# Functional Morphology and Evolution of Tail Autotomy in Salamanders

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ABSTRACT    Basal tail constriction occurs in about two-thirds of the species of plethodontid salamanders. The constriction, which marks the site of tail autotomy, is a result of a reduction in length and diameter of the first caudal segment. Gross and microscopic anatomical studies reveal that many structural specializations are associated with basal constriction, and these are considered in detail. Areas of weakness in the skin at the posterior end of the first caudal segment, at the attachment of the musculature to the intermyotomal septum at the anterior end of the same segment, and between the last caudosacral and first caudal vertebrae precisely define the route of tail breakage. During autotomy the entire tail is shed, and a cylinder of skin one segment long closes over the wound at the end of the body.

It is suggested that specializations described in this paper have evolved independently in three different groups of salamanders.

Experiments and field observations reveal that, contrary to expectations, frequency of tail breakage is less in species with apparent provisions for tail autotomy than in less specialized species. The tail is a very important, highly functional organ in salamanders and it is suggested that selection has been for behavioral and structural adaptations for control of tail loss, rather than for tail loss *per se*.

Tail loss and subsequent regeneration is a well documented phenomenon among the lower vertebrates. Although much is known concerning regeneration, the literature on tail breakage is scattered and scanty. This is particularly true of salamanders, a group that contains a number of species reputed to practice tail autotomy. The present study was undertaken in an attempt to determine those anatomical features that permit and facilitate tail breakage in salamanders. In addition, we wished to investigate morphological specializations in those species reported to practice tail autotomy, and to attempt an analysis of the evolution of such specializations. Our working hypothesis has been that species which demonstrate specialized behavioral patterns resulting in tail loss likely have evolved physiological and anatomical specializations which facilitate the phenomenon. These morphological features might, in turn, provide insight into the processes leading to structural and functional specialization.

Our study has revealed that basal tail constriction in salamanders is an indication of a series of interrelated morphological specializations. In this paper we pre-sent facts concerning anatomical details of the basal tail region, a functional interpretation of the morphology of the region, and a hypothesis concerning the evolution of the observed morphological specializations.

## MATERIALS AND METHODS

Cleared and stained as well as skeletonized specimens of adults of all genera and most species of plethodontid salamanders have been available for the study (see Wake, '66, for complete list). In addition, large numbers of x-rays have been examined to obtain osteological information.

Histological investigations were made on adults of the following species of the family Plethodontidae: *Desmognathus fuscus, D. quadramaculatus, D. ochrophaeus, Pseudotriton ruber, Gyrinophilus porphyriticus, Eurycea bislineata, Hemidactylium scutatum, Plethodon cinereus, P. jordani, Aneides lugubris, Ensatina eschscholtzii, Hydromantes brunus, Batrachoseps attenuatus, B. pacificus, Bolitoglossa subpalmata, B. morio, B. rufescens, Chiropterotriton chiropterus, C. abscondens, C. multidentatus, Pseudoeurycea leprosa, Oedipina uniformis, Lineatriton lineola,* and *Thorius*

*dubitus.* Emphasis was placed on three genera, *Hemidactylium*, *Ensatina*, and *Bolitoglossa.*

Material utilized in the study was fixed in neutral buffered formalin, Bouin's or Zenker's fluid, decalcified in dilute HCl or buffered EDTA, embedded in paraffin or parlodion, and sectioned serially in frontal, sagittal, or transverse planes at 5 to 10 μ. Stains were chosen to best demonstrate connective tissue relationships. These included routine Ehrlich's hematoxylin and eosin, orcein (Mallory, '38), aldehyde fuchsin (Gomori, '50), Heidenhain's azan (Lillie, '54), Van Gieson's connective tissue stain (Lillie, '54), and Bodian's Protargol method of silver staining (Bodian, '36).

Living examples of many species of salamanders have been studied in the field and laboratory, including *Hemidactylium scutatum, Ensatina eschscholtzii, Bolitoglossa subpalmata, B. yucatana, Pseudoeurycea leprosa, Chiropterotriton multidentatus, C. chiropterus, Thorius dubitus, Batrachoseps attentuatus, B. pacificus,* and *Plethodon cinereus.* Large numbers of preserved animals have been studied in the Field Museum of Natural History and the University of Michigan Museum of Zoology.

The classification scheme adopted here for the salamander family Plethodontidae is that proposed by Wake ('66). Because this classification is as yet relatively unfamiliar, it is briefly summarized below (genera in parentheses):

Subfamily Desmognathinae (*Desmognathus, Leurognathus, Phaeognathus*).
Subfamily Plethodontinae
Tribe Hemidactyliini (*Gyrinophilus, Pseudotriton, Stereochilus, Typhlotriton, Eurycea, Typhlomolge, Haideotriton, Hemidactylium*).
Tribe Plethodontini (*Plethodon, Aneides, Ensatina*).
Tribe Bolitoglossini
Supergenus *Hydromantes* (*Hydromantes*).
Supergenus *Batrachoseps* (*Batrachoseps*).
Supergenus *Bolitoglossa* (*Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge, Thorius*).

### Patterns of tail morphology

The term tail autotomy has been used freely in the literature and it is impossible to determine exactly what various authors mean by it. Nevertheless, the end result of tail autotomy is always the same — part or all of the tail is lost. Many authors have reported tail autotomy in salamanders, lizards, snakes, and mammals. The phenomenon is most prevalent and most thoroughly understood in lizards (Quattrini, '52a,b, '54; Etheridge, '67) where breakage is intravertebral. The breakage plane follows an unossified area that extends transversely through from one to many vertebrae, along the caudal side of the associated intermyotomal septum and through the skin. An unsegmented cartilaginous rod and rather atypical musculature and skin is regenerated (Moffat and Bellairs, '64). Breakage is between vertebrae in the other groups, but only in salamanders is there any apparent morphological specialization and only salamanders regenerate a virtually normal tail.

Salamanders may be placed in three very general groups based on the structure of the tail and the pattern of tail breakage (Wake, '66). These groups are not phyletic, but rather represent grades of morphological and functional specialization. Because this classification is convenient and facilitates communication we have adopted it in the present report.

No obvious specializations are associated with the breakage of tails in the more primitive families of salamanders. Breakage is the result of traumatic events, such as attacks by predators, rock falls, entrapment, and similar accidents. These animals usually have tails that are not sharply differentiated from the body and hence are of large diameter basally. Breakage is usually limited to posterior parts of the tail. These animals are said to have *thick-based tails* in this study. Species characteristic of this group included in our study are *Pseudotriton ruber, Desmognathus fuscus,* and *Eurycea bislineata.*

Some members of the family Salamandridae (e.g. *Chioglossa lusitanica*) and many members of the family Plethodontidae (e.g. *Batrachoseps pacificus, Plethodon cinereus*) have what we call *slender-based tails.* In these species breakage may occur at any point in the tail, but the route of breakage is specialized in that the skin break occurs one segment posterior to the muscle break. The result is that, following breakage, the skin covers the open wound and facilitates healing. This pattern, first

mentioned by Piersol ('10), is called the *wound-healing specialization* by us.

A final group that includes almost two-thirds of the species of the family Plethodontidae has *constricted-based tails*. A distinct tail constriction is found at the base of the tail and breakage, when it occurs, is ordinarily at this point. Members of the group have been reported to practice tail autotomy by many authors. We have studied this group more intensively than the others, especially the following species: *Hemidactylium scutatum, Ensatina eschscholtzii,* and *Bolitoglossa subpalmata.* With the exception of some brief and generalized comments, nothing has been written concerning the anatomy of the basal tail region or the mechanisms of autotomy and tail breakage in these species.

### The tail base region

Thick-based tails are well adapted propulsive organs important for locomotion in aquatic to semiaquatic habitats. Such habitats were probably occupied by ancestors of the family Plethodontidae and are still characteristic of most species of the subfamily Desmognathinae and tribe Hemidactyliini (Wake, '66). These groups all have thick-based tails that are often laterally compressed and may have dorsal keels.

Within both of the above groups distinct trends in the direction of terrestriality are found. As species become increasingly terrestrial in habits, for example, the series *Desmognathus quadramaculatus* to *D. fuscus* to *D. ochrophaeus* to *D. wrighti,* tails tend to become round in cross section and increasingly slender near the base. A similar trend is seen in the hemidactyliines, culminating in *Eurycea lucifuga.* Members of the remaining plethodontid genera, grouped in the tribes Plethodontini and Bolitoglossini, are all terrestrial (Wake, '66). No species of these latter groups have thick-based tails. Slender-based tails are found in *Plethodon* and *Aneides* among the plethodonines and *Hydromantes* and *Batrachoseps* among the bolitoglossines.

Constricted-based tails are found only in semiterrestrial (*Hemidactylium,* a hemidactyliine) and terrestrial (*Ensatina,* a plethodonine; *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge,* and *Thorius,* all bolitoglos-

sines) species. The amount of constriction and details of structure differ considerably among the species. Constriction is pronounced in most, but is barely evident in *Oedipina, Lineatriton,* and some species of other genera. A universal feature of the group is the presence of a first caudal segment that is short relative to the segments that immediately precede and follow it. This segment is immediately posterior to the cloacal slit and is the first to entirely surround the vertebral column. Shortening of the segment is most pronounced in those species with obvious basal constriction, such as members of the genus *Bolitoglossa.* In *Hemidactylium,* both the first and second segments are short.

The basal region of species with constricted-based tails is of smaller diameter than some more posterior parts of the tail. Decrease in the thickness of the musculature of the first caudal segment is the primary factor, but the constriction is often accentuated by the abrupt increase in diameter of the tail behind the shortened segment. This increase is the result of hypertrophied dorsal skin glands (Hubbard, '03; Esterly, '04) in some species (e.g. *Ensatina eschscholtzii, Hemidactylium scutatum*). The tail is a site of fat deposition in all species of plethodontid salamanders and, in some of the tropical species (e.g. *Bolitoglossa yucatana*), the tails are extraordinarily swollen.

A series of caudal grooves encircle the tail, marking the position of the intermyotomal septa. These grooves tend to be deep in the basal region of species with constricted tails and especially in the northern highland species of *Bolitoglossa.* The groove at the posterior end of the first caudal segment may be so deep that the skin on either side of it comes into contact. This gives the impression of a clean break in the epidermis, although such a break is not present. Such deep grooves also accentuate the basal constriction.

*The tail defined.* In species with constricted-based tails, breaks occur much more frequently in the basal region than elsewhere. Such breaks extend through the skin at the posterior end of the first caudal segment, between the musculature of the first caudal segment and its anterior attachments, and between the first caudal

vertebra and the vertebra immediately preceding it. This pattern defines the tail, in a functional sense. A more precise definition is possible if one includes all aspects of the morphology of the tail base and immediate postsacral region of salamanders.

A distinct graded morphological series of vertebrae is found between the sacral (identified by its ribs which articulate with the ilia) and the first caudal vertebrae in all salamanders. These have been called the caudosacral vertebrae (Wake, '63, '66) and are two or three in number in plethodontid salamanders. These numbers have taxonomic significance and three is the primitive number. Two are present in the subfamily Desmognathinae, some individuals of several species of *Batrachoseps*, and all species of the supergenus *Bolitoglossa* (including the genera *Bolitoglossa, Oedipina, Pseudoeurycea, Chiropterotriton, Lineatriton, Parvimolge,* and *Thorius*).

Although caudosacral vertebrae are transitional in morphology, they are functionally distinct from caudal vertebrae and must be considered part of the trunk. The cloacal region is in a post sacral position in salamanders and lies directly below the caudosacral series. Some haemapophysial rudiments may be present more anteriorly, but the first fully developed haemal arch is located on the last caudosacral vertebra. This haemal arch is unique in being swept posteriorly so that its distal tip is well behind the posterior end of the centrum. In addition, the arch is greatly broadened distally and lacks the anteriorly directed, median hypophysial spine that characterizes caudal haemal arches. The cloaca and associated structures are firmly attached by massive amounts of connective tissue to the ventral side of the centrum of the last caudosacral vertebra and the expanded, blade-like part of its haemal arch. In addition the caudalifemoralis and ischiocaudalis muscles attach to the intermyotomal septum that is a continuation of the haemal arch of the last caudosacral vertebra, and the caudalipubo-ischiotibialis muscles originate on the margins of that arch. Clearly breakage cannot occur anterior to this point and the tail can be said to start at the intermyotomal septum that connects to the haemal arch, transverse processes and other parts of the last caudosacral vertebra.

*Vertebral column.* A more or less gradual reduction in vertebral length characterizes the region from the sacrum to the tail tip in generalized salamanders, with the most pronounced shortening near the tip. In those species with basal tail constriction, the first caudal vertebra has many specializations, the most obvious being the decreased length relative to the immediately preceding and following vertebrae. The first caudal vertebra of these species is always measurably shorter than the last caudosacral and the second through fifth or more caudal vertebrae, but in *Hemidactylium*, the first and second caudal vertebrae are almost equally shortened. Vertebral shortening is a very conspicuous feature of the most highly specialized members of the group with constricted-based tails, and is especially marked in *Hemidactylium, Ensatina,* and *Bolitoglossa*. Vertebral shortening is much less obvious in the elongated species of *Lineatriton* and *Oedipina*, and is somewhat intermediate between the extremes in the other genera.

Within the family Plethodontidae, postsacral ribs are never found. The caudosacral vertebrae bear long transverse processes, and transverse processes are typically present on most caudal vertebrae. In most of the genera, the transverse processes arise near or slightly anterior to the midpoint of the centrum. The processes may extend almost directly laterally with only a slight posterior bend at the distal tip (*Batrachoseps*), or they may extend posterolaterally forming acute angles between the posteriorly swept process and the long axis of the vertebral column (fig. 1). The angle varies considerably, from very large (e.g. *Hydromantes*), to intermediate (most genera, e.g. *Eurycea, Plethodon, Pseudotriton*), to rather small (*Aneides*). Typically the first caudosacral vertebra bears the longest transverse processes and the processes steadily diminish in size on succeeding vertebrae until they disappear entirely. The point of disappearance of the transverse processes is subject to ontogenetic as well as interspecific and intergeneric variation.
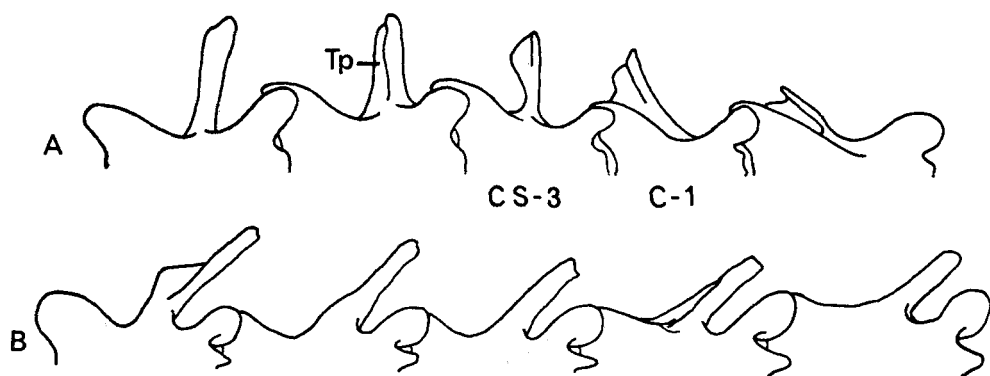
Fig. 1   A dorsal view of the right side of three caudosacral (CS-3) vertebrae and two caudal (C-1) vertebrae of (A) *Ensatina eschscholtzii* and (B) *Plethodon jordani*. Orientation of the transverse processes ($T_p$) in these two species differs considerably.

