

# Tongue Evolution in the Lungless Salamanders, Family Plethodontidae.

## II. FUNCTION AND EVOLUTIONARY DIVERSITY

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**ABSTRACT** A recently presented model of tongue projection dynamics is used to generate a series of predictions concerning morphologies to be expected under selection for increased distance of projection, increased speed of projection, and increased directional versatility. A general understanding of biomechanical events and the model are used as points of departure for making specific predictions concerning details of structure in skeletal, muscular and connective tissue components of the tongue and associated structures. Comparative methods are used to examine these predictions in the genera of plethodontid salamanders. These salamanders are known to project their tongues to different degrees, and this knowledge is used to test the hypotheses concerning morphological specialization. Three distinct groups of plethodontid salamanders have evolved specializations for long distance projection, and these genera differ from one another in important ways in respect to specific character complexes. For example, the tropical genera and *Hydromantes* use CBII as the major force transmission element in the skeleton, while *Eurycea* and its allies use CBI in this role. *Hydromantes* differs from both in having a uniquely proportioned and structured hyobranchial skeleton and associated musculature. Less extreme specializations for tongue projection are found in different combinations in three other groups. Finally, two distinct groups of generalized species having only limited tongue projection capabilities are recognized, each having a unique complex of inter-related features. Each of these eight groups is recognized and characterized as a functional mode, and hypotheses concerning the biomechanical meaning of the character complexes of each are formulated.

The conventional approach to the analysis of structural diversity is classical comparative anatomy, in which data are gathered and interpretations of function and evolution generated from them (e.g., for urodele tongues: Özeti and Wake, '69; Krogh and Tanner, '72). Here we explore an alternate methodology. Our general model of function for the tongue of plethodontid salamanders (Lombard and Wake, '76) is essential background for this paper, and we assume familiarity of the reader with that work. We accept the validity of this general model and extend our methodology to a problem in comparative functional anatomy. The goal of our work presented in the previous, the current and a future paper is the understanding of patterns

of diversification associated with lineage development in plethodontid salamanders. We are here interested in the diversity of themes, both theoretical and realized, in tongue function that can be derived from the general model. We formulate hypotheses concerning the kinds of morphological diversity that might be expected as responses to specific selective pressures. We then test these hypotheses by the comparative method, using our own data and the literature (Smith, '20; Piatt, '35; Tanner, '52; Elkan, '55; Regal, '66; Wake, '66). Interpretations utilize known details of feeding behavior diversity. Our model is, in a sense, typological, and its prin-

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cipal value is heuristic, defining the basic elements available to nature for filling a form-function space whose bounds are determined by behavior (Stephens, '73). In attempting to give shape to that space by defining the theoretically possible, we seek deeper insight into evolutionary processes.

#### PREDICTIONS FROM THE MODEL OF DYNAMICS

Certain patterns of structural diversity might be expected to appear during phylogenesis in a lineage that has diversified in feeding behavior while retaining the same fundamental feeding system (our general model). The questions are, what specific patterns might be expected, and have the appropriate morphologies evolved? Organisms in nature face diverse selection pressures. Related species of rather similar structure living in different places may be subject to very different kinds of selection, as far as feeding mechanisms are concerned. Characteristics of the food resource (for example, distribution of prey sizes, locomotor and defense specializations of the prey, seasonal abundance patterns of prey, distribution of prey in different microhabitats) and foraging habits of the predator (in this case, the salamanders) in relation to the structure of the habitat might vary widely. We will consider three classes of selection pressures and make predictions concerning the kinds of changes they might favor in the evolution of feeding mechanisms. These are selection for increased distance of projection, for decreased time of the feeding sequence, and for increased directional versatility. All would be expected when a large proportion of the prey universe of a species consists of rapidly moving, small insects. Our approach is to focus on specific functions and consider selection associated with their evolution rather than on the conditions of the environment that might produce specific selection pressures.

General morphology has been described in many works (see above); some familiarity with tongue structure in salamanders is presumed. Similarly, general features of feeding in salamanders are known (for example, Noble, '31), and some information is available concerning the relative use of tongues during feeding in the different genera.

Generalizations concerning the degree to which different genera use their tongues during feeding are included in a later section of this paper.

#### *Selection for distance*

##### a. *Skeletal elements*

To increase appreciably distance of tongue projection certain skeletal changes are required. The most significant of these is increased length of the projectile elements comprising the cartilaginous hyobranchium. One might expect the basibranchial (BB) to increase in length. However, this unpaired element lies in the floor of the mouth and is affected by design constraints imposed by surrounding tissues. Anteriorly it is bounded by a part of the tongue pad and the mandibles. Posteriorly, the viscera, especially the heart, impose space constraints. Thus BB length should not change relative to body size even under strong selection for increased projection distance without some reorganization of the tongue tip (which would permit but a small amount of lengthening), or a major change in head shape (elongation relative to body size), which is not apparent in any living plethodontid species. There is an important implication in this prediction: in size series, near isometry in BB length rather than positive allometry is expected in animals with either modest or well developed projection abilities.

The paired ceratobranchials are located posterolaterally to BB. Increases in length of the ceratobranchials might be associated with increased projection distance. The most direct means to accomplish this is an increase in the length of the second ceratobranchial (CBII), which connects to the end of BB in contrast to the first ceratobranchial (CBI), which connects to BB somewhere along its length (figs. 1, 6). There are some spatial constraints. Lengthening the ceratobranchials without a change in their general resting orientation would require, ultimately, a relatively increased head width. The alternative, lengthening of the ceratobranchials together with a change in resting orientation (increase in angle, fig. 1) would force the ceratobranchials to cross the neck region. The ceratobranchial-epibranchial joint is expected to lie in the neck region to facilitate head movement. We thus would not expect reorientation of the ceratobranchials. If the ceratobranchials do increase in length to increase projection distance, we would expect the head to increase in width to some proportional degree. Since no plethodontids have greatly broadened heads, we predict that

## Abbreviations

|                                    |  |
|------------------------------------|--|
| ar, articular                      | oh, omohyoideus  |
| BB, bb, basibranchial              | p, prearticular  |
| br, basiradialis                   | ph, pharyngeus   |
| cal, cerato-articular ligament     | r, radius  |
| CBI, cbI, first ceratobranchial    | ras, rectus abdominis superficialis  |
| CBII, cbII, second ceratobranchial | RCP, rcp, rectus cervicis profundus  |
| cg, circumglossus                  | rcs, rectus cervicis superficialis   |
| ch, ceratohyal                     | rcsl, lateral slip of rectus cervicis superficialis  |
| cyl, cylinder complex of tongue    | SARI, sarl, subarcualis rectus I   |
| projection system                  | se, <i>Schnenplatte</i>  |
| d, dentary                         | sh, sheath surrounding tongue stalk  |
| EB, eb, epibranchial               | sp, suprapeduncularis  |
| gg, genioglossus                   | st, tongue stalk   |
| ghl, geniohyoideus lateralis       | tt, tongue tip   |
| ghm, geniohyoideus medialis        | uh, urohyal  |
| gl, glandular tissue               | x-x', x axis from which $\alpha$ is measured   |
| hga, anterior hyoglossus           | x, x', x'', base line of tractrix on x axis, determined by varying lengths of CBI (x, x') and CBII (x'') |
| hgp, posterior hyoglossus          | $\alpha$ , angle any ceratobranchial forms with x axis   |
| hy, hebstoeropsiloideus            | 1, site of articulation of CBI and BB  |
| ig, intraglossus                   | 2, site of articulation of CBII and BB   |
| ir, interradialis                  | 3, site of articulation of CBI, CBII, and EB   |
| l, glossal ligament                | $\rightarrow$ , distance from tip of BB to jaw   |
| lc, lingual cartilage              |  |

