. Vertebral numbers as in (A). The distalmost origin of the m. caudofemoralis longus traverses less of the regenerated portion of the tail than is the case in (E).

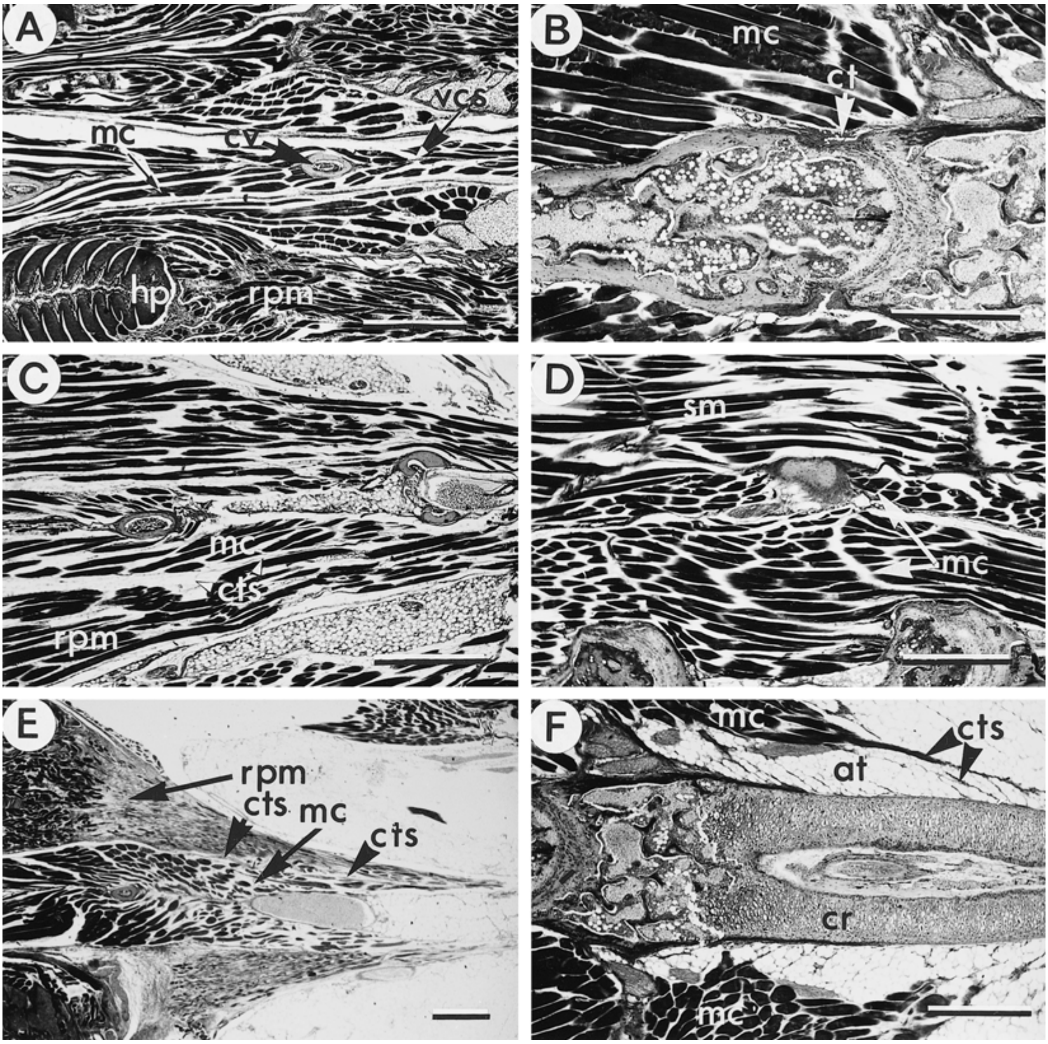

Fig. 2. Histological details of frontal sections of the tail base of *Podarcis hispanica* with reference to the m. caudofemoralis longus and m. retractor penis magnus and their relationship to each other and the caudal skeleton in original and regenerated tails. (A) The ventral pattern of origin of the m. caudofemoralis longus (mc) from vertebral chevrons (cv) and the vertical skeletogenous septum (vcs) in an original tail, male (H77). One hemipenis (hp) is shown with its connection to the m. retractor penis magnus (rpm). (B) A more dorsal site of origin of the m. caudofemoralis longus (mc) from the connective tissue (ct) ensheathing the caudal vertebrae, male specimen (H91) with a regenerated tail. (C) Shared origin of the m. caudofemoralis longus (mc) and the m. retractor penis magnus (rpm) from an intervening connective tissue sheath (cts), male (H77) with an original tail. (D) Dorsal region of origin of the m. caudofemoralis longus (mc) in relation to the segmental muscles (sm) of the tail, male (H77) with an original tail. (E) Thickened connective tissue sheath (cts) of the m. retractor penis magnus (rpm) providing a modified pattern of origin for this muscle and the m. caudofemoralis longus (mc) in a male (H91) with a regenerated tail. (F) Reinsertion of the m. caudofemoralis longus (mc) onto the cartilaginous rod (cr) of the regenerated tail in a male (H91) via connective tissue strands (cts) passing between clusters of adipose tissue cells (at). Scale bar for all panels = 0.5 mm.

posed (Fig. 1C). In males, this externalized portion appears as four lobes of muscle tissue, two on each side, extending beyond the edge of the broken epidermis and dermis, and beyond the edge of the distalmost retained vertebral element (Fig. 1C). The dorsal and ventral lobes all extend to about the same level, but the former are smaller than the latter ones in bulk. The dorsal lobes are extensions of the m. caudofemoralis longus, whereas the ventral lobes consist of closely associated extensions of the m. caudofemoralis longus and the m. retractor penis magnus.