The genera with constricted tail bases differ markedly from the less specialized plethodontid genera in the orientation of the transverse processes in the tail base region. In these genera, the orientation of the processes changes from posterolateral to sharply anterolateral in a space of three to five vertebrae (fig. 1). *Hemidactylium* and *Ensatina* have three caudosacral vertebrae, but other genera with constricted-based tails have two. In all, the pattern of the transverse processes on the first is essentially similar to that in less specialized groups. In *Hemidactylium* and *Ensatina*, the processes of the second caudosacral vertebra form a larger angle with the long axis of the vertebral column than do those of the first. The last caudosacral vertebra in all species with constricted-tail bases bears transverse processes that are almost perpendicular to the long axis. In some species of *Bolitoglossa*, these processes may be directed slightly anteriorly. The usual situation in other species is for the processes to be directed slightly posteriorly or to be almost at right angles with the axis (fig. 1). All caudosacral processes arise near the vertebral midpoints.

Transverse processes on the first caudal vertebrae in genera with constricted tails differ markedly in position and shape from those of other plethodontids. In all these genera, the processes originate near the anterior end of the vertebra and they are directed slightly to strongly anteriorly. In *Ensatina*, and to a lesser extent, in *Hemidactylium*, the transverse processes are very stout structures, rather irregular in shape and dorsoventrally expanded (Wake, '63). The greatly expanded distal tips are oriented almost vertically in *Ensatina*, while the tips of processes on succeeding vertebrae are tilted anteriorly (fig. 1). Processes are better developed and less irregular in shape in *Ensatina* than in *Hemidactylium*.

The other genera with constricted-tail bases differ from *Ensatina* and *Hemidactylium* in that they do not have especially stout processes, but they are similar in having processes that are directed anteriorly rather than posteriorly. The processes arise at the anterior ends of the centra and have relatively broad bases. Typically the processes are spinous with acuminate, anteriorly directed tips (fig. 2, 3). The processes of the first caudal vertebrae are very elongate in most species of *Chiropterotriton* and *Bolitoglossa* and in some species of *Pseudoeurycea*. In species of both *Chiropterotriton* (e.g. *magnipes*) and *Bolitoglossa* (most species), the transverse processes are sinuously curved anteriorly and approach the posteriorly directed processes of the last caudosacral vertebra. Southern species of *Bolitoglossa*, especially *altamazonica* and *chica*, have very long processes that are directed sharply anteriorly. The last caudosacral processes of these species are also directed rather sharply anteriorly; there is thus no overlapping of processes. In many species of *Bolitoglossa*, from Mexico and Central America, the processes of the last caudo-
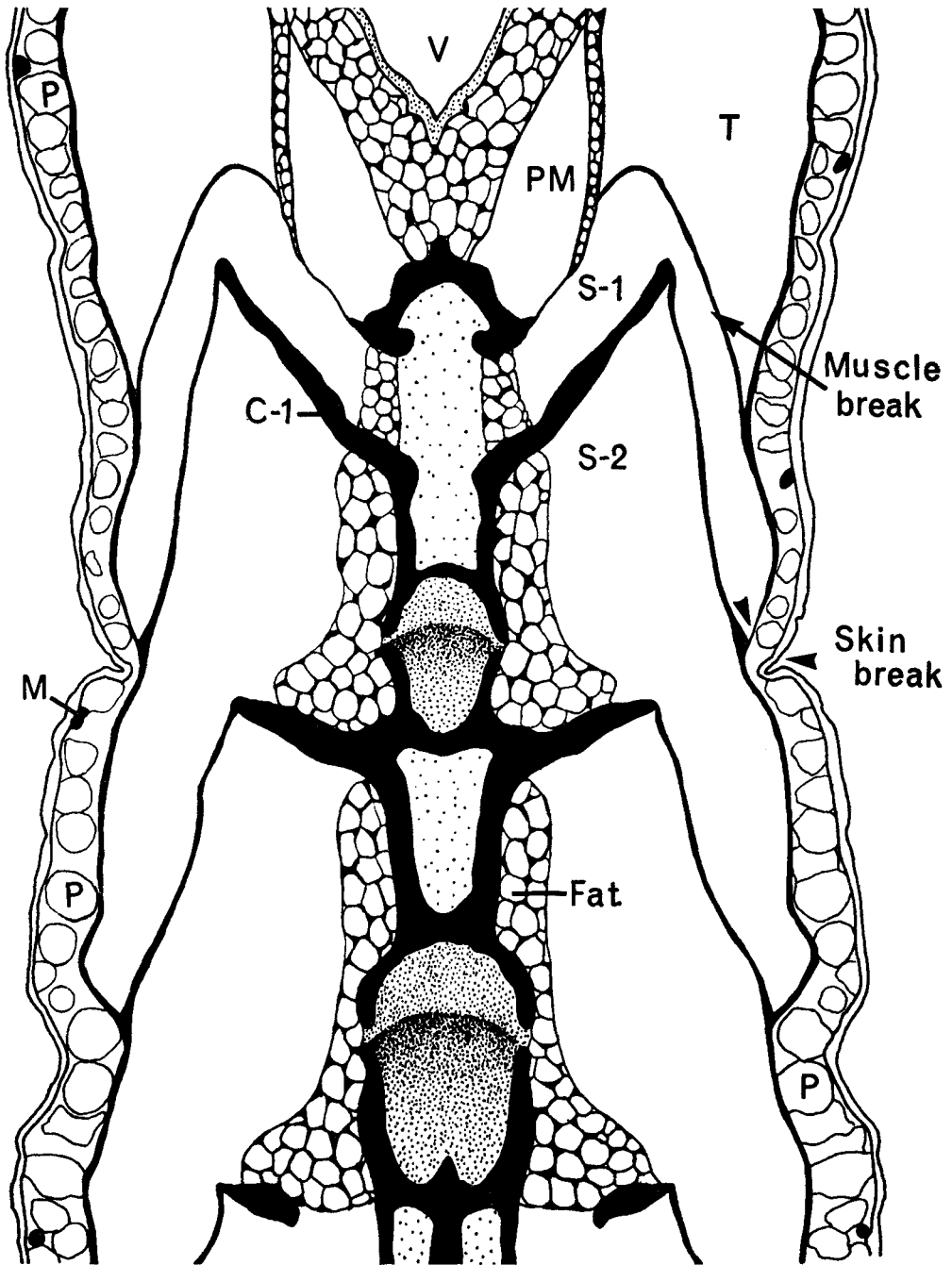
Fig. 2   A slightly oblique frontal section through the tail base of *Bolitoglossa subpalmata*. The first caudal segment (S-1) is much shorter than the second caudal segment (S-2). The transverse processes of the first caudal vertebra (C-1) are directed anteriorly. M, mucous gland; P, poison gland; T, last trunk segment; PM, pelvic musculature; V, cloaca. × 219.
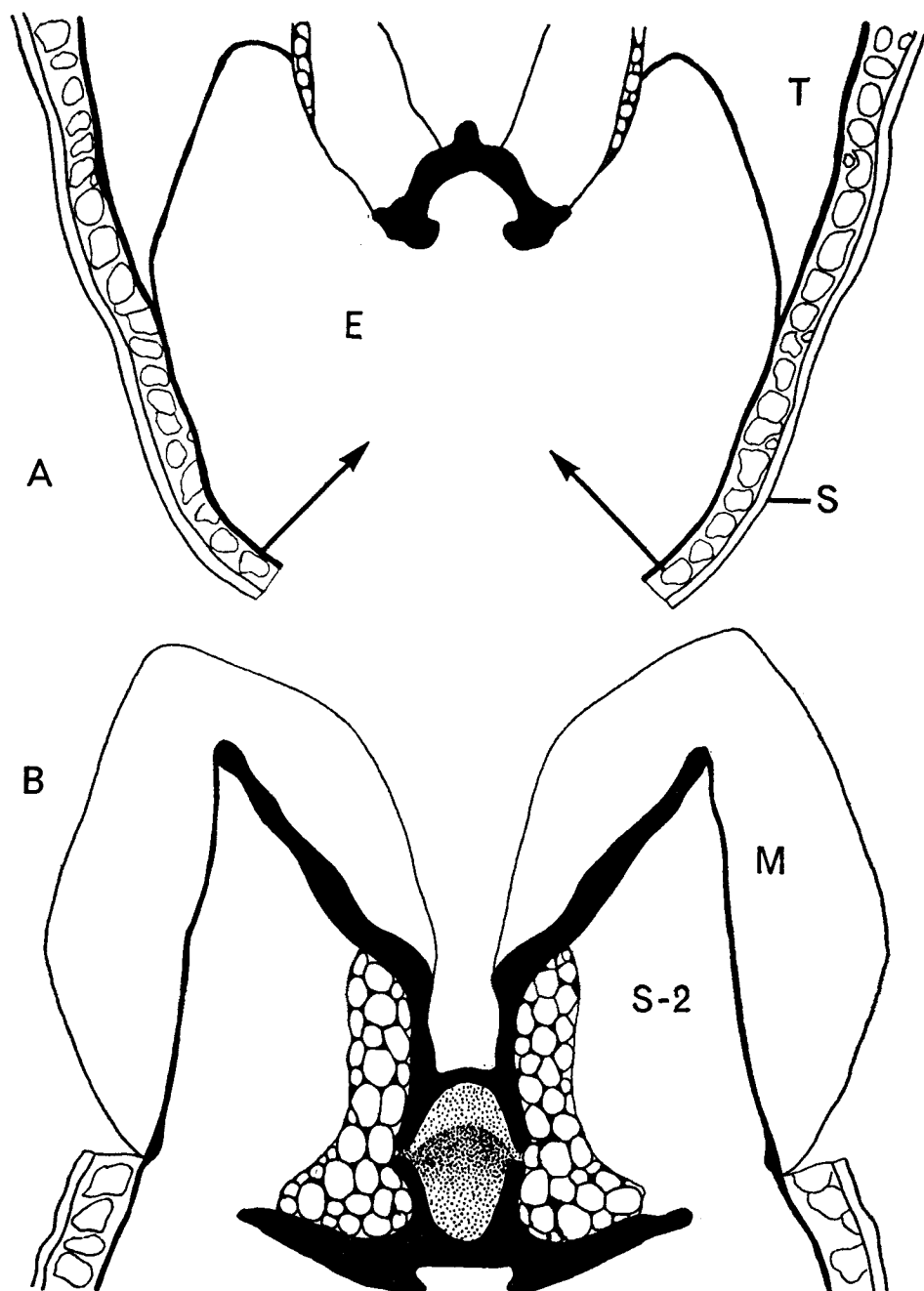
Fig. 3 A slightly oblique, diagrammatic frontal section through a broken tail of *Bolitoglossa subpalmata*. The skin (S) is beginning to close over the broken portion of the body (A). The muscle (M) of the tail (B) is thrust laterally following separation from the body. E, empty space often containing blood clot; S-2, second caudal segment. × 219.

sacral and the first caudal vertebrae overlap, with those of the first caudal being located somewhat ventral to the others. Usually in these species, the transverse processes of the first caudal are bifurcated distally, with the amount of bifurcation reaching a peak in such large species as *B. dunni* and *B. macrinii*. As the bifurcation becomes increasingly pronounced, the area between the widely separated tips becomes filled with bone and the process acquires massive proportions, with two spines and a horizontally oriented web of bone (figs. 4, 5). The intermyotomal septum attaches to the more posterior of these spines. Overlapping processes and distal bifurcation are also encountered in some populations of *Pseudoeurycea leprosa* and some related species in the southern mountains bordering the Mexican Plateau.

Processes of caudal vertebrae beyond the first, in all species with basal tail constriction, become increasingly shortened. Generally, these processes are as sharply or more sharply (*Ensatina*) directed to the anterior than are the processes of the first caudal vertebra. There is considerable variation in the size of the processes. In some forms, such as *Ensatina* and *Hemidactylium*, they diminish in size rapidly and are absent from most posterior vertebrae, but in others they are present on most vertebrae. All are located near the anterior ends of the centra and most are oriented sharply anteriorly, in contrast to the situation in less specialized species. There is a gradual posterior movement of the processes toward the end of the tail (fig. 4). Characteristically, these processes are oriented anteriorly in the most specialized species, in contrast to the primitive condition.