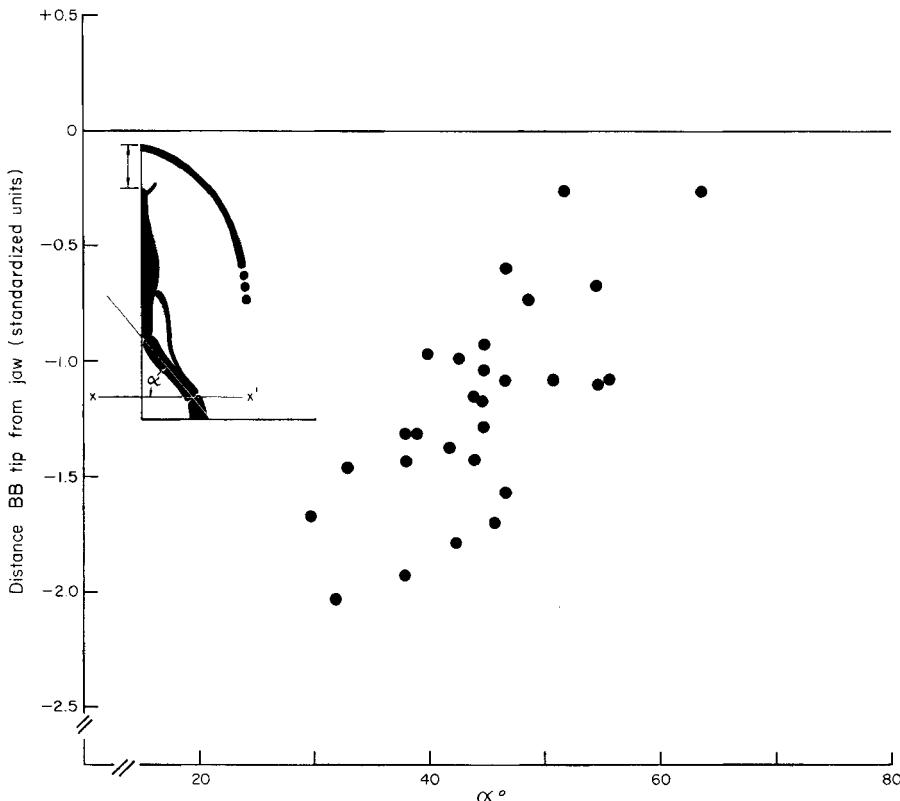


Fig. 1 Relation of distal tip of BB to the jaw during tongue projection. As the ceratobranchials fold the tongue moves forward, and the change in angle  $\alpha$  (insert) is correlated with movement of the tip of BB relative to the anterior margin of the jaw (measured, as example, double-headed arrow). Raw data were converted to standardized units for plotting, thus permitting use of animals having a wide range in size. As these data are derived from bolitoglossine salamanders, in which CBII moves along the tractrix,  $\alpha$  was measured using it rather than CBI, the element used by Lombard and Wake ('76) in their measurements. See text for further explanation.

change in the ceratobranchials would be slight under selection for distance.

The epibranchials (EB) at rest are far lateral in position. These paired elements have essentially no space constraints, for they lie under the dorsolateral skin of the trunk. Theoretically they can extend to the pelvis and beyond, so long as a space between skin and underlying muscle can be tolerated. Since they have favorable orientation and position, we predict that selection for increased projection distance would have its most direct effect in the increased length of the epibranchials.

Finally, the mass of the skeletal elements is expected to be reduced under selection for distance. As a result the tongue could be projected for a greater distance with a given amount of force.

#### b. *Muscular elements*

Only muscles inserting on the projectile parts of the hyobranchial skeleton or tongue pad which have extrinsic origins are considered. Three general changes might be expected: (1) increase in power of projection muscles, (2) increase in length of retractor muscles, and (3) loss of muscles attached to the skeleton which restrict the range of projection, its direction, or both. Ultimately the musculature of projection and retraction is expected to be reduced to the simplest possible arrangement, one projector and one retractor.

The maximum number of muscles attaching to the hyobranchial skeleton or tongue pad in plethodontids is four, viz: subarcualis rectus I (SARI), rectus cervicis profundus (RCP) (directly or through another muscle, see below), omohyoideus (through the lateral slip of the rectus cervicis superficialis—RCS) and genioglossus.

The SARI is the only muscle disposed for projection (Lombard and Wake, '76). Since power in a muscle is roughly proportional to its physiological cross sectional area (Hill, '53; Gans and Bock, '65), positive allometry is expected as increased projection distance is achieved. RCP is a retractor muscle of the tongue (Lombard and Wake, '76), and as projection distance increases, it also must increase in length. A specialization for storage of this lengthened musculature is necessary, such as coiling, looping or pleating. The lateral slip of the RCS-omohyoideus is also a retractor of the tongue apparatus. As projection distance increases, a lengthening of this muscle complex is expected, and storage

methods for the additional muscle are necessary. Loss of one or the other of these muscles might be expected as their functions, at least in part, are redundant. The genioglossus is a rotator of the tongue pad (see below). As projection distance increases the genioglossus must increase in length, and, again, a means of storage is required. Loss of this muscle might occur as the tongue pad becomes freer and increasingly projectile, for it would act both as a drag and a brake.

#### c. *Connective tissues*

Two major changes of connective tissue organization are expected under selection for increased distance of projection. First, the tissues connecting the anterior parts of the tongue to the floor of the mouth and restricting projection might be reduced in strength and lost. Alternatively, the quality of this connection could be changed, say to a highly elastic tissue, to permit projection for distance.

Second, the connective tissue sheath around the projectile elements (BB, CBI, CBII and EB) is expected to increase. As the amount of sheath tissue increases some method of storage in the resting state would be necessary. Pleating seems to be the simplest option for storage of the relatively large amount of sheath epithelium necessary to cover a fully projected tongue stalk.

#### *Selection for reduction in duration of a feeding event*

##### a. *Skeletal elements*

Relative reduction in the mass of all projected skeletal elements is expected under selection for increased acceleration, deceleration, and velocity associated with reduction in duration of a feeding event. Weight reduction is expected if acceleration and terminal velocity are to increase appreciably, and the skeletal elements are the densest portion of the projectile. However, strength must be maintained, and the stress-bearing elements, therefore, are under some constraints.

A reduction in viscous friction is expected to accompany increased velocity. A decrease in surface area of the projected elements would result in a reduction of viscous friction during projection. By maintaining the density of the cartilage, but reducing the diameter of such elements as the epibranchial, both relative decreases in mass and in surface areas would occur. Viscous friction could also be

reduced by a shortening of the time required to fold the apparatus during projection. Folding produces a single bundle of elements with associated reduction in frictional surface area. The time required for the apparatus to fold could be reduced by reducing the length of the second ceratobranchial. This would place the element in a position far along the tractrix (Lombard and Wake, '76) at rest, and such a conformation is favorable for rapid movement to the midline. Finally, lubrication could reduce friction.

If selection for speed is not countered to a degree by selection for distance (as above) all articulated elements might shorten.

#### b. *Muscular elements*

Two major structural changes expected in the retractor musculature are increased fiber length and number. Both of these parameters are related to the speed and force of contraction of muscle (Gans and Bock, '65). An animal with a shorter feeding-sequence time would be expected to have protractor muscles which have more fibers of longer length than one whose feeding time was longer.

#### c. *Connective tissue*

A reduction in viscous friction is expected and some means to this end have already been noted. Two further reductions can be made based on consideration of factors in equation (2) in Lombard and Wake, ('76). An increase in the separation between the sheath of the tongue stalk and the cavity within which it passes ( $L$ , fig. 9a; Lombard and Wake, '76) might be expected. A reduction in the viscosity ( $\eta$ ) of the fluid found in this space might also (and more likely) occur. This lubricant would therefore be expected to be serous in nature, and an appropriate morphology for production of this type of secretion would be predicted.

#### *Selection for directional versatility*

##### a. *Skeletal elements*

The principal factor to be considered in making predictions concerning directional versatility is the relative degree of freedom in the tongue, independent from movements of the head of the animal. The speed of tongue projection and retraction is sufficiently great that specializations for rapid swivelling of the head on the body are not expected. However, one might find modifications of the vertebral column in the vicinity of the cranio-vertebral

joint to increase the total range of head movements relative to the body (Worthington and Wake, '72).

We have discussed the mechanical advantages of a folded as opposed to an unfolded skeleton for increasing projection range (Lombard and Wake, '76: fig. 8). We therefore predict that rapid folding should occur under selection for increased directional versatility. This is most easily accomplished by shortening CBII, relative to other elements, thus creating a proportionally smaller tractrix, and promoting rapid folding after a relatively slight projection.