In females, there are also four externalized lobes of muscle (all of which are exclusively the m. caudofemoralis longus), but their mode of attachment differs. Here, the two lobes form more of a cone along with the remains of the first autotomic vertebra, which also extends beyond the retained cuticle (Fig. 1F). These observations indicate a less extensive detachment of the m. caudofemoralis longus from the vertebral series in females, although the terminus of this muscle still extends beyond the last remaining osseous element. These results are expected because of a shorter region of overlap of the m. caudofemoralis longus and the autotomic vertebrae in females (see above).

From observations of the autotomized portion of the tail, it is apparent that the vertical skeletogenous septum detaches from the first autotomic haemal spine, which remains with the discarded portion of the tail. Posterior to the first autotomic haemal spine, the septum is also shed with the tail. Thus, detachment of the m. caudofemoralis longus from the autotomic vertebrae to which it attaches, in the original tail, is achieved not by the tearing of the muscle but instead by it being pulled away from the underlying bones. It still remains enveloped in a continuous sheet of collagenous connective tissue derived from the vertical skeletogenous septum, which is continuous with the epimysium of the muscle.

Regenerated tails: reinsertion observed from radiographs and histology.—Proximal to the distalmost nonautotomic haemal spine, muscle relationships and origins are unchanged. The vertical skeletogenous septum connects and envelops the haemal spines and is the site of origin of the m. caudofemoralis longus. Beyond the distalmost remaining haemal spine, the skeletogenous septum disappears. It appears to be ‘‘balled-up’’ against the posterior edge of the last haemal spine. At this point, the m. caudofemoralis longus is no longer divided by the skeletogenous septum into right and left halves; instead, the fibers of the two sides converge and make contact.

The connective tissue membrane surrounding the m. retractor penis magnus is thickened toward its point of origin from the last remaining half vertebra. The posterior extremities of the m. retractor penis magnus and the m. caudofemoralis longus are difficult to distinguish, the two muscles sharing points of origin (Fig. 2E).