The last caudosacral and all caudal vertebrae but the most recently formed have posteroventrally sloping haemal arches. Large median hypophysial keels are borne on the anteroventral surfaces of all caudal vertebrae of generalized species. Genera with basally constricted tails differ from other plethodontid salamanders in the shape of the haemal arch of the last caudosacral and first caudal vertebrae. The haemal arch of the last caudosacral vertebra is broad and flat distally, and the resulting lamellate structure is oriented almost transversely in the cloacal region. This structure is much larger, more flattened, and more laterally extended than the corresponding structure in more generalized forms. As in other salamanders, this arch lacks a hypophysial keel. The posterior margin of the arch is usually in very close proximity to the corresponding structure on the first caudal vertebra, a
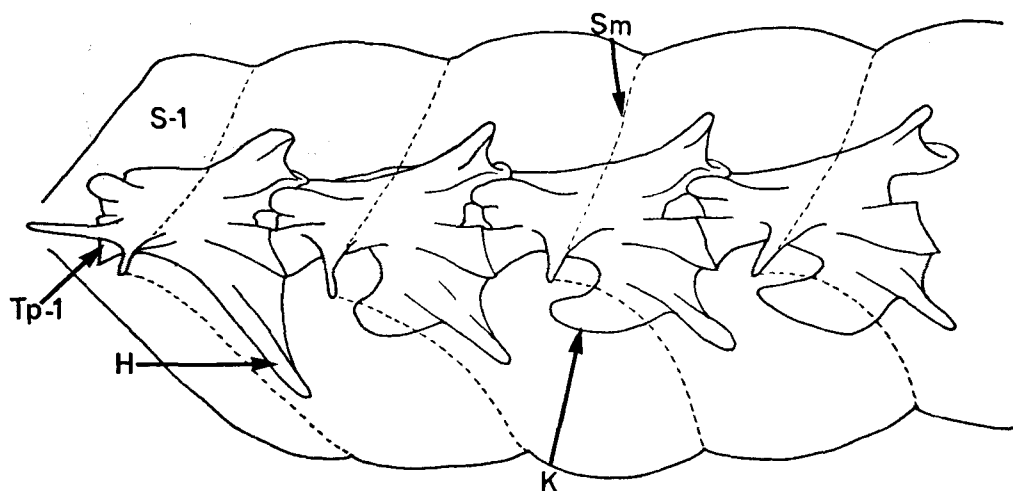


Fig. 4   A left lateral view of the first four caudal vertebrae of a detached tail of *Bolitoglossa rostrata*. Drawn from cleared and stained specimen. The bifurcation of the transverse process of the first caudal vertebra (T$_p$-1) is shown. S-1, first caudal segment; H, haemal arch; K, hypophysial keel; SM, intermyotomal septum. × 15.

situation not encountered in more generalized forms. The haemal arch of the first caudal vertebra of species with constricted-based tails is more vertically oriented than in other species and there is a tendency for the median keel to be reduced or lost. First caudal vertebrae of *Ensatina*, *Hemidactylium*, *Bolitoglossa*, and *Pseudoeurycea* either lack such keels, or have a low median ridge. Keels are very reduced and are little more than median ridges in *Chiropterotriton* and *Lineatriton*. Reduction is less extreme but very evident in *Thorius*, *Parvimolge*, and *Oedipina*. The keels are rather small on the second caudal vertebrae of *Ensatina*, *Bolitoglossa*, *Pseudoeurycea*, and *Chiropterotriton* and increase progressively in size posteriorly (fig. 4). Maximum size is attained at about the fourth to sixth vertebrae. In other genera, keel enlargement is less obvious.

Generalized salamanders have zygapophysial joints in which the amount of contact between post- and prezygapophyses of adjacent vertebrae is relatively great in the anterior portion of the tail, with the amount of contact decreasing posteriorly. In those forms with constricted tail bases, this generalization does not hold true. Perhaps the most extreme conditions are found in the genera *Bolitoglossa*, *Ensatina*, and *Hemidactylium*. Primitively, the post-



Fig. 5   Dorsal view of the first caudal vertebra of *Bolitoglossa morio*. × 36.

zygapophyses of the last caudosacral vertebra are oriented with the articulating facets in an almost horizontal plane, as in the preceding and following vertebrae. In *Ensatina*, in contrast, the entire process, and especially the lateral part, is tilted dorsally, and the articulating facet faces in a somewhat ventrolateral direction. In addition, a well marked zygapophysial ridge, only slightly indicated on other vertebrae, extends from the posterior margins of the prezygapophyses to the postzygapophyses (fig. 1). The combined effect of the upturned postzygapophyses and the well developed zygapophysial ridge lends a depressed aspect to the posterior portion of the neural arch. The prezygapophyses of the first caudal vertebra are twisted dorsally, matching the angle of the upturned postzygapophyses. The net result of these modifications is that the zygapophyses at this particular joint are smaller than at the joints immediately preceding and following, and there is a great reduction in the amount of actual articulation between these zygapophyses.

The arrangement seen in *Ensatina* is repeated in *Bolitoglossa*, but the zygapophysial joint between the last caudosacral and first caudal vertebra is less specialized. The zygapophyses at this joint are reduced in size and are upturned, and there is a distinct decrease in the area of zygapophysial overlap. The situation in *Chiropterotriton* and *Pseudoeurycea* is very similar to that in *Bolitoglossa*, but the zygapophyses are less tilted. Slightly upturned zygapophyses of reduced size are also found in *Lineatriton* and *Oedipina*, but the modifications are slight compared with *Bolitoglossa* and *Ensatina*.

The form of the zygapophyses in *Hemidactylium* differs radically from that seen in the genera discussed above. The neural arches and associated processes on the postsacral vertebrae are very high in *Hemidactylium*. In addition, there has been much dorsal and posterior growth of the posterior margin of the neural arch of the last caudosacral vertebra. Thus, the margins of the neural arch of this vertebra and the associated hyperapophyses are massive. The posterior growth of the neural arch and associated structures of the last caudosacral vertebra is so great that the
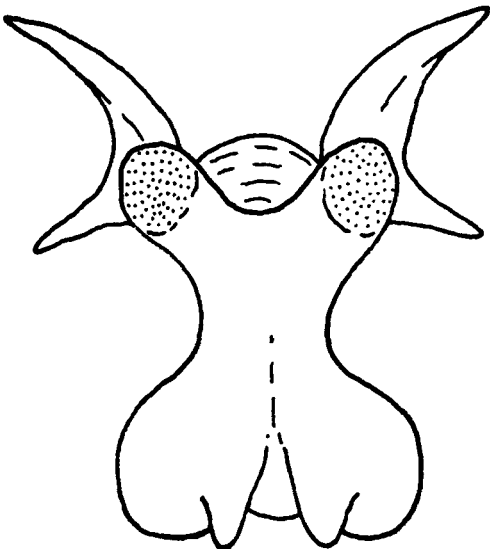
region almost contacts the anterior margin of the arch of the first caudal vertebra. As a result, the fibers of dorsal musculature binding these vertebrae are greatly reduced in length and numbers. The posterior margins of the neural arch of the last caudosacral vertebra extend to a point dorsal to the anterior limit of the centrum of the first caudal vertebra. The postzygapophyses of the last caudosacral vertebra are reduced in size, somewhat tilted laterally and elevated. However, the processes are located in a position rather simliar to that in generalized species and have not been carried posteriorly by the growth of the neural arch. The effect of the posterior growth of the neural arch has been to increase the distance between the postzygapophyses of the last caudosacral vertebra and the prezygapophyses of the first caudal vertebra. As a result the latter are very elongated. The articulation between the zygapophyses at this joint is more reduced than that at the preceding or following joints and the lateral margins of the processes are tilted dorsally, but to a lesser extent than in *Bolitoglossa* and *Ensatina*. It is apparent that the zygapophysial joints of the species with constricted tail bases are weaker than those in the more generalized species.

*Musculature.* The first caudal segment starts at the intermyotomal septum attached to the last caudosacral vertebra. The musculature of this segment differs in configuration from that of the caudosacral region in that the septum at the anterior end of the segment encircles the vertebra. In contrast, the musculature of the caudosacral region is limited to the dorsal and lateral sides of the vertebrae and is replaced ventrally by the pelvic musculature. Musculature of all caudal segments encircles the vertebrae and individual fibers are oriented primarily parallel to the body axis.

In primitive salamanders, including generalized plethodontids, the length of the caudal segments gradually decreases from the base to the tip of the tail. Basal segments are usually about equal in length and the first is at least as long as the next few segments and longer than the remainder. In sharp contrast is the reduced first caudal segment found in species with constricted-based tails. Two factors are involved in the reduction and subsequent constriction: (1) shortening of the segment as a whole and thus of the individual muscle fibers, (2) reduction in the thickness of the musculature as a result of apparent decrease in the number of muscle fibers in the segment. The result of these factors is a tail that is structurally weaker and more flexible at its base than it is a short distance posteriorly.

Shortening of the first caudal segment is related to the forward movement of the transverse processes of the first caudal vertebra. Such a position for these processes is found only in those species with constricted-based tails. The anterior position of the processes causes the intermyotomal septum, which attaches to the distal tip of the transverse processes, to be moved anteriorly. In those groups, such as some species of *Bolitoglossa*, in which the transverse processes are not only moved anteriorly but are also very elongated and extend far anterolaterally, the effect is profound and segment shortening is great. In members of one species group of *Bolitoglossa*, in which the processes are overlapped by those of the last caudosacral vertebra, muscle fiber shortening reaches an extreme. A further complexity is the terminal bifurcation of the transverse processes of the first caudal vertebra in members of this species group. The bifurcation occurs only in those forms in which anterolateral extension of the process is pronounced. The intermyotomal septum that joins the first and second caudal segments attaches to the more posterior projection. The anterior projection is elongated and extends into the first caudal segment. As a result, the muscle attached to the anterior projection is very short and the bone of the enlarged process occupies space normally occupied by muscle fibers. The bifurcation is also important because it allows extreme segment shortening without inordinate lengthening of the second segment. As a result, the "normal" tail segmentation pattern is restored in about three segments (fig. 4).

The circumference of the first caudal segment is much less than that of the last caudosacral and the second caudal segments, in those species with constricted-base tails. The result of this diminution is

that there is less musculature to be separated from the intermyotomal septum of the first caudal segment than in the segment that immediately follows. Consequently, the junction of the first caudal with the last caudosacral segment is an area of potential weakness.

The genus *Hemidactylium* differs from the other genera with constricted-based tails in that the second caudal segment also is shortened, although to a lesser degree than the first. In addition, the second segment has a smaller circumference, based on thickness of musculature and ignoring the skin, than the third. Thus in *Hemidactylium* the normal segmental relationships are restored somewhat more gradually than in other genera. In *Hemidactylium* there is a constricted region rather than a constricted segment at the tail base.

### Comparative Microscopic Anatomy

*Skin and subcutaneous connective tissue.* Skin of the tail base region of species with thick-based tails, such as *Desmognathus quadramaculatus,* consists of a relatively thin epidermis and a very thick dermis. The dermis contains a few, small mucous glands and moderate numbers of much larger poison glands which lie in a bed of relatively loose connective tissue (fig. 6). The glandular region lies between the basement membrane (in the sense of Hay, '66) and a deep, very thick layer of collagenous connective tissue. Between this layer and the underlying musculature is a subcutaneous layer of loose connective tissue. This fairly extensive tissue is most fibrous in the intersegmental regions, where the fibers of the intermyotomal septa join it. The fibers of the subcutaneous region are essentially in continuity with those of the intermyotomal septa.

Some variation is encountered within the group with thick-based tails. *Pseudotriton ruber* has a very thin epidermis and an extraordinarily thick dermis. Dermal glands are small and widely dispersed, and the dense dermal layer is much thicker than that in *D. quadramaculatus.* In contrast, some of the more terrestrial species of *Desmognathus* (e.g. *D. ochrophaeus*) have skin resembling that found in species with slender-based tails. Here the epidermis is relatively thick and the dermis has

many glands and much loose connective tissue.

The dermal and subcutaneous layers of slender-based tails are thinner than the corresponding layers in thick-based tails. The deep layer of the dermis is relatively thin and less dense, and the subcutaneous region is greatly reduced. Dermal glands are abundant and the poison glands are especially numerous and large. The epidermis is somewhat thicker than in thick-based tails. No distinction between inter- and intramyotomal regions is noted in either thick-based or slender-based tails, except for the fact that the attachment of the intermyotomal septum causes the entire skin to be pulled medially, toward the body axis. The result is the conspicuous caudal groove seen in these species. Caudal grooves are generally less marked in species with thick-based tails.

Skin of the lateral and ventral surfaces of species with constricted-based tails resembles that in species with slender-based tails. Mucous glands of the dorsal and dorsolateral skin are also somewhat similar in the two groups but tend to be larger in some genera with constricted-based tails, especially *Ensatina* and *Hemidactylium.* In other respects, however, there are striking differences. The dermal and subcutaneous connective tissue forms a fibrous sheath surrounding the tail in all salamanders. In species with thick- and slender-based tails, there is no regional differentiation in the sheath and it is about equally thick throughout the basal region. The same condition prevails, except at the tail base, in species with constricted-based tails (fig. 7). In contrast, a marked differentiation in this sheath is found at the level of the posterior end of the first caudal segment in species with basal tail constriction. At this point, the dermal and subcutaneous connective tissue is reduced or absent. Details of this connective tissue discontinuity in one highly specialized group and comparisons with other groups are presented below.

Adult individuals of several species of *Bolitoglossa* have very well marked constrictions at the bases of their tails. In addition to the shorter and smaller first caudal segment, there is a deep groove marking the junction of the first and sec-

ond caudal segments. This groove is so marked in some (e.g. *B. rostrata*) that it gives one the impression that the skin is interrupted at that point. The groove is somewhat less marked in *B. subpalmata*, but is still pronounced (figs. 8, 9). Several factors are involved. The first is the marked reduction in thickness of the epidermis at that point. More important is the reduction in size and number of the dermal glands in the groove region. The result is that the epidermis rests directly on the connective tissue sheath, a condition not encountered elsewhere in the tail (fig. 9). Finally, the connective tissue sheath of the tail is greatly reduced in thickness immediately anterior to the groove. As one nears the intermyotomal septum at the end of the first caudal segment, the connective tissue decreases in thickness and density. There is essentially an interruption in the sheath immediately anterior to the point where the intermyotomal septum joins the skin (see below), and only a few fibers join the dermis of the first caudal segment with that of the second. Certainly this area is one of structural weakness.

The intermyotomal septum between the first and second caudal segments in *Bolitoglossa subpalmata* is oriented posterolaterally from its origin on the first caudal vertebra. As the thick, dense collagenous sheet nears the skin it curves posteriorly and joins smoothly with the subcutaneous connective tissue (figs. 8, 9). As a result, the deep dermal and subcutaneous fibrous layers of the second caudal segment pass without interruption into the intermyotomal septum at the anterior end of the segment. This continuous fibrous layer approaches a straight line orientation in the region where the skin of the first segment joins that of the second (fig. 8). It is at this junction that the connective tissue discontinuity is most apparent and it is here that the skin separates during tail breakage.

The cutaneous groove is ordinarily not so obvious in other genera as in *Bolitoglossa*. Nevertheless, although there are slight differences in general morphology, the connective tissue specialization in other genera approaches the condition in *Bolitoglossa*. In *Ensatina*, a groove is usually evident and, in the area of the groove,

there is a decrease in the amount of dermal and subcutaneous connective tissue. Only a few cutaneous fibers are continuous between the first and second segments, and obviously the region is structurally weak. The skin of *Ensatina* does not become as thin in the area of constriction as in *Bolitoglossa* because the dermal glands tend to be somewhat larger and a moderate amount of loose connective tissue is present (figs. 10, 11). The greatest reduction occurs in the deep layer that ordinarily consists of densely packed collagenous tissue. At the end of the first caudal segment in *Ensatina*, this layer cannot be distinguished.

