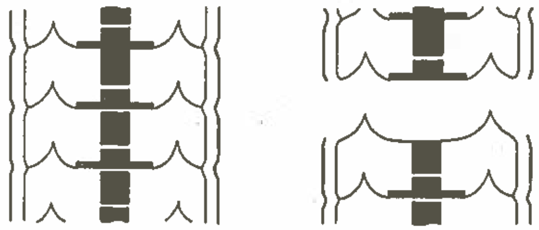
VERTEBRAL COLUMN (TAIL)

by Dr. David Wake

Vertebral column (tail)

Tails of terrestrial vertebrates are important organs serving a variety of functions, including locomotion, prehension, fat storage, and courtship behavior. Despite its many functions, salamanders, lizards, snakes, and mammals have all independently evolved mechanisms which either produce or facilitate tail loss. These mechanisms combine behavioral, morphological, and physiological components and are operative under conditions of moderate to extreme stress. When voluntary control is present, the phenomenon is termed autotomy. Tail loss is very common in some species, and presumably it confers survival value. Most predators are visual feeders, and the violently twitching shed tail is a distraction which covers the flight or concealment of the prey. The selective value of such a phenomenon is clear, and predation is thought to be the most important factor in the evolution of specializations for tail loss. This article discusses recent information on tail loss in salamanders.



(a) (b)

Fig. 1. Tail breakage pattern in lizard. Anterior at top. (*a*) Portion of unbroken tail which includes one nonautotomic and two autotomic vertebrae. (*b*) Break extends through the skin and intermyotomic septum, then through the specialized autotomy septum of connective tissue within a vertebra.

Structure and regeneration patterns. Vertebrates display a variety of patterns of tail loss. Breaks are relatively rare and are traumatic in snakes and mammals, resulting from forcible removal of the tail. The break usually is intervertebral, but may be intravertebral. Regeneration is slight, involving only the immediate vicinity of the break.

For lizards, in which tail autotomy and subsequent patterns of regeneration are relatively well known, frequencies of tail loss as high as 0.72 have been recorded. An autotomy plane passes through the skin, behind the intermyotomal septum, and through a fibrous zone which divides certain vertebrae (from one to many) in two parts (Fig. 1). Autotomy breaks are intravertebral, but breaks may be intervertebral in species with no autotomy planes. Following breakage of any sort, a peculiar ablation of the stump (involving about one-quarter of a vertebra) occurs, and regeneration commences. Abberant skin and muscle appear, and the skeletal member, an undivided cylinder of cartilage, surrounds the regenerating spinal cord.

Tail breakage is rare to common in salamanders. Several distinct patterns occur, but the break is always intervertebral and may occur at any point posterior to the cloaca. Regeneration of a nearly perfect tail follows, including apparently normal skin, segmental muscle, spinal cord, and vertebrae; only the notochord is absent.

Recent studies of salamanders reveal a seemingly paradoxical situation: A high degree of morphological specialization for tail breakage is found in species which have a surprisingly low frequency of natural tail loss. An analysis of this problem has elucidated the adaptive processes leading to such specializations.

Autotomy in salamanders. Salamanders have three types of tail morphology. Species with thick-based tails have no obvious specializations for autotomy, and tail breakage (usually distal) results from trauma. Species with slender-based tails usually lose only part of the tail, and they have a wound-healing specialization. The skin break occurs at the posterior end of one of the relatively simple, cylindrical segments, and the muscle fibers separate from their anterior attachment to an intermyotomal septum in the same segment. When the tail is lost, an empty cylinder of skin remains with the animal, and its collapse over the wound provides protection and facilitates blood clotting and regeneration. The most specialized species are those with constricted-based tails. This group is characterized by a slight to marked constriction of the tail base, including wound-healing specializations. This type is restricted to the family Plethodontidae, in which unique patterns of specialization for autotomy have evolved in three separate lineages (*Hemidactylium*, of eastern North America; *Ensatina*, of western North America; and *Bolitoglossa*, *Chiropterotriton*, *Lineatriton*, *Oedipina*, *Parvimolge*, *Pseudoeurycea*, and *Thorius*, of the New World tropics).

Constricted tail bases. The most striking feature associated with tail constriction is the shortening of the first caudal segment (third or fourth postsacral) and vertebra. This is as far anterior as tail breakage can occur, because pelvic muscles and the cloaca are attached to the second caudosacral vertebra in the neotropical species and to the third in *Ensatina* and *Hemidactylium*. Shortening of the segment is correlated with anterior placement and elongation of the transverse processes of the first caudal vertebra, to which the intermyotomal septum at the end of the segment attaches (Fig. 2). The anterior placement of the transverse processes effectively shortens the musculature of the segment. The shortened segment, with reduced musculature, provides an area of weakness at the tail base, where autotomy of the entire appendage may occur.

A variety of additional specializations, unique to this region, further weaken the tail base. The dermal and subcutaneous fibrous layers of skin at the posterior end of the shortened segment are greatly reduced or absent. This is the site of skin rupture. The anterior attachment of the individual muscle fibers of the segment is greatly weakened compared with other parts of the tail. Fibrous tissue

(a) (b)

Fig. 2. Tail breakage pattern in salamanders. Anterior at top. (*a*) Salamanders with constricted tail bases have a short and specialized first caudal vertebra, and a much shortened and weakened first caudal segment. (*b*) When the tail breaks, vertebrae are separated and the skin of the first caudal segment remains with the body, collapsing over the wound to facilitate blood clotting and healing.

joining the last caudosacral and first caudal vertebrae is much reduced and may be absent in some areas, such as around the centrum.

Initiation. Experiments show that autotomy is initiated by violent contractions of the myotomic musculature and a twisting of the body around its long axis. The initial event is the apparently voluntary separation of the muscle fibers from their anterior attachment. The intermyotomal septum to which these fibers remain attached is directed anteriorly, toward the tips of the transverse processes of the first caudal vertebra. The orientation of the septum is such that the contracted, detached fibers of the first segment exert a large force against the surrounding skin cylinder, especially posteriorly where the skin is weakened, and the skin ruptures. The nearly simultaneous muscle detachment, skin rupture, and body twisting result in a mechanical separation of the spinal cord, breaking the tail.

Tails with constricted bases seem to be very weakly attached and might be expected to be lost readily. On the contrary, although the frequency of natural tail loss in species with thick-based and slender-based tails may be as high as 0.33 and 0.28, respectively, the highest value in species with constricted tail bases is 0.19 (mode for 13 species, 0.074). Because tail regeneration is more complete and takes longer than in lizards, an evolutionary "compromise" has occurred. The tail is so important in the biology of the organisms that a high degree of control over tail loss has evolved. Only under the most extreme conditions of stress is the appendage shed. Yet, the many specializations ensure that the entire tail is lost. Convergent evolution of such features in different groups of salamanders suggests that an entire, rather than partial, twitching tail is a more effective decoy.

For background information see SALAMANDROIDEA in the McGraw-Hill Encyclopedia of Science and Technology. [DAVID B. WAKE]

Bibliography: R. Etheridge, *Copeia*, 1967(4): 699–721, 1967; D. B. Wake and I. G. Dresner, *J. Morphol.*, 122(4):265–305, 1967.