Increased elasticity of elements of the hyobranchial skeleton might also be expected. This is particularly true of the very long EB's, which would bind if the tongue were projected from the corner of the mouth unless they were highly elastic. One would least expect BB to increase in elasticity, for it is the leading element and is the principal stress-bearing member.

The ceratohyals remain in the floor of the mouth, but muscles associated with directing the tongue are attached to them. The ceratohyals are expected to become increasingly elastic, and perhaps to become cylindrical and less flattened in order to increase flexibility in all planes.

##### b. *Muscular elements*

The musculature associated with the opening in the floor of the mouth through which the tongue passes is expected to undergo some modification. This musculature includes the suprapeduncularis, the lateral geniohyoideus and the SARI (fig. 18; Lombard and Wake, '76: fig. 12). All of these muscles attach to the anterior ends of the ceratohyals, elements strengthening the dorsolateral margins of the tongue opening. Change in orientation or size is expected as specialization for aiming the projectile evolves.

The genioglossus muscle attaches the tongue pad to the region of the mandibular symphysis (fig. 2a) and it restricts projection of the tongue to an increasing degree as the line of projection moves away from the midline. Adaptive change might take two forms. One possibility is complete loss of the muscle. An alternative is reorientation such that the muscle passes from the tongue pad caudally to a new attachment rather than anteriorly to the midline of the jaw. This would provide a situation in which the muscle could follow

projections off the midline without restricting them.

#### *Predictions for the tongue tip*

Our model of dynamics dealt only briefly with the tongue tip, a complex of glandular tissue, muscle, cartilages and nerves. It is the part of the tongue that meets the prey and delivers it to the mouth. Accordingly, we would expect to find more diversity in structure and function of the tongue tip than with other parts of the tongue apparatus. Tongues that are projected only slightly are expected to have large mass, strong muscular attachment to the jaws and to the tissues of the floor of the mouth, relatively complex intrinsic musculature, and independent mobility. Under conditions of selection for increased distance of projection, increased velocity of projection, and increased directional versatility, one would expect the mass of the tongue tip to decrease, the connections to surrounding tissues to diminish or be lost, or to at least increase in elasticity, and both the intrinsic musculature and independent mobility of the tongue pad on the tip of the hyobranchial apparatus to decrease. Mechanisms for tongue pad rotation should be tied to the projection system *per se*, both for efficiency and speed.

#### MATERIALS AND METHODS

A discussion of the materials used and our methods of preparation were presented in a previous work (Lombard and Wake, '76). Briefly, a total of 344 specimens representing 72 species of 21 plethodontid genera were examined and at least one specimen of each genus represented was dissected. In addition, at least one specimen of each genus was cleared and stained and at least one serially sectioned for microscopic examination. In many cases serial graphic reconstructions (Lombard, '77) of the tongue were made in both the resting and projected state. These materials were used for testing the predictions made in the preceding section.

The taxonomy used is that of Wake ('66; summarized in Wake and Dresner, '67). The following terms are used in the text: desmognathine (for Subfamily Desmognathinae), hemidactyliine (for Tribe Hemidactyliini) plethodonine (for Tribe Plethodontini), and bolitoglossine (for Tribe Bolitoglossini, including all members of the Supergenera *Bolitoglossa*, *Batrachoseps*, and *Hydromantes*).

#### OBSERVATIONS

##### *Elements related to projection and retraction*

###### a. Distance

Our predictions concerning features which would be expected to change under selection favoring increase in projection distance were tested by examining diversity in structure relative to ecology and behavior of the different groups of plethodontids. These predictions and the results will be considered in order of presentation (above).

###### 1. Skeleton

###### *Basibranchial*

BB length increases isometrically with increasing size throughout the family (fig. 3). We predicted this relationship. The significance of this fact is discussed above. Members of all genera but one (*Hydromantes*) are very similar in the BB/standard length relationship, despite the great differences in relative distance of tongue projection. *Hydromantes* has a relatively longer BB than any other genus; here change in BB length has been a significant factor in the evolution of a projectile tongue.

###### *Second ceratobranchial*

If CBII length is plotted against body size for the three groups (Tribe Hemidactyliini, Supergenus *Bolitoglossa*, Supergenus *Hydromantes*) that have free tongues and are known to project their tongues for great distances, two distinct plots are seen (fig. 4). Hemidactyliines and *Hydromantes* show one relationship (close to, but slightly shorter than that seen in less specialized plethodontids), and members of the Supergenus *Bolitoglossa* have a markedly different one. Members of the Supergenus *Bolitoglossa* have significantly shorter CBII than other plethodontids. No change in CBII length was predicted, but phylogenetic decrease is better accommodated within the model than would be increase.

###### *Epibranchial*

Epibranchials are very long in all species with known capabilities for long range projection of the tongue consistent with our predictions. In figure 5 the proportions of the articulated elements of the hyobranchial apparatus are indicated for the four major groups within the family. In the Desmognathinae and Pleth-

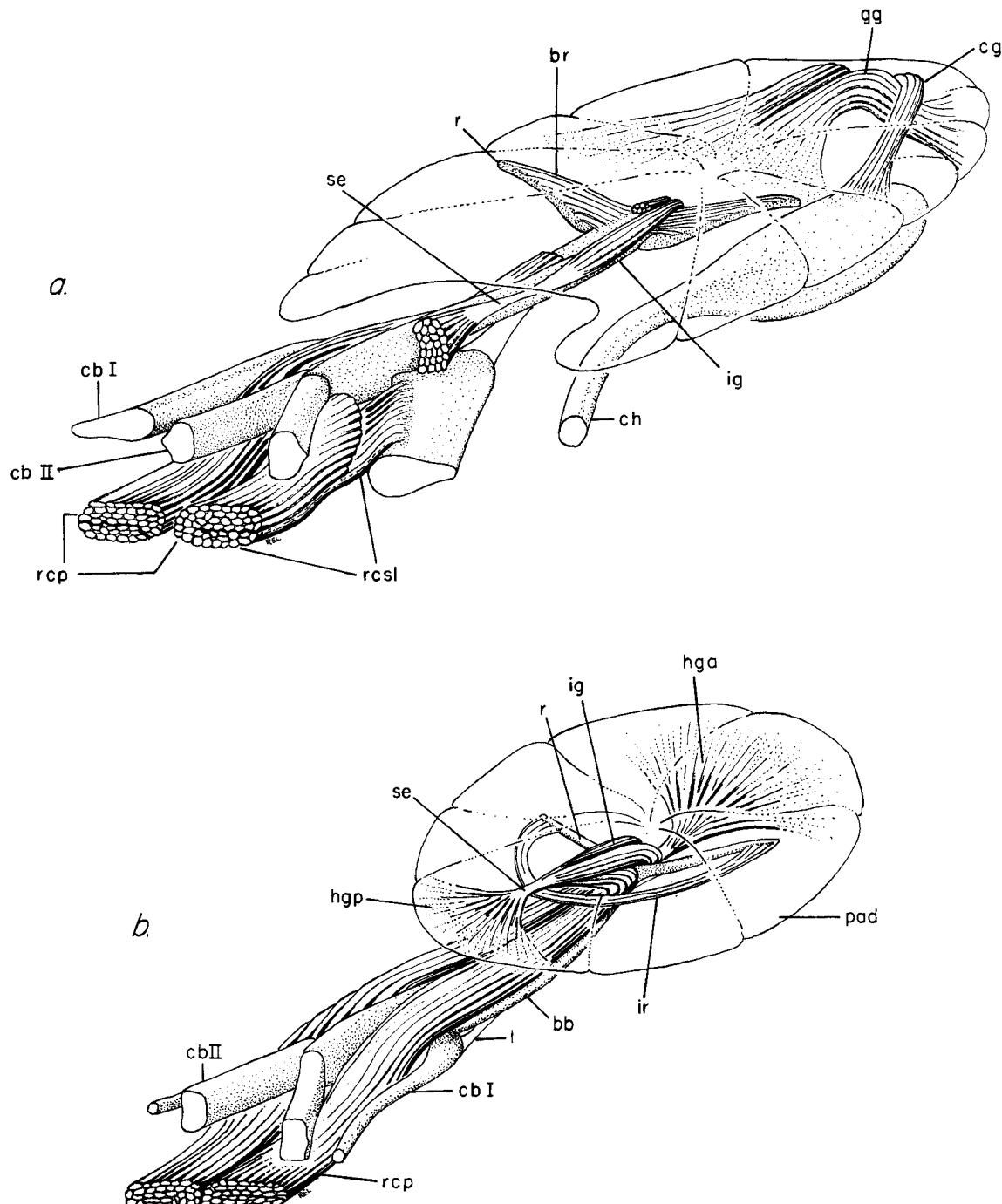


Fig. 2 Tongue tips and associated structures in *Plethodon* (a), *Bolitoglossa* (b). These are generalized, three-quarter view drawings based on reconstruction of sectioned and dissected tongues of several species, designed to illustrate the arrangement of cartilages, ligaments, and muscles within the tongue pad. In (a) the hyoglossus muscle is not illustrated, for clarity, and in (b) the ceratohyals are not shown, for they have no relation to the tongue pad in this mode.