A discontinuity in the connective tissue sheath is present at the end of both the first and second caudal segments in *Hemidactylium* (figs. 12, 13, 14). The dermal and subcutaneous connective tissue at the anterior ends of these segments is about as thick as that in other tail segments. At about the midpoint of the segment the connective tissue layer begins to diminish in thickness and, near the end of the segment, very little remains. Glands are absent or greatly reduced in size in the skin near the ends of these segments and the epidermis rests almost directly on the underlying musculature, close to the posterolaterally oriented intermyotomal septa. Our observations on cleared and stained, as well as on museum preserved specimens, indicate that breakage occurs at the end of the first segment, but, in view of the weakened nature of the skin at the end of the second segment, breakage could also be expected at that point.

In all species of *Pseudoeurycea, Chiropterotriton, Lineatriton,* and *Thorius* examined, the connective tissue defect is less pronounced than in *Bolitoglossa, Ensatina,* or *Hemidactylium*. Grooves may be present, but they are usually not as well developed as in *Bolitoglossa*. The connective tissue defect at the posterior end of the first caudal segment is present, but it is much less obvious than in the above genera. In *Thorius,* the connective tissue simply appears to be diminished in thickness and the dermal glands reduced in size and density in the area of the groove.

Diminution in the amount of fibrous connective tissue at the end of the first

caudal segment is the major skin specialization related to weakness or fragility in *Ensatina* and *Hemidactylium*. This feature is of considerable importance in *Bolitoglossa, Chiropterotriton,* and *Pseudoeurycea* as well, but in these genera, and possibly in *Ensatina,* another factor is also important. In the most specialized condition, such as is seen in *Bolitoglossa subpalmata* and *Pseudoeurycea leprosa,* the subcutaneous region of only the first caudal segment contains a number of small, highly basophilic cells (fig. 15). These cells form a distinct layer below the dense connective tissue layer at the base of the dermis. Posteriorly this cellular layer contacts the posterolaterally oriented intermyotomal septum at the end of the segment. The cells follow the septum to the point at which it becomes continuous with the fibrous layer of the second caudal segment. Here the cell layer turns rather sharply toward the surface and extends almost to the base of the epidermis (figs. 16, 17). The cell layer thus forms a partition between the dermis of the first and second caudal segments. One can also find inward extensions of the epidermis at the point where the cell line is located. The orientation of these cells and of those in the epidermal invagination forms a separation plane that orients and facilitates breakage of the skin at this point (fig. 17).

Weakening of the skin at the end of the constricted region results from a simple decrease in the amount of connective tissue in some species. In the most highly specialized groups, the insertion of a partition of cells of unknown origin and function into the dermis results in a separation in the dermal and subcutaneous connective tissue sheath that further weakens the skin at this region. Currently, investigations are in progress as to the origin and biological properties of these cells.

*Intermyotomal septa — muscle fiber relationships.* The attachments of the individual muscle fibers to the intermyotomal septa in the tails of all salamanders are identical, with the exception of the first caudal segment of species with constricted-based tails. Typically each muscle fiber is firmly attached to the septum proper by a rather dense bed of collagenous fibers, and there is no obvious separation of the fibers

at any point in the tail from the septum (figs. 11, 18).

In contrast, some of the species with constricted-based tails have a unique pattern of muscle fiber attachment in the first caudal segment. The attachment at the posterior end of the segment is normal, but that at the anterior end is apparently weaker than at any other point in the tail. Among the species studied, the most extreme condition is encountered in *Bolitoglossa subpalmata.* The anterior side of the intermyotomal septum at the anterior end of the first caudal segment is identical to muscle septum relationships elsewhere in the body and tail. On the posterior side of the same septum, however, the muscle fibers of the first caudal segment are delicately attached to the main mass of collagenous fibers in the septum by slender bundles of collagenous fibers (fig. 19). The fibers in this bundle are relatively few in number and small in diameter. In addition, the bundle contains small cells with large nuclei, which apparently result in a further weakening of the attachment by displacing fibrous elements.

Breakage occurs at this point, and the connective tissue of the delicate bundle either separates from its attachment to the fiber or breaks, and the sarcolemma of the muscle fibers normally ruptures. This situation is somewhat analogous to the rupture that occurs at the myotendinous junction in most vertebrates (Barrnett, '66). Rupture of the sarcolemma results in an expansion of the released end of the muscle fiber, producing a mushroom-like cap (figs. 21, 24).

Cells that are found in the delicate attachment bundle may contribute to the blastema of the regenerating tail. Their functional versatility was apparent in one individual of *Pseudoeurycea leprosa* in which the muscle had become separated from the septum on one side of the tail. The cells of the attachment bundles increased greatly in number, and some moved posteriorly (fig. 20). These latter cells were apparently transformed into myoblasts, and all intermediate stages are encountered. Detailed studies of the attachment of the muscle fibers to the septum and of the regenerative capacities of these peculiar cells are currently under

investigation. Whatever the significance of the anatomical detail, the delicate attaching bundle of connective tissue is much weaker than the attachment at any other point in the tail.

The pattern described in *B. subpalmata* is not nearly as apparent in the other species examined. However, in all available specimens of *Bolitoglossa, Thorius, Lineatriton, Pseudoeurycea,* and *Chiropterotriton,* the attachment of the muscle fibers of the first caudal segment to the septum joining the last caudosacral and first caudal segments exhibits relative weakness. Generally the fibers are pulled slightly away from this septum and a delicate bundle of connective tissue, occasionally containing cell bodies, joins the muscle to the septum. Most of our material was infiltrated with paraffin and doubtless the condition seen in our slides is in part an artifact of preparation. However, since the condition is observed only at this position it is obvious that the attachment of the muscle to this particular septum in these species is much weaker than in neighboring segments.

The picture is even less clear in the other species with constricted-based tails. In some specimens, a few of the connective tissue bundles at the anterior end of the first caudal segment are visible, but the condition is certainly not typical. The muscle usually appears to be less tightly attached than elsewhere in the tail, and this suggests that the region is one of relative weakness. We have determined experimentally that the breakage plane extends across these attachments.

Tail breakage occurs with apparent ease in species of genera with slender-based tails, for example, *Batrachoseps* and *Plethodon.* We have been unable to detect any differences between the muscle attachments on the anterior and posterior sides of the intermyotomal septa of these forms.

*Intervertebral attachments.* In generalized salamanders, successive vertebrae are bound very tightly together by relatively large amounts of collagenous connective tissue. The connective tissue is particularly well developed between the pedicel walls, around the zygapophysial capsules, and around the margins of the centra. The thick, relatively dense bands of connec-

tive tissue bind all vertebrae together and there is no localized differentiation in the column.

The amount of intervertebral connective tissue is reduced in quantity, thickness, and density in those species with slender-based tails in which tail breakage may occur basally or at any place within the tail. No differentiation of one intervertebral joint relative to any others is apparent.

A remarkable differentiation is found in forms that have marked tail constriction. In all specimens of *Bolitoglossa, Chiropterotriton, Pseudoeurycea, Thorius, Ensatina,* and *Hemidactylium* that we have examined, the amount of connective tissue binding the first caudal to the last caudosacral vertebra is dramatically reduced. The connective tissue between neural arch pedicels is restricted to a few randomly distributed strands of collagen and there is essentially no connective tissue between the centra (fig. 22). The amount of connective tissue in the zygapophysial capsule is reduced relative to the joints immediately in front of and behind this joint. The region is certainly one of weakness relative to other parts of the tail. For example, the joint between the first and second caudal vertebrae might be considered "normal," that is, large amounts of connective tissue bind all parts of the vertebrae together (fig. 23).

*Thorius* is a diminutive species that does not have an obviously constricted tail. Yet it seems fully as specialized as those species with marked constriction, in terms of lack of connective tissue between the last caudosacral and first caudal vertebrae. In addition to its absence in sectioned material of unbroken tails, no connective tissue is evident in the articular region in one specimen of *Thorius dubitus* which was induced to break its tail. The caudal part of the broken tail was sectioned and stained, and as is apparent from figure 24, the margins of the centrum are entirely devoid of connective tissue.

A summary of characters associated with tail base morphology is presented in table 1.

DISCUSSION

Within the Order Caudata, specializations related to tail breakage have evolved

TABLE 1

| | Thick-based tails | Slender-based tails | Constricted-based tails |
|---|---|---|---|
| Break pattern | Skin and muscle break at same point | Skin break at posterior and muscle break at anterior end of segment (wound-healing specialization) | Skin break at posterior and muscle break at anterior end of first caudal segment (wound-healing specialization) |
| Length of first caudal segment | Equal to or longer than adjacent posterior segment | Equal to or longer than adjacent posterior segment | Shorter than adjacent posterior segment |
| Length of first caudal vertebra | Equal to or longer than adjacent posterior vertebra | Equal to or longer than adjacent posterior vertebra | Shorter than adjacent posterior vertebra |
| Orientation of transverse processes on anterior caudal vertebrae | Sharply posterolateral | Moderately to sharply posterolateral | Sharply anterolateral |
| Epidermis | Thin | Thick | Thick |
| Dermal glands | Relatively small and scattered | Relatively large and numerous | Very large and numerous; largest and most concentrated on dorsal part of tail |
| Deep fibrous layer of dermis | Thick; continuous between first and second caudal segments | Thin; continuous between first and second caudal segments | Thin; discontinuous between first and second caudal segments |
| Attachment of muscle fibers at anterior end of first caudal segment | Strong; identical to that in other segments | Strong; identical to that in other segments | Weaker than in other segments |
| Connective tissue fibers between last caudosacral and first caudal segments | Numerous and dense | Numerous and dense | Few and scattered; absent between centra. |

in at least two families, the Salamandridae and the Plethodontidae. The lowest grade of specialization is the wound-healing mechanism, a breakage pattern in which the cutaneous break occurs at the posterior end and the muscle break at the anterior end of a given caudal segment. Although this specialization basically results from no more than a slight topographic reorientation of the intermyotomal septa, it is highly significant to the organism. When the tail breaks, all of the muscle of the segment in which the break occurs is lost. The end of the body then consists of the exposed vertebra and the intermyotomal septum that extends from the vertebra in all directions out to the segment-long cylinder of skin. Orientation of the septum relative to the skin is such that the skin of the segment in which the break occurs is pulled toward the exposed vertebra. The folded skin collapses over the wound, facilitating both immediate blood clotting and subsequent healing and regeneration. Regeneration characteristically proceeds rapidly with a tail blastema forming that regenerates all tissue except the notochord (see also, Holtzer, Holtzer and Avery, '55). The earliest reference to this pattern of breakage is a brief discussion by Piersol ('10). He discussed the protective function of the collapsed skin and the effect exposure of the muscle would have on increasing the rate of the contortions of the severed tail. Since that time, nothing of significance has been added on the subject, but his observations have

been repeated by several authors on several species.

We have not widely sampled families other than the Plethodontidae, but wound-healing specializations are present in other groups and the feature has apparently evolved several different times. *Chioglossa lusitanica* is an exceptionally long-tailed salamandrid that has been available for study. It clearly has the same kinds of wound-healing specializations that occur in plethodontids. We have not found similar specializations in other families.

Within the family Plethodontidae, wound-healing specializations are rather widespread. Wake ('66) has recently placed plethodontid salamanders in four major groups. The subfamily Desmognathinae contains three genera, *Desmognathus*, *Leurognathus*, and *Phaeognathus*. In all three, tail breakage is apparently common but the wound-healing specialization is not present, or at least, not well developed. When an animal breaks its tail, always by trauma or by mechanically twisting the body away from the restrained tail, the skin and muscle breaks occur at approximately the same spot. Occasionally, however, the skin break may occur relatively far posteriorly and may partially cover the exposed wound. The skin break usually extends in a rather jagged-edged ring around the tail.

The Tribe Hemidactyliini includes a rather diverse array of genera and species. The more primitive genera (*Stereochilus*, *Gyrinophilus*, *Pseudotriton*) include species that have thick-based tails and no specializations for tail breakage. Members of the genus *Eurycea* and some close relatives (*Typhlomolge*, *Typhlotriton*, *Haideotriton*) vary from thick-based (e.g. *E. aquatica*) to an almost slender-based (e.g. *E. lucifuga*) condition. Tails of these species are laterally compressed and, when breakage occurs, a partial closure of the wound follows. Analysis of sectioned material reveals that the skin and muscle breaks are identical in topography at the caudal side of an intermyotomal septum. Wound closure is the result of the sharp posterolateral orientation of the intermyotomal septa and transverse processes from the centra of the caudal vertebrae. The transverse processes are located at

about the midpoint of the vertebrae and this feature tends to accentuate the posterior shift of the segment attaching to the caudal half of each vertebra. As a result of this posterior shift of the segments and the lateral compression of the tail, the tissue that extends beyond the point of skeletal separation collapses medially and a vertically oriented wound closure ensues. This is quite a different and less effective kind of wound-healing specialization than is found in other plethodontids and seems to be the result of evolutionary convergence. The genus *Hemidactylium* is also a member of this tribe.

The Tribe Plethodontini includes the genera *Plethodon, Aneides* and *Ensatina*. Wound-healing specializations are especially well developed in *Plethodon*, particularly in those species grouped as Eastern Small Plethodons by Highton ('62). Long, slender tails characterize members of this group and tail breakage is common. The specialization is equally well developed in the larger species of the genus and we have been able to demonstrate it in eastern large species such as *Plethodon jordani* and western species such as *Plethodon vehiculum*. Members of the genus *Aneides* are close relatives of *Plethodon* and the wound healing specializations also occur commonly in the more terrestrial species, *A. flavipunctatus* and *A. hardii*. Tail breakage is rare in *A. lugubris*, *A. ferreus*, and *A. aeneus*, climbing species which use their tails in locomotion.

The final group of lungless salamanders, the Tribe Bolitoglossini, includes a variety of forms. The genus *Hydromantes* uses its tail as a propulsive and supportive organ during terrestrial locomotion (Stebbins, '47) and we know nothing concerning break patterns. Tail breakage is rare in the genus. *Batrachoseps* demonstrates very well developed wound-healing specializations. This genus includes very long-tailed species which have tails that may be twice the body length. Breaks occur at any point along the slender tail. Although basal tail breaks are uncommon, the genus must be considered to be somewhat transitional in tail morphology, between the slender-based and constricted-based groups. Breaks occur with ease in *Batrachoseps* and tend to be most common in the distal parts of the

tail. In large individuals with extensive fat deposits in the tail, a region at the base of the tail has a distinctly smaller diameter than adjacent posterior regions. This region is at least as constricted externally as is the corresponding region in *Oedipina*, a genus we place in the constricted-based group. The first caudal segment of *Batrachoseps* appears to be slightly shorter than the second in our sections. However, within *Batrachoseps*, no sharp demarcation is evident between the caudosacral and caudal vertebrae, such as occurs in other plethodontids (Wake, '66). It is the only plethodontid genus in which caudosacral vertebrae vary in number and there is no vertebral shortening in the tail base region. Wound-healing specializations are very well developed, but there is no evidence of a connective tissue defect or other specializations associated with basal tail constriction. Other members of this tribe have basally constricted tails.