In males, the m. retractor penis magnus does not extend as far dorsally as the m. caudofemoralis longus, and the latter expands laterally and somewhat longitudinally, extending alongside the cartilaginous rod of the regenerated tail. At this point, no robust connective tissue membrane covers the m. caudofemoralis longus. The bulk of this muscle does not come into direct contact with the cartilaginous rod, but instead adipose tissue intervenes between the rod and the muscle. Between the adipose cells, thickened strands can be observed connecting the m. caudofemoralis longus to the cartilaginous rod and running posteromedially (Fig. 2F). In this way, the m. caudofemoralis longus in males establishes new contact with the axial skeleton in the regenerated part of the tail. Even more dorsally, this insertion becomes somewhat tighter, the muscle fibers lying closer to the cartilaginous rod. Such anatomical relationships may change with time, but the evidence available clearly indicates that the m. caudofemoralis longus not only detaches from the distalmost points of its axial skeletal attachment without tearing but that it also reattaches, even if weakly so, to the axial portion of the regenerated tail (Figs. 1E, 2F).

In females (Fig. 1F), there is one main difference in tail base morphology, excluding lack of hemipenes and associated muscles. A very thin connective tissue membrane surrounds the m. caudofemoralis longus on its lateral edge. This membrane, in the position of the m. retractor penis magnus, protects the m. caudofemoralis longus and is retained in the regenerate. The vertical skeletogenous septum is also retained to a greater degree.

DISCUSSION

Mechanism of detachment, persistence, and reinsertion.—The m. caudofemoralis longus (and the m. retractor penis magnus) does not originate directly from the bone of the more distal vertebrae with which it is associated but from the vertical skeletogenous septum, and extensions thereof, that connects and envelops the vertebrae. Therefore, it is not the muscle that must detach from the bone during autotomy but the septum. This prevents damage to the actual muscle tissue of the m. caudofemoralis longus and the m. retractor penis magnus. The dorsal lobe of the m. caudofemoralis longus detaches from the autotomized part of the tail quite readily because of the gap present between it and any adjacent segmental muscular tissue.

Upon autotomy, both the m. caudofemoralis longus and the m. retractor penis magnus muscles are exposed to the environment and, therefore, must be protected from desiccation and infection. This is apparently accomplished by the system of connective tissue membranes. The m. retractor penis magnus is enclosed in its own membrane. The m. caudofemoralis longus is covered by the vertical skeletogenous septum on its medial margin and by the medially facing membrane of the m. retractor penis magnus on its lateral edge.

It is suggested that, upon regeneration of the tail, the membrane of the m. retractor penis magnus thickens, with some of the muscle tissue being displaced by additional fibers. This facilitates the reattachment of the m. retractor penis magnus and the m. caudofemoralis longus to the cartilaginous rod. The thickening of this enveloping membrane may occur while the muscles are exposed, prior to the commencement of regeneration.

Dorsally, because the m. caudofemoralis longus no longer has a common bounding membrane to facilitate reinsertion, another mechanism must exist for this reattachment. Here, adipose tissue differentiates between the m. caudofemoralis longus and the cartilaginous rod. Within this, tissue strands form that connect the m. caudofemoralis longus fibers to the cartilaginous rod (Fig. 2F). This attachment appears to be much weaker than the original, or for that matter, the ventral reattachment involving the strengthened membrane of the m. retractor penis magnus (Fig. 2E). Again, however, this reestablished dorsal origin may become stronger with time.

In females, the m. retractor penis magnus is not available to protect the m. caudofemoralis longus. Alternatively, a very thin membrane surrounds the m. caudofemoralis longus in females.

Function, constraint, and evolutionary significance.—In light of the findings presented in this paper, we comment on their ultimate significance with respect to the ecology, evolution, and mechanism of tail loss. The relationships of the nonsegmental muscles in the tail base are also considered.

Because of the many functions of a tail, loss of it has costs (Barbadillo et al., 1995). The tail stores the hemipenial apparatus in males, and is used in locomotion and predator escape (Barbadillo et al., 1995). The latter two functions are in opposition to one another. Locomotion is optimal when the tail is present, whereas predator escape involves the loss of the tail. We have here attempted to explain how evolution has coped with this paradox and how tail autotomy occurs in this region of compromise.