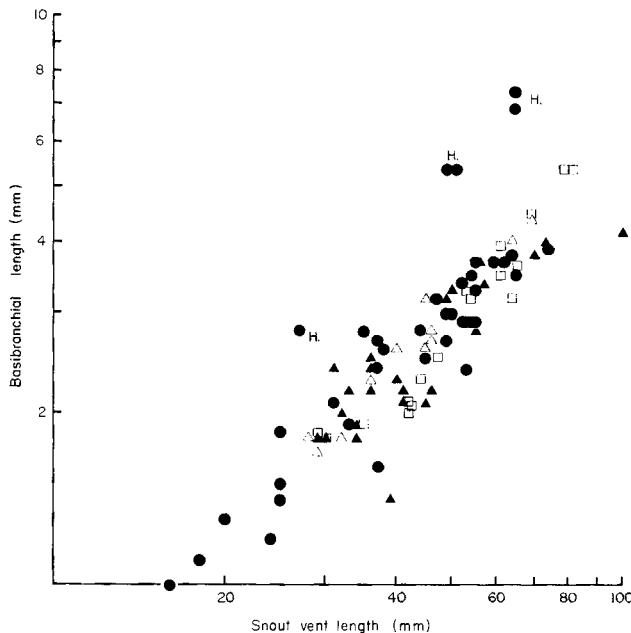


Fig. 3 Relation of basibranchial length to snout-vent length. ● Bolitoglossini, ▲ Hemidactyliini, □ Plethodontini, △ Desmognathinae. H indicates members of the genus *Hydromantes*.

odontini, BB comprises between 25 and 35% of the total linear dimension of the apparatus, while CBII and EB comprise between 30 and 40% and less than 40%, respectively. In hemidactyliines EB comprises between 40 and 50% of the total, and in bolitoglossines the EB is from over 50 to nearly 70% of the total. Epibranchials proportionally increase very greatly, and, as is clear in figure 6, the increase in length of EB relative to size is also very great.

Ceratobranchials become increasingly short both in terms of internal proportions of the hyobranchial apparatus and relative to body size from the desmognathines and plethodontines, through the hemidactyliines (and *Hydromantes*) to the bolitoglossines, where they comprise as little as 10% of the total (fig. 5). In contrast, BB is between about 20 and 35% of the total in all groups, with the figure dropping below 25% in a few hemidactyliines and many bolitoglossines.

## 2. Muscles

The tongue pad is connected to the body of the generalized plethodontids by three groups of muscles—the genioglossus, the RCS (lateral slip), and the RCP. The genioglossus

muscles are characteristically present in generalized terrestrial salamanders. They are a pair of relatively stout muscles which arise on the anteroventral surface of the dentary, near the mandibular symphysis, and converge immediately to the ventral midline. There they pass under or between the two geniohyoideus medialis muscles and extend into the tongue pad. They effectively tie the anterior part of the tongue pad to the mouth, although a certain amount of flexibility is present so that some extension of the tongue is possible (Özeti and Wake, '69; Severtsov, '72). The two rectus cervicis muscles are also present in generalized salamanders. The RCS extends directly from the sternum to the posterior margin of CBI, with from a few fibers to a major slip extending to the urohyal. The RCP is a direct anterior continuation of the rectus abdominis profundus and extends forward between the two ceratobranchials into the tongue pad, where it variously connects to BB, to radials, or to connective tissue in the fleshy part of the pad (see below).

All plethodontids are capable of extending the tongue out the mouth to catch small prey, and relative to such groups as the ambystomatids and most salamandrids, they have

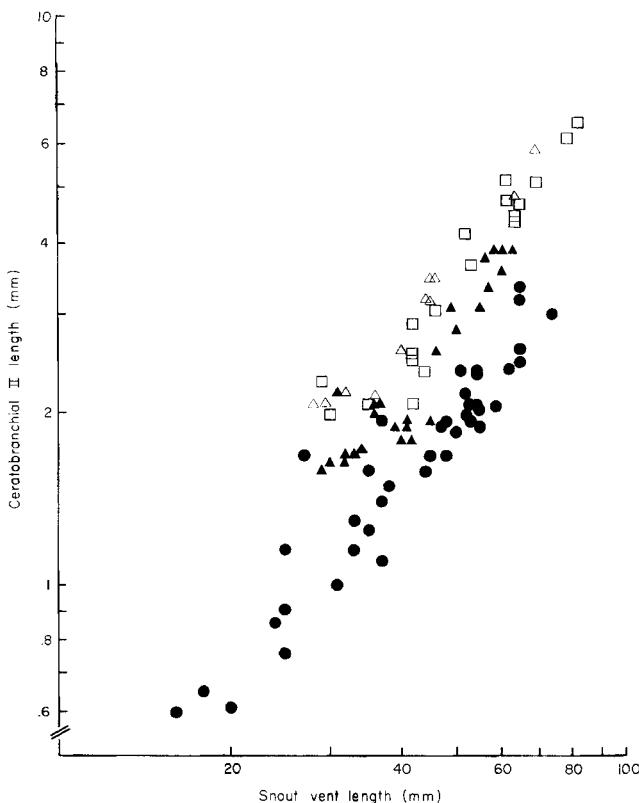


Fig. 4 Relation of second ceratobranchial length to snout-vent length. ● Bolitoglossini, ▲ Hemidactyliini, □ Plethodontini, △ Desmognathiniae. Log-log plot.

highly protrusible tongues. One expects modifications of all of the muscular connections of the tongue in plethodontids, and these are found.

#### *Genioglossus*

Genioglossal muscles are longer in plethodontids than in most other salamanders. The muscles pass superficial to the geniohyoideus muscles before proceeding dorsally, and this produces a small increase in length relative to the condition in other families. This situation is found in the desmognathine genera and in *Plethodon* and *Aneides*. In *Ensatina* the genioglossal muscles are shifted in origin from the symphyseal region to a more posterior position along the dentary (fig. 7). The fibers are oriented perpendicular to the midventral line, and, as a result of the lateral excursion of the mandible, the length of the muscle is effectively increased. A similar situation is seen in *Hemidactylium* (also

Wake, '66). In *Batrachoseps* the genioglossus muscle is very greatly elongated as a result of the origin having shifted posteriorly almost to the end of the mandible (Piatt, '35). This is by far the greatest elongation of the muscle encountered in any salamander. The genioglossal muscles are absent in all hemidactyliines except *Hemidactylum* and in all bolitoglossines except *Batrachoseps*, and any restriction of tongue projection produced by these muscles is correspondingly absent.