*Tail constriction.* Basal tail constriction is found only among members of the family Plethodontidae. However, this family is by far the largest family of salamanders, and the more than 115 species that demonstrate basal tail constriction constitute about 40% of all living species of salamanders.

In its most extreme expression, such as in a fat-tailed old adult of *Bolitoglossa rostrata*, the constriction is very conspicuous, but, in some members of every species in which constriction occurs, individuals are found which do not demonstrate obvious external tail constriction. Such individuals are usually the most emaciated and slender to be found. In this study we have emphasized three genera with very conspicuously constricted tail bases. *Hemidactylium scutatum* is the most terrestrial member of the Tribe Hemidactyliini and lives in woodlands bordering bogs and low-lying areas primarily in the northern sections of eastern North America. It has a tail with a large, rounded dorsal surface and an almost knife-edged ventral surface. The conspicuous tail constriction is located at the base of the tail, immediately behind the vent and in front of the area of dorsal skin gland enlargement. *Ensatina* is perhaps the most terrestrial member of the tribe Plethodontini. The single species, *E.*

*eschscholtzii,* ranges from extreme southern California into Canada, west of the Sierra Nevada-Cascade Mountains crests. The strongly constricted tail has a similar shape to that of *Hemidactylium*. The genus *Bolitoglossa* is a diverse assemblage of about 50 species of neotropical salamanders. Members of the genus range from northern Mexico into South America. All of the species are terrestrial. The constriction is usually strongly marked, especially in the highland species such as *B. rostrata* and *B. subpalmata*. Tails tend to be almost round and dorsal concentrations of skin glands are not so obvious as in the above genera. The constriction in many species of *Bolitoglossa* is emphasized by thinning of the skin at the posterior margin of the first caudal vertebra. In healthy individuals with fat tails, this region tends to be pulled in, toward the vertebral column, by the intermyotomal septum. A very conspicuous, deep groove results.

All remaining genera that have constricted tail bases are also members of the tribe Bolitoglossini. Although species of *Bolitoglossa* have the most obviously constricted tails, constriction is also very evident in members of the genera *Chiropterotriton* and *Pseudoeurycea*. In the genera *Parvimolge*, *Lineatriton* and *Thorius* tail constriction is much less obvious. The last three are all diminutive forms with few fat stores in their tails and no great hypertrophy of the dorsal tail glands. *Lineatriton* has a secondarily elongated tail in which the length of vertebral centra as well as numbers of tail vertebrae are increased relative to more primitive groups. These factors all tend to deemphasize the constricted area. Finally, the highly specialized, extremely long-tailed species of the genus *Oedipina* have slight to no external tail constriction. *Parvimolge*, *Lineatriton*, *Thorius*, and *Oedipina* must be considered members of the functional category that includes forms with constricted tail bases. All have first caudal vertebrae that are shorter than either the last caudosacral or the second caudal vertebrae. This is a character found elsewhere only among species with obviously constricted tail bases. Confirmation has been obtained from serial sections of species of *Lineatriton*, *Thorius*, and *Oedipina* which reveal

that the muscle fibers of the first caudal segment are distinctly shorter than are those of the segments that immediately follow.

*The pattern and mechanism of tail breakage.* Before discussing the mechanism of breakage, a brief review of the morphology of the tail base region of species with constricted-based tails is necessary. Throughout the discussion, emphasis will be placed on the most highly specialized of the genera that display constricted tail bases, *Hemidactylium, Ensatina,* and *Bolitoglossa.* Despite numerous differences, all three genera share at least some features. In all genera, the centra of the first caudal vertebrae are markedly shorter than those of immediately surrounding centra. All have a haemal arch on the first caudal vertebra that is more vertically oriented than are those of surrounding vertebrae. The arch has relatively short anterior-posterior dimensions and either lacks a median keel or has but a low ridge on its broad, anterior face. This surface is in close proximity to the broad posterior flange of the haemal arch on the last caudosacral vertebra. Zygapophysial articular surfaces of the last caudosacral and first caudal vertebrae have smaller dimensions than those of surrounding vertebrae. The anterior part of the neural arch of the first caudal vertebra tends to be raised, and the transverse processes arise very near the anterior margin of the vertebra. The processes tend to be oriented more perpendicularly relative to the longitudinal body axis than in less specialized forms, and in many species, the processes are directed anteriorly.

Muscle fibers in the first caudal segment are noticeably shorter than those in surrounding segments. The decreased length of the first caudal vertebra is not sufficient to account for the rather dramatic muscle fiber shortening. Major contributing factors are the movement of the transverse processes of the first caudal vertebra to a more anterior position and a more vertical orientation of the haemal arch on that vertebra than is found elsewhere. Since the intermyotomal septum between the first and second caudal segments attaches to the process and the haemal arch, the change in orientation of these structures

effectively shortens the first caudal segment. The combination of perpendicular to somewhat posterior orientation of the transverse processes of the last caudosacral vertebra and acute anterior orientation of the processes of the first caudal vertebra contributes further to segment-shortening.

The insertion of the intermyotomal septum into the subcutaneous connective tissue is almost perpendicular in primitive salamanders. Measurements have been made on frontal sections through the centra of a variety of salamanders to determine the angle formed by the intermyotomal septa and the connective tissue sheath of the tail base region. The septum between the last caudosacral and first caudal segments has been pulled far forward, and the angle between the septum and the fibrous connective tissue sheath is much more obtuse in those forms in which tail constriction is marked than in more generalized species. In *Pseudotriton,* the angle is something over 90°. In *Desmognathus ochrophaeus,* a species with a rather slender-based tail, the angle is about 130°. In *Hemidactylium* the angle approaches 150° –155°, and in *Bolitoglossa* the angle may be as large as 165°. Increasing the angle has functional significance in increasing the efficiency of the tail breakage phenomenon and especially the wound-healing specialization. As the angle becomes large, the connective tissue of the intermyotomal septum forms almost a straight line with the subcutaneous connective tissue (fig. 8). If the angle is measured relative to a line laid along the connective tissue surrounding only the second caudal segment rather than the whole tail, it is very close to 180°. An additional factor is the angular relation of the subcutaneous connective tissue of the first segment to that of the second and to the intermyotomal septum. Orientation of the septum and the connective tissue in the anterior part of the second segment results in essentially a straight line of fibers. The fibers in the posterior part of the first caudal segment join this line and form an angle of more than 50° with the septum. Such an arrangement would favor a break on the cranial rather than the caudal side of the attachment of the septum to the skin. Anterior orienta-

tion of the intermyotomal septa throughout the tail, with an acute cranial and an obtuse caudal angle relative to the skin of the tail as a whole, occurs in all species that have wound-healing specializations. Regional differentiation with a great exaggeration of the trend in the first two caudal segments occurs only in forms with constricted tail bases.

The gross organization of the tail discussed above forms a clear morphocline, with the most primitive condition having intermyotomal septa almost perpendicularly oriented relative to the skin. There is a gradual transition to forms that have all septa extending anteriorly from the skin to the axial skeleton. In the most extreme condition, such as is found in *Plethodon* and *Batrachoseps,* wound-healing specializations are very well developed and breakage readily occurs at virtually any point in the tail. At the derived end of the morphocline is the group of species that have constricted tail bases. Here the anterior septa are sharply directed anteriorly from the skin, but more posteriorly along the tail, the septa become increasingly perpendicularly oriented. In this group, features associated with wound-healing are concentrated anteriorly and breakage of posterior parts of the tail is uncommon. A cutaneous connective tissue defect on the cranial side of the first caudal intermyotomal septum concentrates breakage tendencies in the area of constriction. Additional features involved in tail constriction are the decrease in dorsal skin glands in the basal tail region and a decrease in the number of muscle fibers, and hence in the thickness of the segmental muscle layer, in the first caudal segment, relative to immediately more posterior parts of the tail.

In earlier sections of this paper, we discussed the several unique histological features of the first caudal segment. These include diminution or complete absence of the cutaneous and subcutaneous connective tissue at the caudal end of the first segment, immediately anterior to the intermyotomal septum. The skin glands may be absent from a small area just anterior to this septum. In addition, the epidermis may be thin in this region. Several forms have a layer of specialized cells inserted

between the muscle and the skin. These cells approach the epithelium at the caudal end of the segment and effect a complete separation of the fibrous layers of the two segments. Attachment of the muscle fibers of the first caudal segment to the anterior intermyotomal septum is weaker than in any other surrounding segments. Finally, the amount of fibrous connective tissue between vertebrae in the area of constriction is much less than that found elsewhere, and no fibrous tissue has been found between the centra of the last caudosacral and first caudal vertebrae.

The areas of greatest structural weakness correlate exactly with the break pattern, as determined experimentally. We have broken the tails in individuals of *Bolitoglossa subpalmata, B. yucatana, Ensatina eschscholtzii,* and *Thorius dubitus.* In all the break pattern is similar to that illustrated in figure 3. The skin breaks at the posterior end of the first caudal segment and the muscle separation is at the anterior end of the same segment. Thus the route extends through the few subcutaneous fibers that join the skin of the first caudal segment to the underlying musculature. More internally, the break extends through the paravertebral fat deposits and between the first caudal and last caudosacral vertebrae. The notochord, blood vessels, and finally, the spinal cord are also severed at that point.

All plethodontid salamanders exhibit a characteristic behavioral response when restrained by their tail. The animal twists the body sharply and violently in a 360° arc around the body axis. Often the result is tail breakage at a point in advance of the point of tail immobilization. In forms with basal tail constriction, the entire tail is lost except when the extreme caudal tip is held. In oder to determine the sequence of events during tail breakage, we have performed a number of simple erperiments and have obtained sufficient information to be able to outline the gross aspects of tail breakage.

Tail breakage in forms with slender-based and constricted-based tails occurs rapidly as part of a violent behavioral pattern. It seems likely that mechanical factors alone are involved in the species with slender-based tails, the unrestrained parts

of the animal simply being twisted from the restrained parts. In the forms with slender-based tails there is no evidence that autotomy, in the sense of voluntary tail loss in the absence of mechanical factors, can occur.

Apparently, a combination of voluntary and mechanical factors are involved in the breakage of tails at points of constriction, at least in the most highly specialized species. When an animal is in an excited state, as a result of being rolled or shaken, and is held in the tail base region, one can detect the violent contraction waves in the caudal myotomes. Our hypothesis is that the first event in "autotomy" in these forms is the separation of the musculature of the first caudal segment from the intermyotomal septum that joins the first caudal to the last caudosacral segment. We have demonstrated above that this area is one of relative weakness. Immediately following its separation from the septum, the muscle contracts in the direction of the intermyotomal septum joining the first and second caudal segments. These freed, contracted muscle fibers orient themselves at right angles to the intermyotomal septum to which they remain attached. Because this latter septum is oriented at angles from 140° to 160° relative to the tail surface, the diameter of the constricted segment will suddenly be greatly increased. The result is a greatly increased force directed on the skin of the posterior part of the first caudal segment, particularly at a point immediately craniad to the point at which the intermyotomal septum between the first and second caudal segments joins the connective tissue of the skin. This is precisely the area that we have shown to be structurally weak. It is likely that, in the most highly specialized forms, breakage of the skin at the posterior end of the first caudal segment follows immediately upon separation of the muscle of the segment from its anterior attachment. In most forms, twisting of the body from the tail produces the actual skin break. Intervertebral attachments are weak and presumably the violent movements of the partially detached tail are sufficient to effect final separation, although when the body is twisted, the skin, vertebrae, notochord, blood vessels and

spinal cord are separated in the same motion.

We have never observed completely voluntary tail breakage, or true autotomy. One individual of Bolitoglossa subpalmata was restrained by its tail, just posterior to the area of constriction. The segments contracted violently for a few seconds, then a sinusoidal wave was produced down the back musculature and onto the tail at the same time as the animal propelled itself forward with its limbs. Basal breakage occured and the animal walked away from the tail. A young Bolitoglossa yucatana lost its tail as is was being rolled in a human hand. The tail was broken readily and the animal had no opportunity to twist its body from its tail. It was not possible to detect the sequence of events during breakage because of the speed of the movement.

Very little information can be found in the literature concerning the mechanism of tail breakage in forms with basal tail constriction. Almost all of the information available deals with Ensatina and Hemidactylium, and it is very scanty. Hubbard ('03) states that only under the most extreme provocation (being eaten by a snake, dropped into "killing fluid") will Ensatina lose its tail. Esterly ('04), on the other hand, noted that an individual of Ensatina that had been inadvertantly trapped among debris in a terrarium became very agitated upon gaining its freedom and began moving about "swinging its tail from side to side like an angry cat." After five minutes of such behavior Esterly "merely touched the tail" and it was suddenly "thrown off." Stebbins ('51) stated, in regard to tail loss in Ensatina, "the tail may shed but usually only under stress, commonly breaking at the basal constriction." In 1954, Stebbins added that the tail can be shed under stress or when injured. He did not elaborate further on the process of breakage, but did discuss the route of separation. This discussion, although very short, is the most complete to be found in the literature. It should be modified in regard to two points. The break, if perfect, leaves no exposed musculature on the end of the body, but only the connective tissue of the intermyotomal septum and skin in the areas away from the nerve cord, notochord, blood vessels and bone at the center

of the tail. Also, the cloaca is functionally part of the trunk and is protected from tearing because it is attached to the specialized last caudosacral vertebra, and not because it is protected by a specialized caudal vertebra. In the same paper, Stebbins ('54) reported that a good indication of the critical maxium temperature of *Ensatina* was that temperature at which "spasmodic twitching, and sometimes autotomy of the tail" occurred.

Gnaedinger and Reed ('48) reported observations on Oregon *Ensatina* that are at some variance with those of the workers cited above, all of whom worked with central and southern California populations. They found that salamanders in their laboratory lost tails if handled at all roughly and that tail loss would "invariably result within a short time if an animal were held suspended by the tail". Stebbins ('54) deliberately tested the degree of "caudal fragility" by picking up animals in the field by their tails. He reports that only one of some forty individuals lost its tail and, in this animal, the tail was pinched as the salamander hung in a suspended position. Charles Brown (personal communication) reports that none of hundreds of *Ensatina* that he has collected in California over several years have voluntarily broken their tails at the time of collection.

We have been unable to discover any accounts in the literature of the precise behavior and movements of the animal immediately prior to tail breakage. In our experience, twisting the body around the axis is the only way in which the tail can be broken in *Ensatina*. We have conducted a number of experiments with California *Ensatina*, including placing the animal in deep and shallow water and raising the temperature slowly above the critical thermal maximum, dropping the animals into water heated to the critical temperature, dropping animals directly into 10% formalin solutions, placing a drop of dilute acid on the back and tail, feeding the animals to water snakes (*Natrix*), pricking the tail with a variety of instruments, and suspending the animal from its tail and pinching the tail. Unless the individuals were able to twist the body around the long axis, breakage did not occur.