Originally it was thought that the m. caudofemoralis longus and m. retractor penis magnus, being nonsegmental muscles, were not involved in autotomy and that this placed a constraint on how far proximally the tail could be autotomized (Russell and Bauer, 1992; Zani, 1996). This was disputed by Barbadillo et al. (1995), who noted that the m. caudofemoralis longus actually bridged one or more fracture planes in the tail. The present study demonstrates, however, that the nonsegmental muscles of the tail are involved in tail autotomy but that they do not tear.

It has been suggested that the m. retractor penis magnus is the major constraining force in males in determining the most proximal point of autotomy (Arnold, 1994; Barbadillo et al., 1995). This assertion can now be modified. Because the m. caudofemoralis longus shares muscular attachment with the m. retractor penis magnus ventrally, both muscles can be considered to constrain caudal autotomy about equally.

From an evolutionary perspective, it is suggested that, in the context of predator escape, assuming that the absolute size of the autotomized tail affects predator behavior (satiation vs pursuit), one would expect the autotomizable portion of the tail to be maximized. This, in turn, is constrained by hemipenial musculature in males and by the m. caudofemoralis longus and its role in the evolution of greater sprint speed (Brown et al., 1995; Dial and Fitzpatrick, 1984) in both sexes. Autotomy is maximized by a partial sacrifice in locomotor performance (Dial and Fitzpatrick, 1984; Barbadillo et al., 1995; Brown et al., 1995), which is temporary. This sacrifice in locomotor performance is only partial, because of the numerous points of origin of the m. caudifemoralis longus from the caudal vertebrae (Raynaud et al., 1975). In *P. hispanica*, the nonsegmental muscles that extend distally are not torn and reattach during regeneration. The origin of the m. retractor penis magnus and the ventral part of the m. caudofemoralis longus originate by way of shared collagenous connective tissue, giving strength for renewed function of the muscles. The weaker origin in the dorsal section of the m. caudofemoralis longus may serve for stability rather than function. It appears that the efficiency of the m. caudofemoralis longus is reduced in instances of maximal caudal autotomy, as suggested by Arnold (1994), but is not physically damaged in the process.

Zani (1996) suggested that the m. caudofemoralis longus restricts tail loss. Because this muscle is involved in caudal autotomy, one can conclude that, instead of preventing tail loss, this muscle constrains it. This, however, does not preclude the view of Arnold (1994) and Zani (1996) that the spread of the m. caudofemoralis longus and the other nonsegmental muscles of the tail may be associated with loss of autotomic ability in some taxa (i.e., Varanidae, Helodermatidae, etc.). This remains a valid hypothesis for future testing.

Overlap of the autotomic tail and the nonsegmental muscles at the tail base has been noted in other taxa as well (Russell and Bauer, 1992: table 1). In *Anolis garmani* (Polychrotidae), the amount of overlap is similar to that found in *P. hispanica*: one to two vertebrae (Russell and Bauer, 1992). In such a case one might expect a similar mechanism to that described here. In the Teiidae, the overlap can have a much broader range (1–6 vertebrae) (Russell and Bauer, 1992). In the Tropiduridae, the overlap may be greater still (5–9 vertebrae); yet autotomy still occurs (Russell and Bauer, 1992). How much, if any, of a bridging area exists in such taxa is not known, and such cases are of particular interest for the further study of some of the arguments presented here, particularly in the context of minimization of damage to the m. caudofemoralis longus and the loss of autotomy in some taxa.

MATERIAL EXAMINED

Photographs of cleared-and-stained specimens UAMB (Universidad Autonoma de Madrid, Biology Department): Males: H18, H20, H22, H23, H36, H37, H53, and H54; Females: H19, H24, H40, H41, H55, and H56. Alcohol preserved specimens UAMB: Males: H74, H76, H77, H81, H85, H86, H91, and H94; Females: H75, H79, H83, H95.

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