#### *Rectus cervicis superficialis and omohyoideus*

In plethodontids the primary anterior attachment of the RCS is on the urohyal, and only a relatively long and slender lateral slip (the rectus cervicis lateralis of Tanner, '52) represents the principal attachment of the muscle found in such groups as salamandrids. This lateral slip retains its primitive insertion, on the posteromedial edge of the first ceratobranchial (fig. 8). Between the sternum

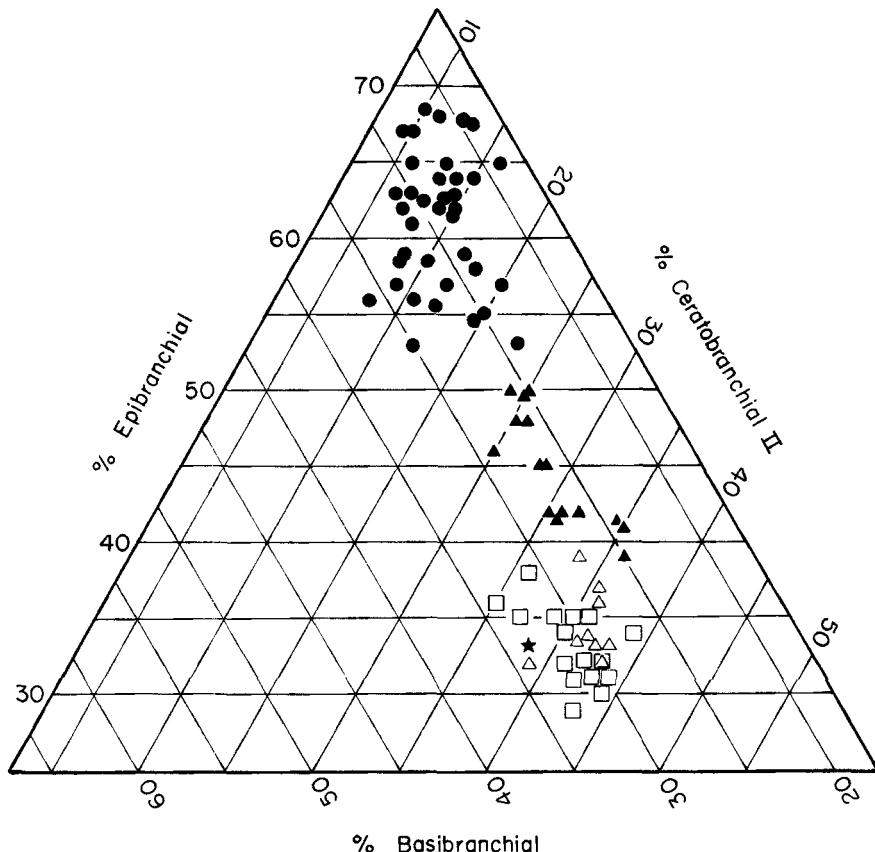


Fig. 5 Relative proportions of BB, CBII, and EB in plethodontid salamanders. For any specimen the sum of the three percentages is 100. The star indicates the proportion 1:1:1. ● Bolitoglossini, ▲ Hemidactyliini, □ Plethodontini, △ Desmognathinae.

and the urohyal, the lateral slip is joined by a relatively slender omohyoideus muscle, which extends anteromedially from the forelimb. This complex of two muscles, like the genioglossus, plays a minor role in retraction of the tongue, but limits excursion of the tongue from the mouth. Desmognathines and plethodontines have the generalized arrangement described above. The attachment is less extensive than in more primitive families, but clearly places some limit on tongue protraction. In hemidactyliines the same general pattern is seen, but the lateral slip is slender and "loose" and the omohyoideus and the lateral slip of RCS are very slender. In *Hydromantes* and all members of the Supergenus *Bolitoglossa* both the lateral slip of the RCS and the omohyoideus are absent (fig. 9). These observations contrast with those presented by Tan-

ner ('52), who failed to trace the lateral slip to its correct anterior attachment in some genera and failed to find it in others in which it is present.

#### *Rectus cervicis profundus*

The principal retractor of the tongue in plethodontids is the RCP. This muscle arises with the hebstoeypsiloideus (not previously reported in the plethodontids) at a myocomma at the level of the sternum. Both muscles represent anterior continuations of the rectus abdominis profundus. In the most generalized plethodontids (desmognathines and plethodontines) the RCP is a relatively stout, very long, cylindrical muscle (fig. 8). In the hemidactyliines it lies rather loosely in the throat region, especially in the area immediately in front of the heart and deep to the urohyal. In

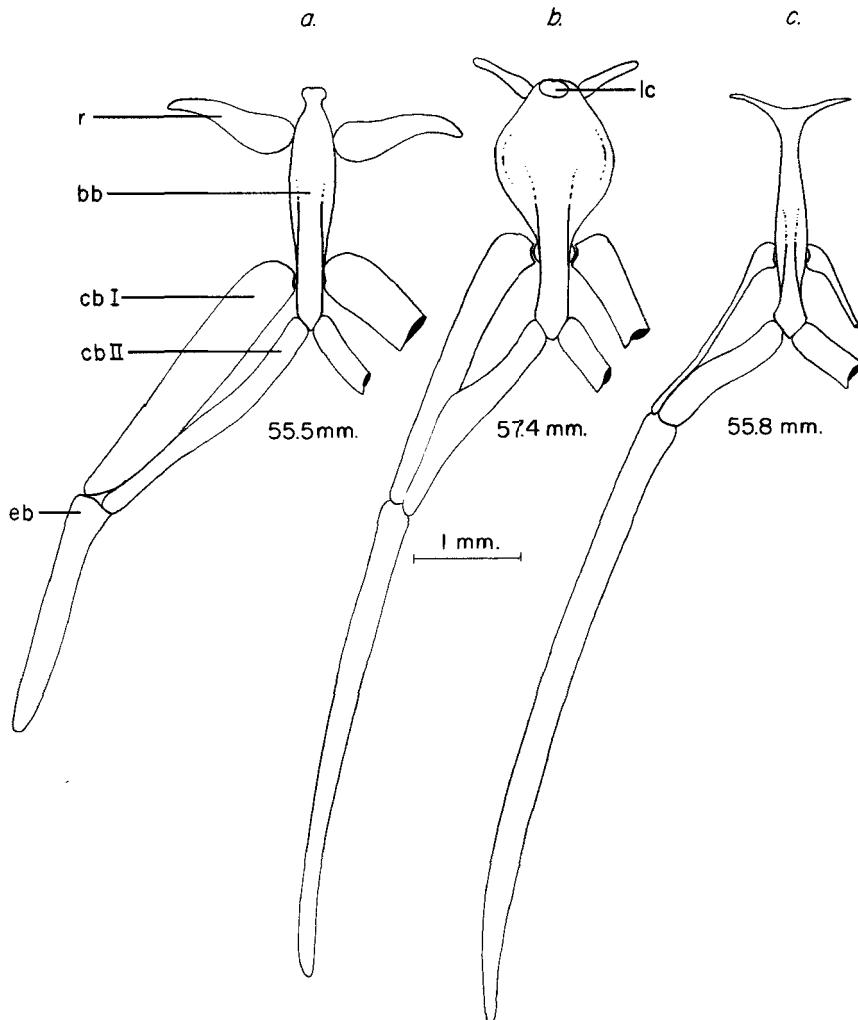


Fig. 6 Articulated hyobranchial apparatus in adult *Plethodon jordani* (a), *Eurycea longicauda* (b), and *Bolitoglossa subpalmata* (c). Ceratohyals are not shown, and the urohyal, present in (a) and (b), is not shown. The snout-vent length of the specimens is indicated under each skeleton. Note that while the BB is of about equal length in all three individuals, the other elements vary greatly in length. Note the reduction in length of the ceratobranchials and the increase in length of EB from (a) to (b) to (c). CB I is stouter than CBII in (a) and (b) but not (c). Free radii are present in (a) and (b), but not (c). Only (b) has a lingual cartilage. Dorsal view, with tongue at rest in mouth.

all of the bolitoglossines remarkable features lead to a significant lengthening of this muscle. In *Batrachoseps* the connective tissue sheath surrounding the muscle in the throat is rather loosely attached, and the muscle at rest is folded in a zig-zag, or accordion pleat within the sheath. Upon projection of the tongue the muscle unfolds and greatly increases from its resting length. In *Hydro-*

*mantes* and all genera of the Supergenus *Bolitoglossa*, the muscle is thrown into a loop, or in the most extreme instances, into a coil at the level of the gular fold, just in front of the heart (fig. 9). In one large *Hydromantes genei* 10 mm of muscle were found to lie coiled in a 2-mm linear distance in the throat. Upon projection of the tongue, the muscle straightens and greatly increases from its resting length.