The senior author has had considerable experience with *Ensatina* in California, Oregon and Washington. Animals have never broken their tails in the field, unless found partially pinned in rotted logs that were being torn apart. Individuals have frequently been picked up by their tails and it has been noted that tails of northern animals appear to be lost more readily than those of the southern animals. Two animals collected in Tacoma, Washington in June, 1966, broke their tails, but only after being allowed to twist their bodies around the long axis while the tail was being held.

Much less information is available concerning *Hemidactylium* than for *Ensatina*. Bishop ('20) stated "a specimen in captivity was induced to cast off the tail by touching the back with a drop of dilute acetic acid." He reported that a "single violent wrench of the body sufficed to separate it from the tail," but added that breakage was uncommon in specimens handled in captivity. Noble ('31) stated that *Hemidactylium* has a basal constriction that is a "provision for quick autotomy." Bishop ('41) stated, concerning *Hemidactylium*, "perhaps the most striking habit is the voluntary dropping of the tail," but did not elaborate. Other workers repeat these statements. We have had only two living *Hemidactylium* available for this study. Both were frequently picked up by their tails but they were not given an opportunity to twist their bodies while the tails were held. Several times they were released about midway through the twist, but neither animal lost its tail.

There is virtually nothing in the literature concerning tail breakage in neotropical salamanders of the supergenus *Bolitoglossa* apart from general statements concerning the nature of the basal tail constriction and allusions to its possible use. Dr. L. C. Stuart (personal communication) reports that, by placing members of the genus *Bolitoglossa* in water and rapidly raising the temperature above the critical thermal maximum, he has been able to induce autotomy in some individuals. In these, the tails simply appeared to drop off.

From our studies on large numbers of museum preserved specimens, it is appar-

ent that the muscle separation must precede the skin break. Most workers prepare animals for fixation by immersing them first in a solution of a narcotizing agent such as chloretone, in warm water, or in a weak alcohol solution. Some simply drop the living animal in the fixative. In most instances there is no opportunity for the organism to wedge itself against an object to break the skin. Occasional specimens are found that have unbroken tails but in which the constriction of the anterior part of the first caudal segment is much more pronounced than in other individuals, and in which the posterior part of the same segment is bulged out. Dissection reveals that the musculature is separated from the intermyotomal septum at the anterior end of the segment. This observation demonstrates that, at least in these individuals, the muscle separation precedes the skin separation and suggests that this is the normal sequence of events during voluntary tail breakage. Presumably muscle separation is partially voluntary and skin and vertebral separation are strictly mechanical, as a result of expansion of musculature, application of external force, or other factors.

*Evolutionary implications.* It is evident that basal tail constriction and associated phenomena have evolved in parallel in three separate phyletic lines (Wake, '66). Ancestors of the three groups probably had wound-healing specializations. Concentration and accentuation of these specializations in the basal tail region led to the evolution of the extremes of specialization reported in this paper.

One can distinguish subtle differences between the three groups that display basal tail constriction. For example, the shortened vertebra is the fourth post sacral in *Hemidactylium* and *Ensatina,* but the third in all members of the supergenus *Bolitoglossa.* Both first and second caudal vertebrae are specialized in structure and both first and second caudal segments are shortened in *Hemidactylium,* but not in the other genera. The cutaneous groove at the caudal end of the first caudal segment of *Hemidactylium* and *Ensatina* is never as sharply defined as in some members of the genera *Bolitoglossa, Chiropterotriton,* and *Pseudoeurycea.* Details of structure of the first caudal vertebrae differ rather sharply in the three groups. Tails tend to be rounder in the supergenus *Bolitoglossa* than in *Ensatina* and *Hemidactylium.* The extremes of segment shortening and of specialization in the attachment of the muscle fibers of the first segment found in members of the genus *Bolitoglossa* are not closely approached by *Ensatina* or *Hemidactylium.* These and other characters tend to support the hypothesis, based on other features (Wake, '66), that tail constriction specializations have evolved separately on three occasions.

Basal tail constriction has evolved only in forms that are largely or completely terrestrial in habits, since, in aquatic and semiaquatic habitats, tails have a very important propulsive function. It is likely that selective factors which led to the evolution of tail constriction specializations were in some way associated with the acquisition of terrestrial habits or of adaptation to some particular aspect of the terrestrial way of life, such as predation by terrestrial organisms. *Hemidactylium* is the most aquatic of the genera that have basal tail constriction, yet it is the most terrestrial member of its tribe (Wake, '66). Although it has an aquatic larval stage, metamorphosis proceeds early and relatively rapidly. The organisms are terrestrial, woodland-inhabitants throughout life except during egg-laying and brooding periods (Blanchard, '23; Bishop, '20, '41). *Ensatina* is as terrestrial as any member of the family Plethodontidae and is probably the most terrestrial and xeric adapted member of its tribe (see also Stebbins, '54). All members of the supergenus *Bolitoglossa* lack aquatic larval stages; their eggs undergo direct terrestrial development (Storer, '25; Brame and Wake, '63).

Patterns of evolution in the supergenus *Bolitoglossa* require special comment. This group includes over two-thirds of the species of plethodontid salamanders. Many species have a very large number of special adaptations. Within this adaptive radiation are found genera with bizarre body forms. Among these are *Lineatriton,* an elongated, poorly known, monotypic genus, and *Oedipina,* an elongate, semiburrowing group of about 20 species. Both groups demonstrate only slight constrictions of

their very long tails. The genera *Thorius* and *Parvimolge* include diminutive species that are the smallest species of salamanders. These species do not have conspicuous tail constrictions. Members of all of these genera have at least some features that we associate with tail autotomy (shortened first caudal segment, specialized first caudal vertebra). Thus we suggest that the ancestral stock of the supergenus *Bolitoglossa* combined the features related to tail autotomy encountered in primitive members of the modern genera *Chiropterotriton*, *Bolitoglossa*, and *Pseudoeurycea*, the most generalized members of the group (Wake, '66). All members of these three genera now have basally constricted tails; this was probably true of ancestors of the supergenus and thus basal tail constriction may be considered a primitive condition in these Neotropical salamanders. Selection has apparently been for increased tail length and possibly for increased tail function in *Lineatriton* and *Oedipina*. Under such conditions, continued selection for tail autotomy specializations could be expected to be relaxed, and in these genera only the grosser features of the specializations have been retained.

One would expect that organisms such as *Hemidactylium*, *Ensatina*, and *Bolitoglossa*, which have localized areas clearly specialized for facilitating tail breakage, would have a high proportion of broken or regenerated tails in nature. Since salamanders regenerate virtually all parts of the tail, including vertebrae but excluding notochord (Holtzer et al., '55), it is impossible to determine whether or not a slightly shorter than normal tail is regenerated without making histological preparations. Therefore all data presented by us and others must be considered to be minimal estimates. However, since Stebbins ('54) has shown that salamanders take over two years to regenerate a tail and, since most salamander species seem to live on the order of five to seven years, it is unlikely that a significant number of individuals with complete regeneration have been missed. We have found data in the literature only for *Ensatina* as far as natural incidence of tail breakage is concerned. Gnaedinger and Reed ('48) report that 4.9% of 169 *Ensatina* had "recently

lost their tails." They stated that 14 others had partially regenerated tails, some regenerating from the base but others from more distal points. The figure for basal tail loss thus lies somewhere below 13% for their sample. Stebbins ('54) reported that 46 of 603 animals (7.7%) studied by him had regenerated all or part of the tail.

In an attempt to obtain information concerning the natural incidence of tail loss in plethodontid salamanders we have examined large series of preserved animals in the Field Museum of Natural History, the Museum of Zoology, University of Michigan, and the Carnegie Museum. An attempt was made to use large samples collected at one time and place, but it was impossible to be assured of nonselective collecting (i.e., the collection of all individuals regardless of size and condition of tail). The collector of the series of 349 *Bolitoglossa morio* was paid for every animal collected and apparently took everything that he encountered. Most of the other series were also collected by individuals or groups such as classes that were thought to be nonselective. Most animals counted were adults. In general, the figures presented represent minimal values.

Data presented in table 2 are based on examination of museum collections. Breakage figures for species with constricted-based tails were obtained by counting individuals with obviously regenerated tails or with tails that were broken prior to death. If breakage occurs after fixation, skin in the break area does not close over the wound, and such individuals were eliminated. It is not as simple to detect breakage in species with slender and thick tail bases, but we accepted as broken only individuals in which approximately one-half of the tail or more had been lost or regenerated. Because the patterns of breakage in species with thick-based tails differ greatly (rarity of basal breaks, no wound-healing specializations) from those with constricted-based tails, we have not attempted any statistical analysis. The species with slender and constricted tail bases are comparable to a greater degree, and we have compared the combined data for the two groups for statistical significance. Chi Square analysis reveals that the figures of 23% with broken tails for the slender-

TABLE 2

| Species | Number | Broken tails |
|---------|--------|--------------|
|  |  | % |
| **Thick-based tails** |  |  |
| Desmognathus fuscus | 239 | 33.4 |
| Desmognathus monticola | 169 | 11.2 |
| Desmognathus wrighti | 420 | 6.9 |
| Eurycea bislineata | 96 | 8.3 |
| **Slender-based tails** |  |  |
| Plethodon cinereus | 273 | 13.0 |
| Plethodon jordani | 455 | 28.2 |
| Plethodon ouachitae | 147 | 19.8 |
| Totals (SBT) | 875 | 23.0 |
| **Constricted-based tails** |  |  |
| Ensatina eschscholtzii | 62 | 9.7 |
| Hemidactylium scutatum | 139 | 4.3 |
| Chiropterotriton chiropterus | 397 | 7.1 |
| Chiropterotriton multidentatus | 214 | 5.1 |
| Pseudoeurycea leprosa | 757 | 7.4 |
| Bolitoglossa altamazonica | 46 | 10.9 |
| Bolitoglossa morio | 349 | 18.9 |
| Bolitoglossa platydactyla | 269 | 7.1 |
| Bolitoglossa rostrata | 202 | 11.4 |
| Bolitoglossa rufescens | 275 | 6.2 |
| Bolitoglossa subpalmata | 142 | 7.7 |
| Thorius macdougalli | 184 | 5.4 |
| Thorius narisovalis | 56 | 17.8 |
| Totals (CBT) | 3092 | 9.5 |

based species and 9.5% with broken tails for the constricted-based species differ significantly at the level, $p = < 0.001$. Thus tail loss is less frequent in our samples of species with constricted tail bases than in those with slender tail bases at a level of high significance.

There are many difficulties with data such as these. We have no information, for example, concerning patterns of variation in a single species from different habitats, different parts of its range, or in samples collected at different times of the year. No data are available for different size classes. Figures from three of the four samples of species with thick tail bases (table 1) do not differ significantly from the figure for species with constricted tail bases, yet the fourth has the highest incidence of tail loss encountered. Nevertheless, it is apparent that tail constriction does not lead to an increase in the incidence of tail loss.

Tail breakage can occur in all salamanders and is so frequent in many species (e.g. Batrachoseps; Hubbard, '03) that it must be important in increasing survival.

However, the tail is a very important organ with locomotor, food storage, behavioral, and respiratory functions. Tail loss in species with basal constriction is more complete but less frequent than in their less specialized relatives. A complete tail, discarded and twitching violently, is probably more efficient in distracting a predator, or acting as a decoy, than part of a tail. It is thus to be expected that morphological specializations that facilitate tail breakage would be localized in the tail base region. Some control over tail loss would probably be necessary before selection for localization and accentuation of breakage specializations could become effective. Because the tail has many important functions and because tails regenerate slowly, those organisms that have some control over tail loss would be favored over those in which tail loss was indiscriminate.

Tail loss occurs only under conditions of extreme stress in most animals with basal tail constrictions. This may be the result of an evolutionary compromise in which an important organ has become highly specialized in a way which may directly in-

fluence survival of the organism. Use of the specializations by the organism results in loss of all other functions. In salamanders with basal tail constriction and associated morphological specializations, selection has resulted in highly adapted organisms that take full advantage of the primitive functions of the tail. However, they have also evolved a high degree of behavioral control over loss of the complete tail, a function that under certain conditions is of possibly crucial significance for survival.

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## PLATE 1

### EXPLANATION OF FIGURE

6  Epidermis (E) and dermis (D) of *Desmognathus quadramaculatus*. The intermyotomal septum (SM) is continuous with the thick subcutaneous connective tissue (SC). $\times$ 293.

David B. Wake and Ian G. Dresner
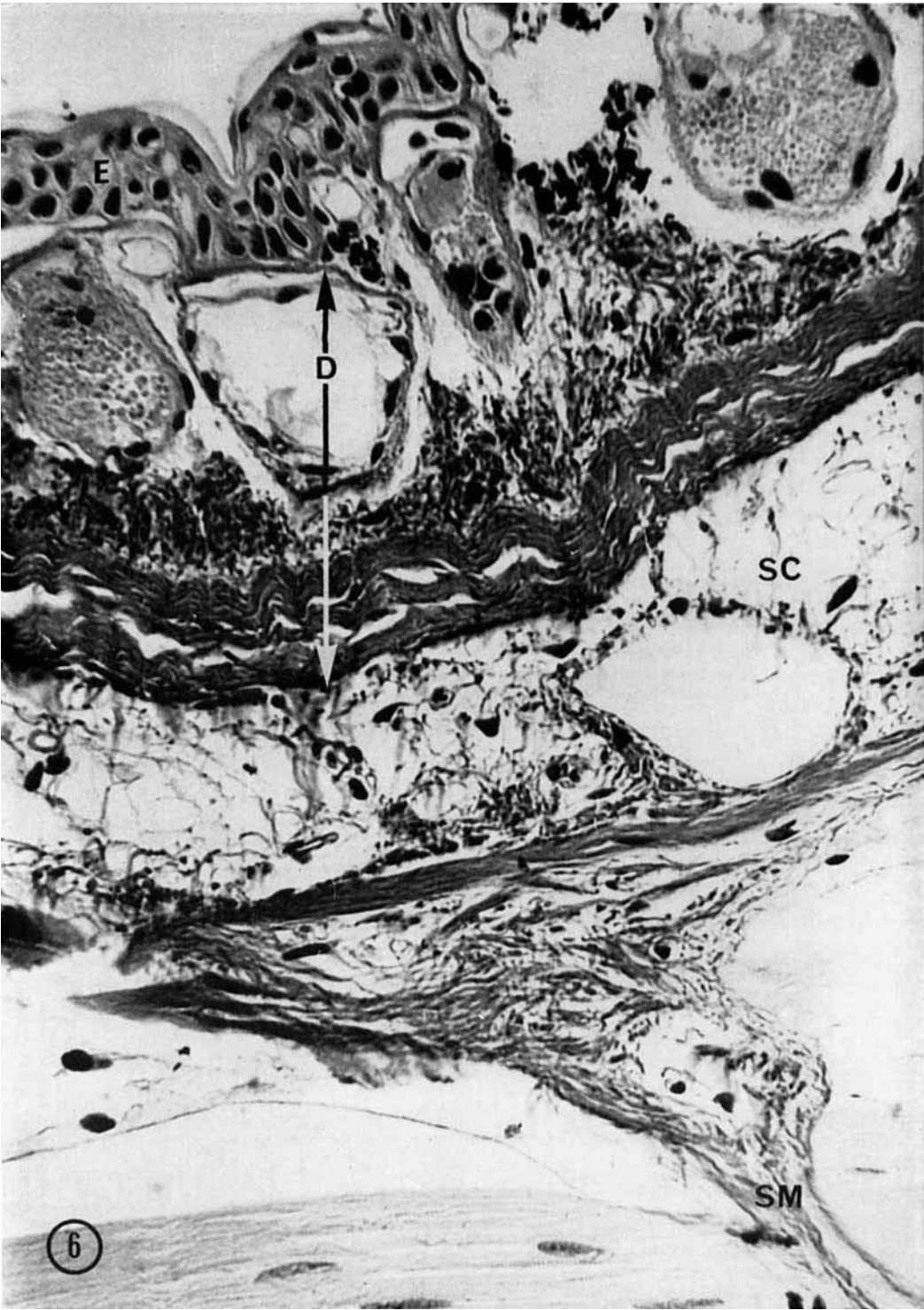
7 Section of skin between third caudal segment ($S_3$) and second caudal segment ($S_2$) of *Bolitoglossa subpalmata.* Note the continuity of the thick fibrous layer between segments. $\times$ 150.

8 Section of skin between first ($S_1$) and second ($S_2$) caudal segments. The dermal connective tissue (D) is much reduced anterior to the tail constriction. CP, cell partition. $\times$ 150.

David B. Wake and Ian G. Dresner
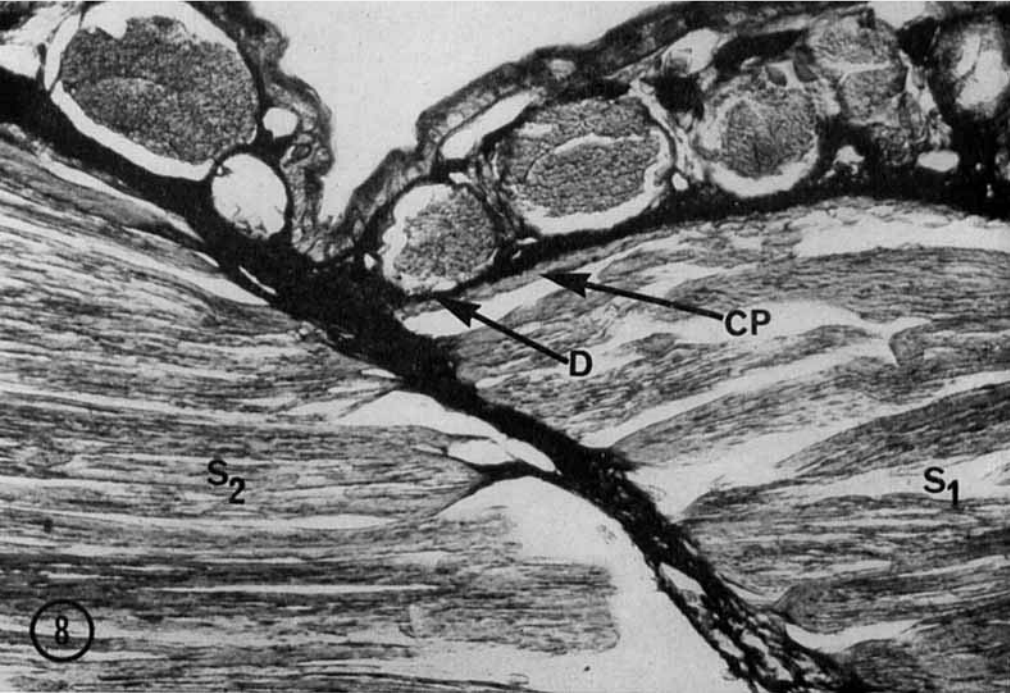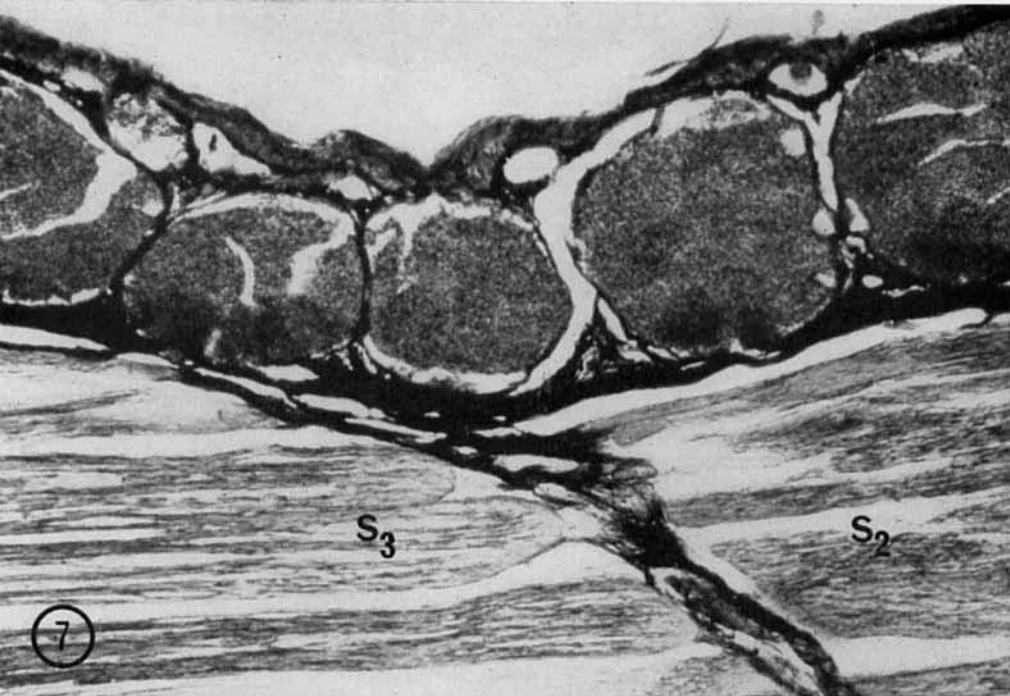
9   Magnified view of the tail constriction in figure 8. The break in the
skin will extend from B — to — B. Note the epidermis is in contact
with the dermal connective tissue. $S_1$, first caudal segment; $S_2$, second
caudal segment; M, mucous gland; P, poison gland; $D_1$, dermis of
first caudal segment; $D_2$, dermis of second caudal segment. $\times$ 683.
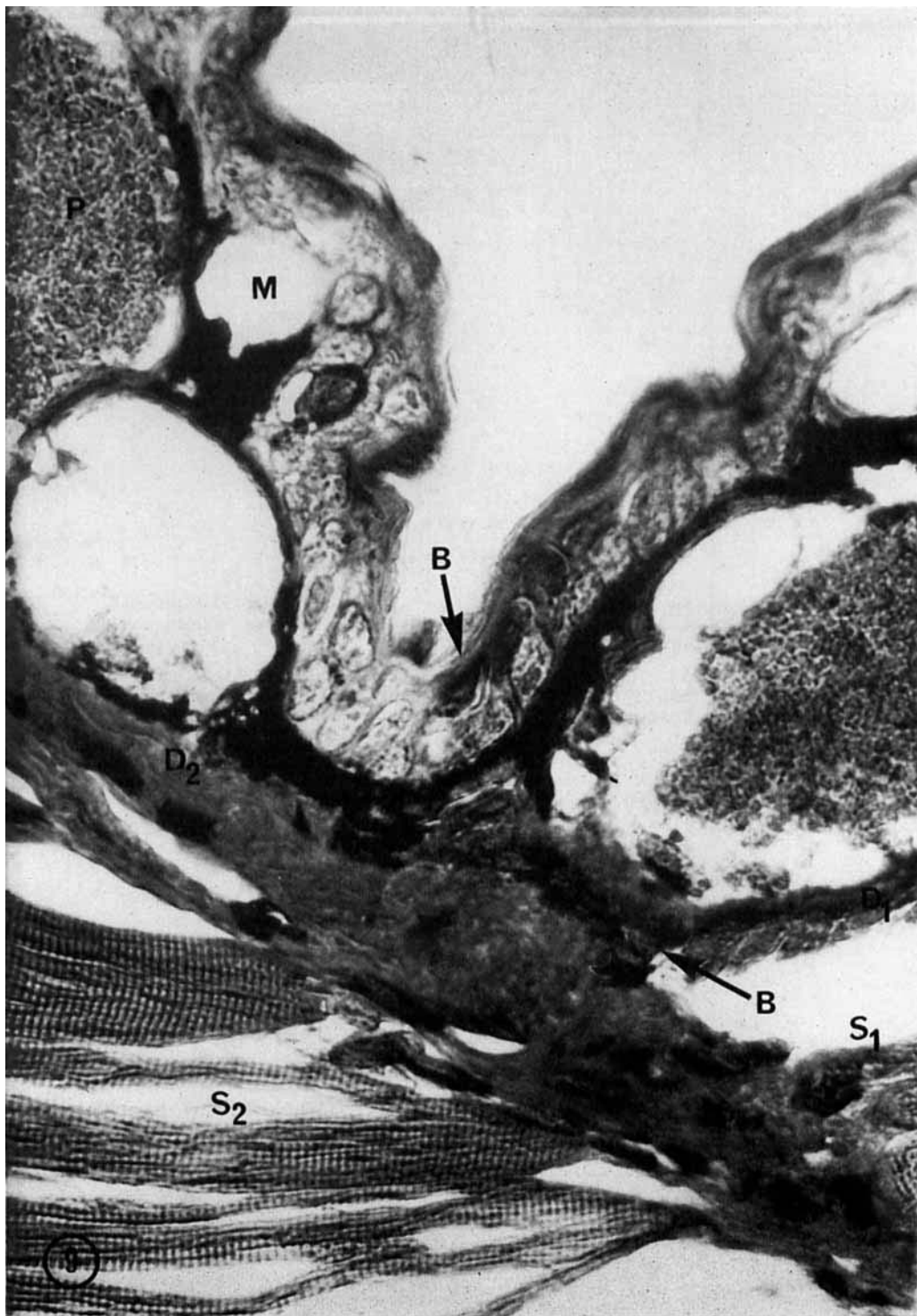
PLATE 3

10  Section of skin between second ($S_2$) and third ($S_3$) caudal segments in *Ensatina eschscholtzii*. The dermal connective tissue is thick and continuous between segments. $\times$ 150.

11  Section of skin at the tail constriction in *Ensatina eschscholtzii* between first ($S_1$) and second ($S_2$) caudal segments. The dermal connective tissue is absent (A) anterior to the constriction. $\times$ 163.
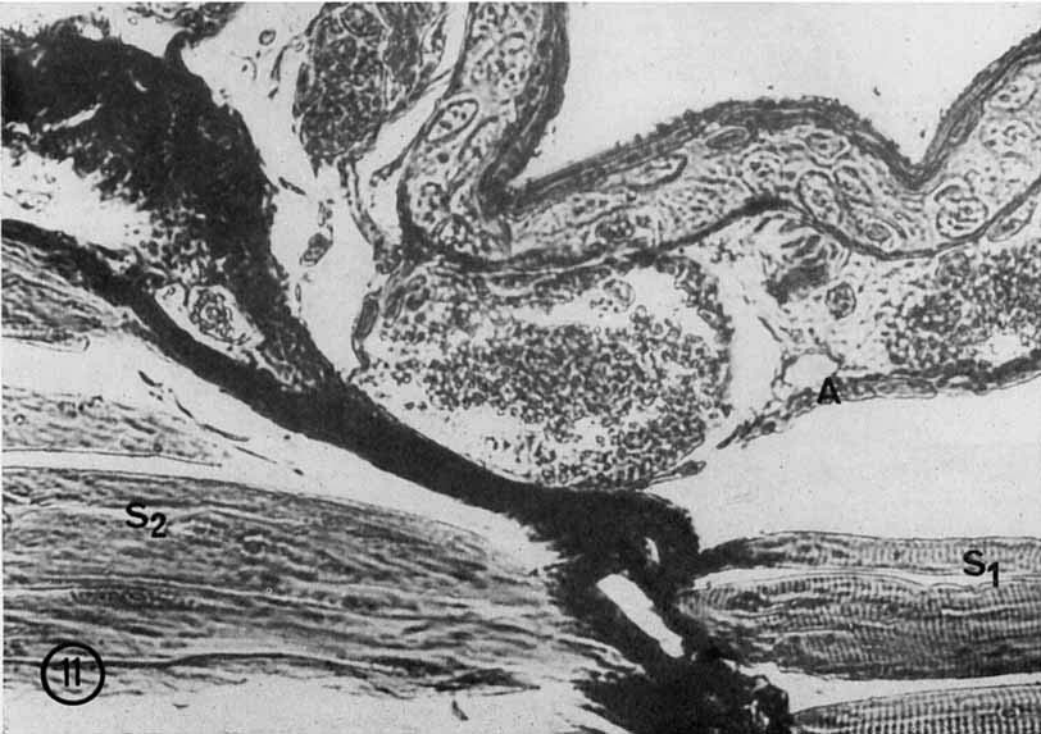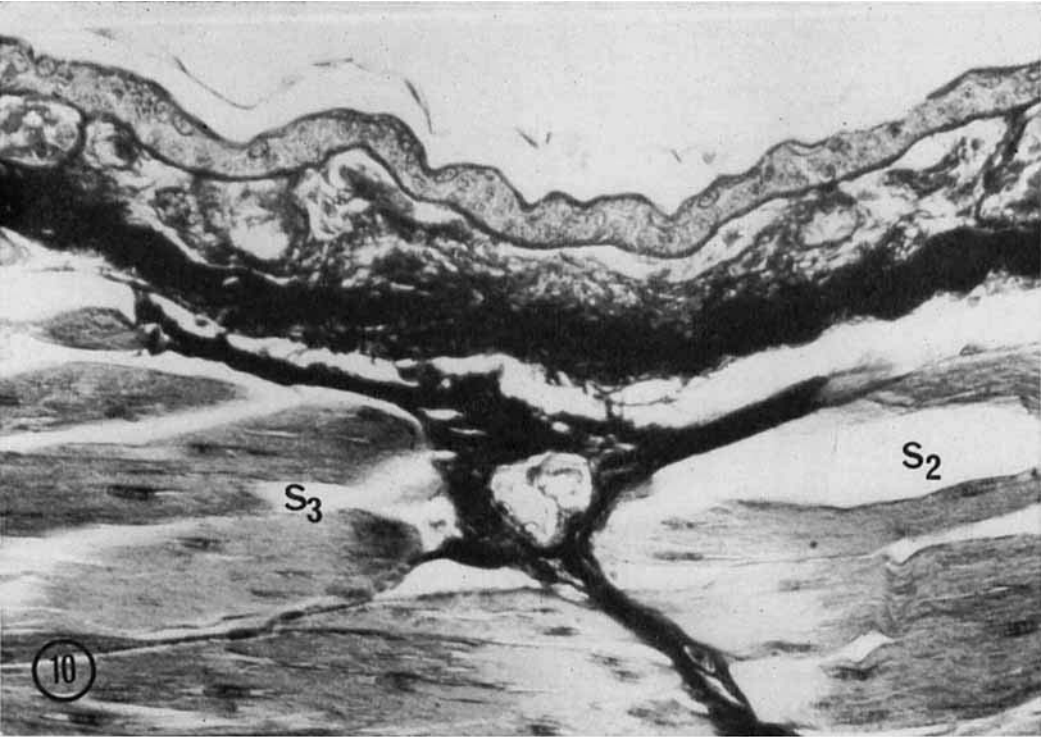
12  Frontal section between third ($S_3$) and fourth ($S_4$) caudal segments of *Hemidactylium scutatum*. $\times$ 75.