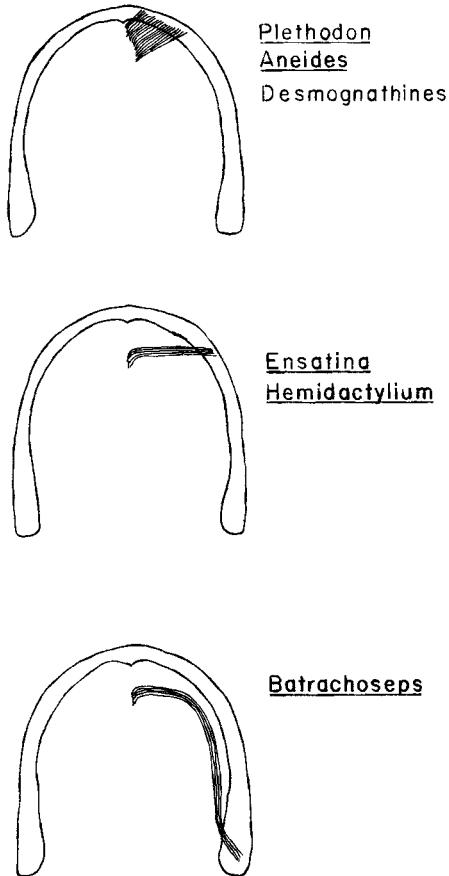


Fig. 7 Diagrammatic ventral views of the lower jaw of plethodontid salamanders, showing the course of the genioglossus muscle on one side of the organism.

The RCP is pleated to some degree within a surrounding fibrous sheath in all plethodontids (see also remarks of Francis, '34, regarding *Salamandra*).

#### *Subarcualis rectus I*

We predicted that the SARI muscle should increase in size in species that project the tongue for relatively great distances. Figure 10 shows the relation of smallest cross sectional diameter of the muscle to snout-vent length. The bolitoglossines, with a relatively great projection, do not appear to have noticeably more robust muscles. Near isometry is observed with increase in size (fig. 10). The total bulk of SARI does increase, however, as EB increases in length. The length of EB increases regularly in the morphocline,

Desmognathinae-Plethodontini; Hemidactyliini; Bolitoglossini. The cline also is in the direction of greater tongue projection distance, so the bulk of the SARI muscle is increasing with projection distance. Changes in fiber arrangement or type which might be expected were not examined in this study.

#### 3. Connective tissue

In desmognathines, *Aneides*, and *Plethodon* the tongue is clearly connected directly to the lower jaw by the genioglossal muscles and surrounding connective tissue. This is an elastic connection relative to some primitive salamanders, but is the tightest connection to be found among plethodontids. The attach-

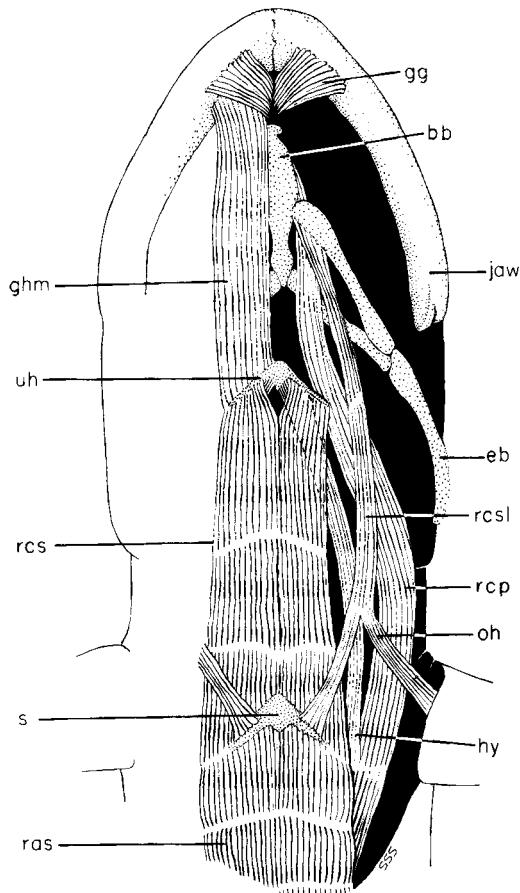


Fig. 8 Some important muscles and certain skeletal elements of the tongue and throat in *Desmognathus quadramaculatus* (75 mm, snout-vent length). Partially dissected, with various elements not drawn. Ventral view.

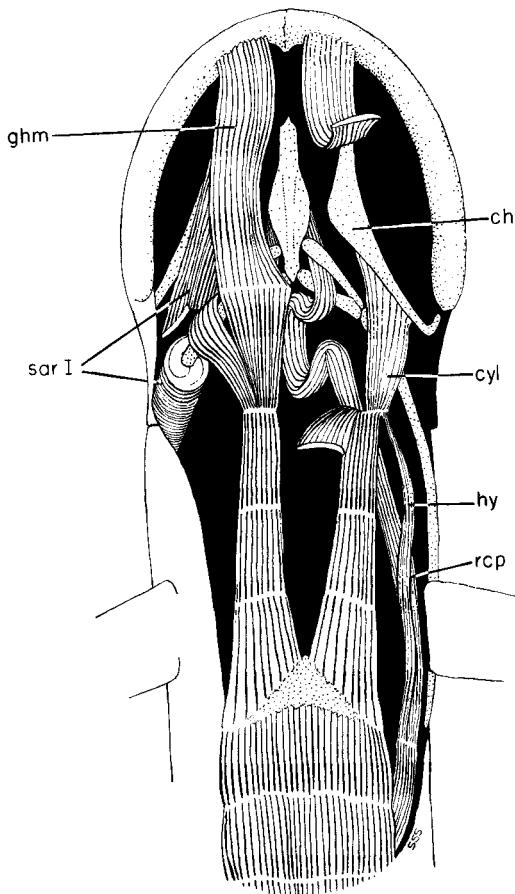


Fig. 9 Some important muscles and certain skeletal elements of the tongue and throat in *Hydromantes brunus* (75 mm, snout-vent length). Partially dissected, with various elements not drawn. Ventral view.

ment to the lower jaw is increasingly loose in the series *Hemidactylum*; *Ensatina*; *Batrachoseps*. In *Stereochilus* and *Typhlotriton* there is a cutaneous attachment, but no muscular attachment (Piatt, '35). In all other hemidactyliines, in *Hydromantes*, and in all members of the Supergenus *Bolitoglossa*, this attachment is absent, and the only connection of the tongue pad to the rest of the body is via the hyobranchial apparatus and associated rectus cervicis musculature and surrounding connective tissue. The sheath itself is modified in those species with the greatest tongue projection, the supergenera *Bolitoglossa* and *Hydromantes*. Here the sheath at rest is extensively folded around the enclosed car-

tilages and musculature, and has an accordion-pleat appearance (fig. 11a; see also Elkan, '57: plate 7). When the tongue is fully projected this sheath is pulled taut (fig. 11b).

#### 4. Tongue pad

The tongue is both reduced in mass and is simplified in terms of numbers of components in the species that have the greatest tongue projection abilities. The maximal condition of tongue mass is encountered in desmognathines and plethodontines. For example, in *Plethodon* one finds the largest tongue pad in the family (figs. 2a, 12d), and most muscular and skeletal components are present. The cartilages that are projected become relatively more slender in groups with great tongue projection, and both size and number of muscles that accompany the projectile are reduced. Marked size reductions occur in the tongue pad as well. The most extreme specializations occur in the bolitoglossines. Ceratobranchial size is markedly reduced relative to other groups, including hemidactyliines (figs. 2, 4). Most bolitoglossines have lost the lateral slip of RCS and omohyoideus musculature, and the RCP is reduced in diameter. All species lack the urohyal, and the musculature associated with this structure is incorporated into an aiming cylinder (see below).

The tongue pad of all plethodontid salamanders is tied closely to the hyobranchial skeleton in terms of dynamics. A strong glossal ligament (described here for the first time) extends from CBI below the BB to attach to the anterior projection of BB, to the lingual cartilage, or to a connective tissue mass (fig. 21). When the hyobranchial skeleton folds during projection the ligament becomes taut. An important contribution to pad rotation is the result. This is discussed in detail in a later section.

Tongue pads are variable in size within the family, and all species with marked tongue projection capacities also have reduced tongue pad size (figs. 12, 13). This is apparent within subfamilies and tribes. For example, *Plethodon* has a markedly longer tongue pad than *Ensatina* (fig. 12c,d), a species with a slenderer hyobranchial skeleton, longer EB, and longer genioglossus muscles, which projects its tongue for relatively great distances. *Hemidactylum* is the only hemidactyline with genioglossus muscles, and its tongue pad is distinctly larger than that of *Eurycea*,

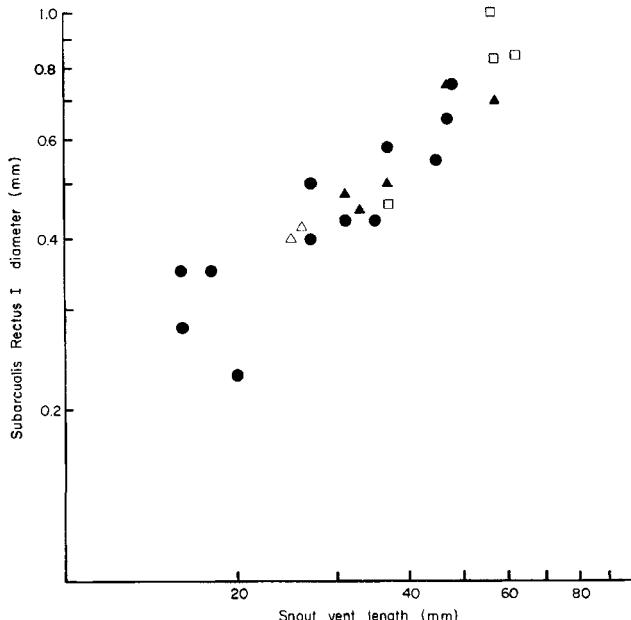


Fig. 10 Relation of the diameter of SARI to size (snout-vent length) in plethodontid salamanders. The muscle was measured from sectioned material of specimens with tongues at rest. Three measures at different locations were taken and averaged for each specimen. ● Bolitoglossini, ▲ Hemidactyliini, □ Plethodontini, △ Desmognathinae. Log-log plot.

which has excellent tongue projection abilities (cf. figs. 12b, 13a). All of the bolitoglossines have small tongue pads.

#### b. Time reduction

Factors of importance in selection for reduction of feeding sequence time are: reduction in mass of the projected elements; increased speed and force of contraction in the protraction musculature; and a reduction of the viscous forces which retard movement. In bolitoglossines time from start of electrical activity to contact of the tongue pad with the prey may be as short as 8-10 msec (Thexton et al., '77). It is in these animals that the first factor definitely occurs and the morphological correlates of the second two are evident. In the following sections interspecific comparisons relate to animals of equivalent size (as measured by snout-vent length).

All the distal elements of the hyobranchial skeleton are reduced in bulk in bolitoglossines, as compared with other plethodontids. The BB is slenderer and lacks the spatulate pattern found in other groups (Wake, '66: figs. 10, 11). CBI (fig. 14) and CBII are reduced in girth. The reduction of the first is extreme and

the second is shortened (figs. 6, 15). The ceratobranchials and basibranchials in bolitoglossines are more gracile than in other plethodontids. The general bulk of the tongue pad also is reduced in the bolitoglossines (figs. 12, 13).

The major protractor and retractor muscles of bolitoglossines show modifications that are compatible with the idea of faster contraction, more powerful contraction, or both. The SARI muscle gains bulk as the EB's increase in length. This implies an increase in projectile force in species with the longest EB's (bolitoglossines) as compared with those having the shortest (plethodonines and desmognathinae). The RCP increases in length in a morphoclade: Desmognathinae and Plethodontini; Hemidactyliini; Bolitoglossine. This implies a correlated trend in increased contraction speed. Physiological specializations in these muscles are possible, but, as yet, uninvestigated.

To increase velocity for a given force, at least three modifications of the apparatus might occur to reduce friction. The separation between the two moving surfaces could increase. The area of the surfaces could de-

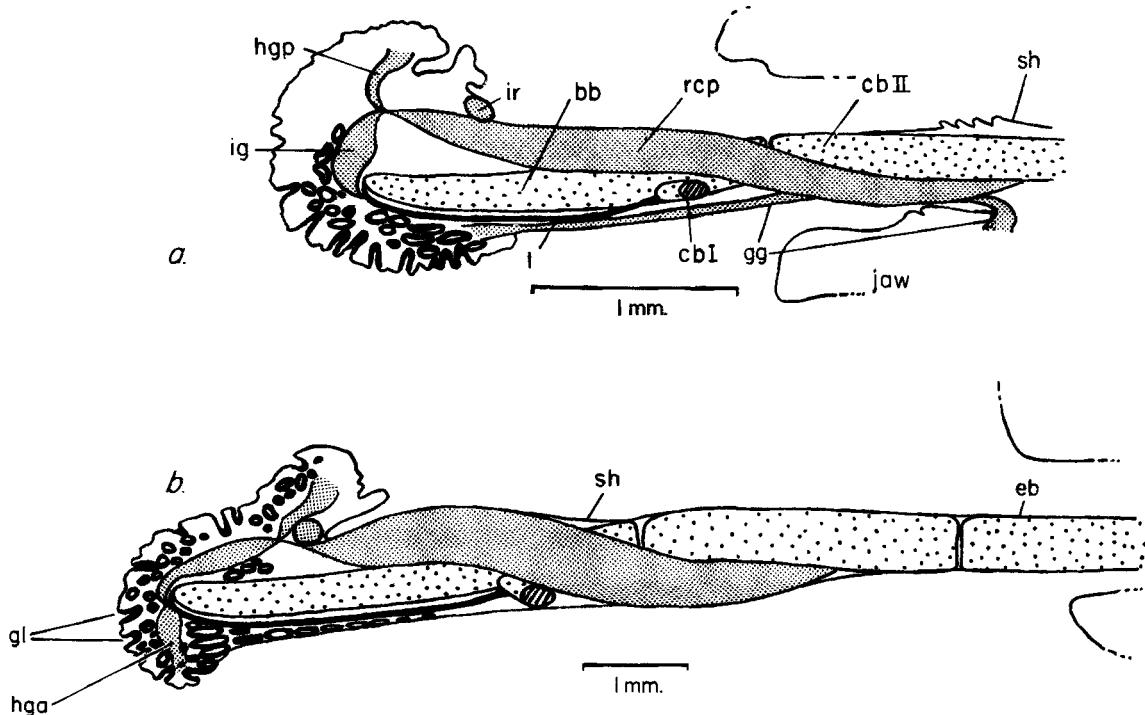


Fig. 11. Semi-diagrammatic reconstructions of partially projected tongues in (a) *Batrachoseps attenuatus* and (b) *Pseudoeurycea leprosa*. Only the distal tips of CBI are shown (cross-hatch indicates section of CBI). Note the glossal ligament extending from the region of the tip of BB to CBI; the long genioglossus muscle in *Batrachoseps*; the linear arrangement of EB, CBI, and BB; the folded sheath in the partially projected specimen. Drawn from specimens embedded in plastic and sectioned.

crease. The viscosity of the fluid between the surfaces could be reduced. Accuracy of measurements is inadequate to test the first possibility. The second possibility has been discussed previously (Lombard and Wake, '76) in the general case. The same logic applies to more specific comparisons, but it would be difficult to measure accurately. Measurement of the viscosity of the lubricating fluid was not done for this study. The morphology of the glandular fields presumed to produce lubricating fluid suggests a serous secretion. Further, this glandular tissue is at its greatest development in bolitoglossines (figs. 24, 25). In some members of the group the glands extend from the floor of the mouth down into the sheath cavity along the stem of BB as far as the joint between BB and CBI. This glandular tissue is low in quantity and poorly organized in desmognathines and plethodonines.

#### c. Directional versatility

Modifications of both the skeletal and

muscular components are expected under selection for directional versatility. It is assumed that one of the advantages of the folded mode of tongue projection seen in the plethodontids is increased directional versatility (Lombard and Wake, '76). Given this assumption, folding the skeleton relatively early in the projection sequence should also be advantageous. The cylindrical configuration of the projectile is more easily directed than a flatter, less flexible unit. To fold the skeleton more rapidly, only shortening of the ceratobranchial which rides the tractrix is required.