13  Frontal section between second ($S_2$) and third ($S_3$) caudal segments in *Hemidactylium scutatum*. $\times$ 75.

14  Magnified view of the tail constriction from figure 13 between second ($S_2$) and third ($S_3$) caudal segments. The dermal connective tissue is absent (A) anterior to the constriction. $\times$ 390.
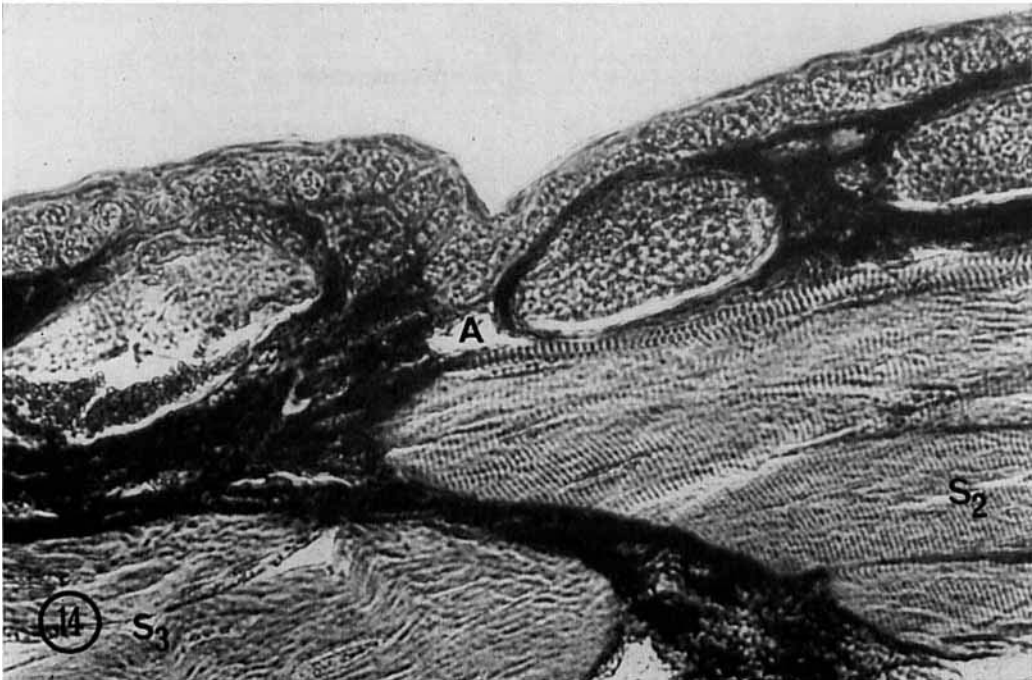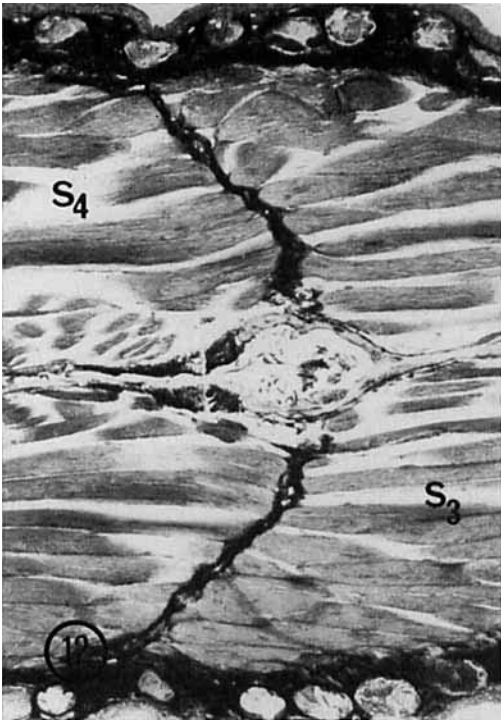
15  Section demonstrating the cell partition (CP) extending beneath the skin in the first caudal segment ($S_1$) in *Bolitoglossa subpalmata*. D, dermis. × 357.

16  Section at the tail constriction of *Bolitoglossa subpalmata* demonstrating the cell partition (CP) as it nears the constriction. D, dermis. × 260.

17  Section of skin at the tail constriction in *Bolitoglossa subpalmata* showing the cell partition extending (CPE) almost to the epidermis. CP, cell partition; D, dermis; SM, intermyotomal septum. × 420.
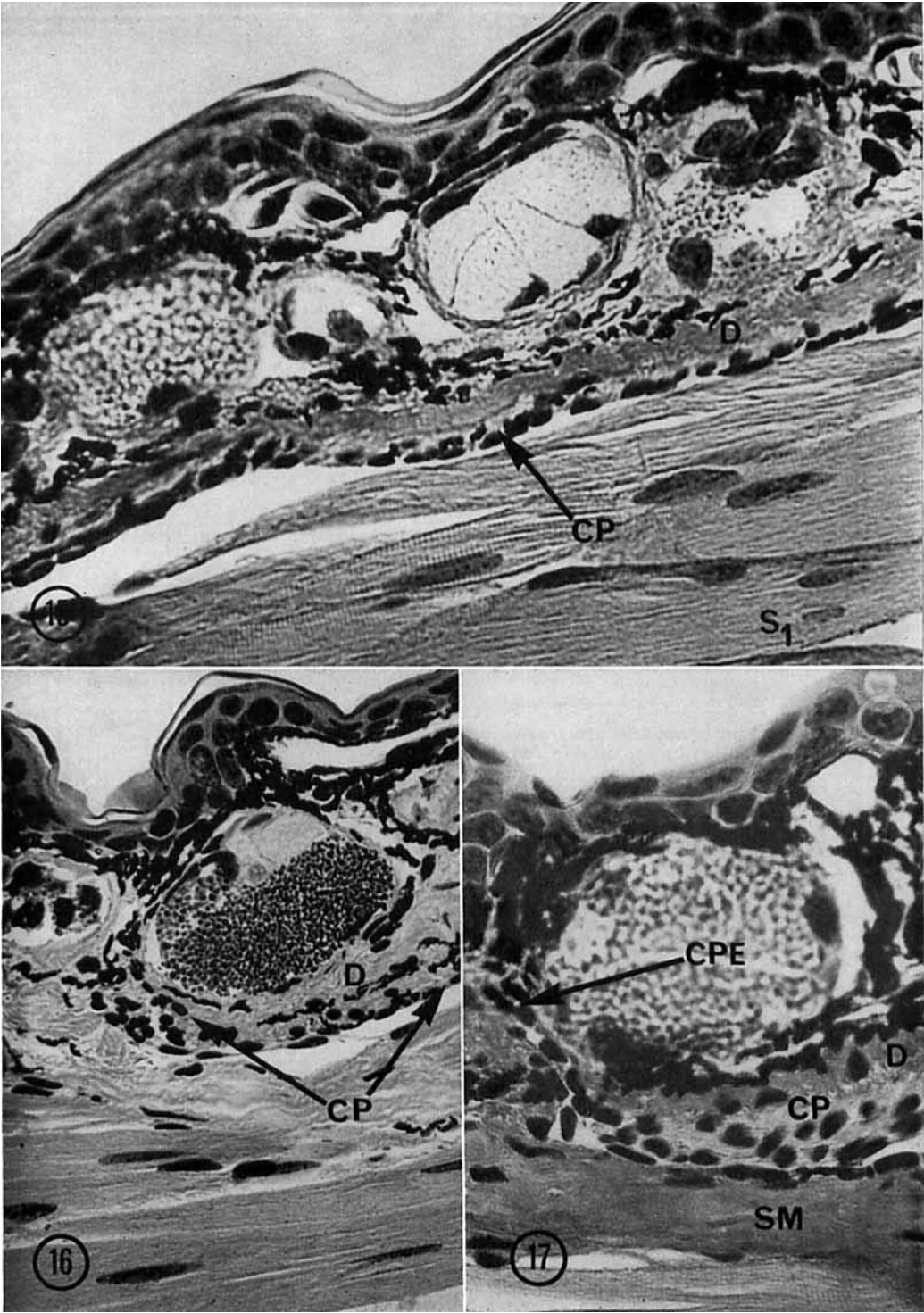
18  Muscle attachment to an intermyotomal septum in *Desmognathus quadramaculatus.* × 260.

19  Muscle attachment to the intermyotomal septum in *Bolitoglossa subpalmata.* Note the specialized attachment to the septum in the first caudal segment (S). CS, last trunk segment. × 260.

20  Muscle contracted away from the intermyotomal septum in *Pseudoeurycea leprosa.* Note the great proliferation of cells (PC) which follows. S, first caudal segment. × 260.

21  End of muscle fibers after breaking away from the intermyotomal septum in *Bolitoglossa subpalmata.* × 420.

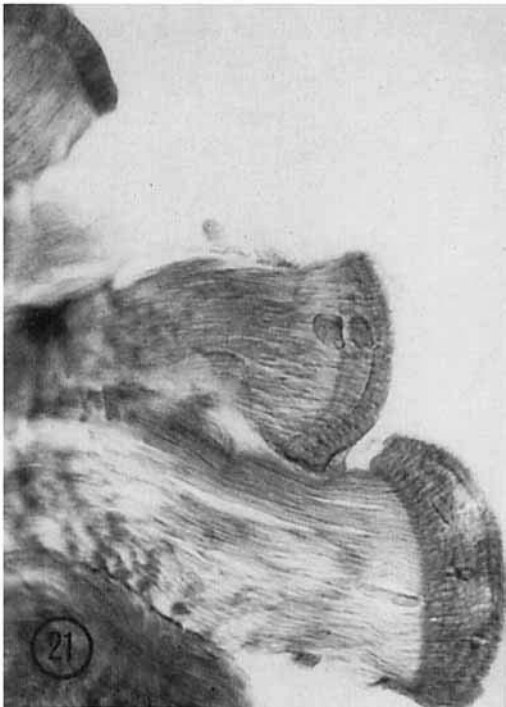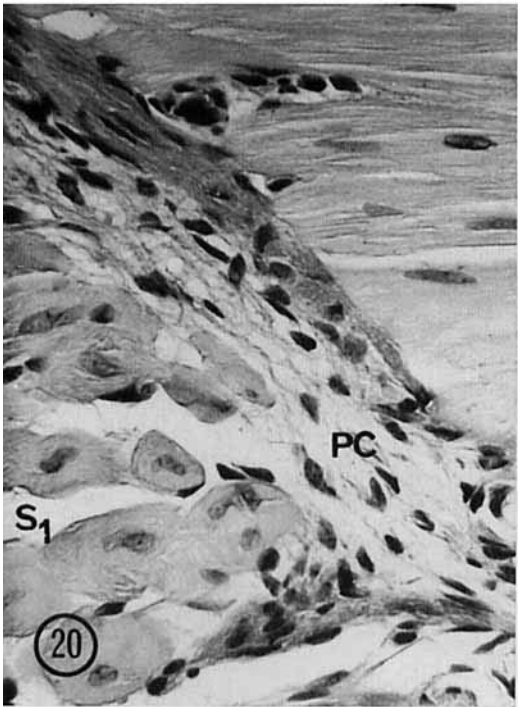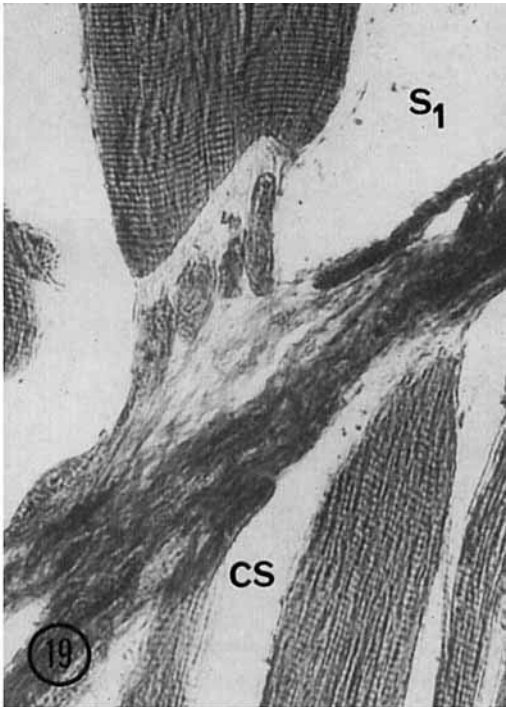David B. Wake and Ian G. Dresner

22 Junction between the last body vertebra and first tail vertebra show-
ing absence (A) of binding connective tissue in *Hemidactylium
scutatum*. × 163.

23 Comparable section at the junction between first and second caudal
vertebrae showing large fibrous bundle (F) binding vertebrae in
*Hemidactylium scutatum*. × 163.

24 Anterior end of a broken tail of *Thorius dubitus*. × 138.

PLATE 8

TAIL AUTOTOMY IN SALAMANDERS
David B. Wake and Ian G. Dresner