When folded the bolitoglossine skeleton is organized so that CBII is in line with EB (fig. 15) on the axis of projection. In the other plethodontids it is CBI which is relatively in line with the EB (figs. 15, 16). This observation is not predicted from our model, and implies two different modes of projection. In the bolitoglossine configuration the route of force transmission during projection is: EB, CBII, BB. In the other plethodontids the route

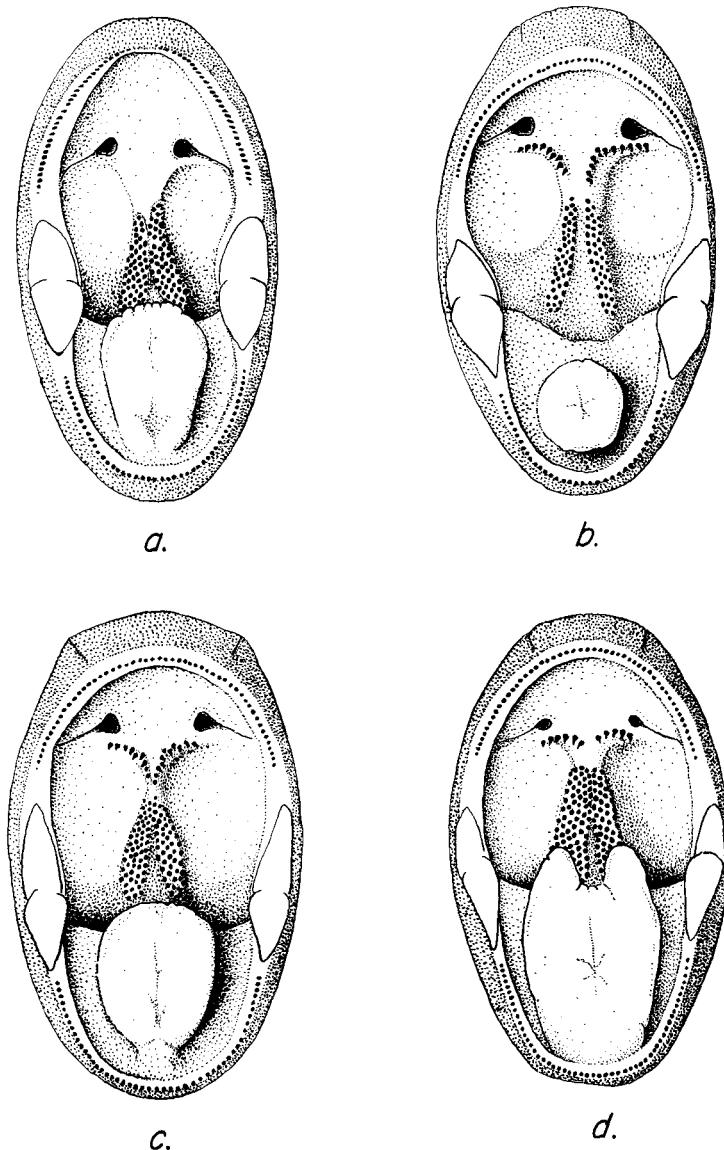


Fig. 12 Superficial structure of the mouths of various species of plethodontid salamanders, showing the tongue in relation to surrounding structures. (a) *Desmognathus monticola*, (b) *Eurycea longicauda guttolineata*, (c) *Ensatina eschscholtzii*, (d) *Plethodon glutinosus*. The adductor mandibulae muscles have been cut. The specimens are of approximately equal snout-vent length.

is: EB, CBI, BB. This observation was predicted by the mineralization patterns noted by Uzzell ('61). Mineralized cartilage in large animals occurs mainly in CBI in non-bolitoglossines and in CBII in bolitoglossines (also Wake, '66). This indicates a site of compressive stress which can be understood in the light of the folding patterns.

These observations imply a much more rapid folding of the bolitoglossine than of the hemidactyline tongue skeleton. CBII is the element which rides the track in the bolitoglossines. In the remainder of the plethodontids it is CBI (fig. 17). The shorter CBII along the track permits more rapid folding than would be possible with the longer CBI on the

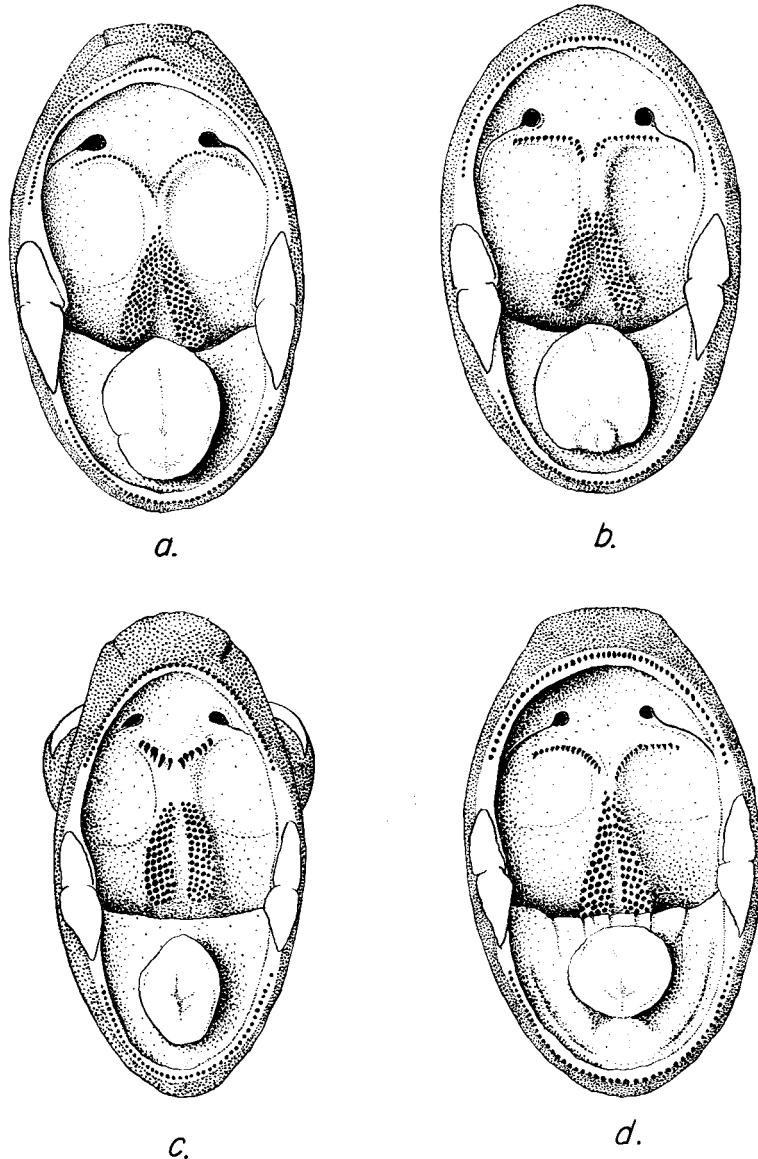


Fig. 13 Mouths of plethodontid salamanders: (a) *Hemidactylum scutatum*, (b) *Hydromantes brunus*, (c) *Batrachoseps attenuatus*, (d) *Bolitoglossa subpalmata*. Same as figure 12, but specimens vary in size.

track. A morphocline in decreasing relative length of the element that rides the tractrix would thus be: desmognathines-plethodonines; hemidactyliines and *Hydromantes*; *Batrachoseps*; Supergenus *Bolitoglossa*. CBI in the bolitoglossines is exceptionally slender (figs. 6, 15) and is curved. This morphology, we suggest, is related to use of CBII in the projectile chain. When CBII is the force transmitt-

ing member, CBI must be very flexible in order to conform to the tractrix so that binding does not occur. Its retention is probably related to the role of CBI in rotating the tongue pad (see below).

An unexpected finding is the "disarticulation" of the hyobranchial apparatus in some small bolitoglossines. In *Thorius* the slender CBI loses its attachment to the BB during

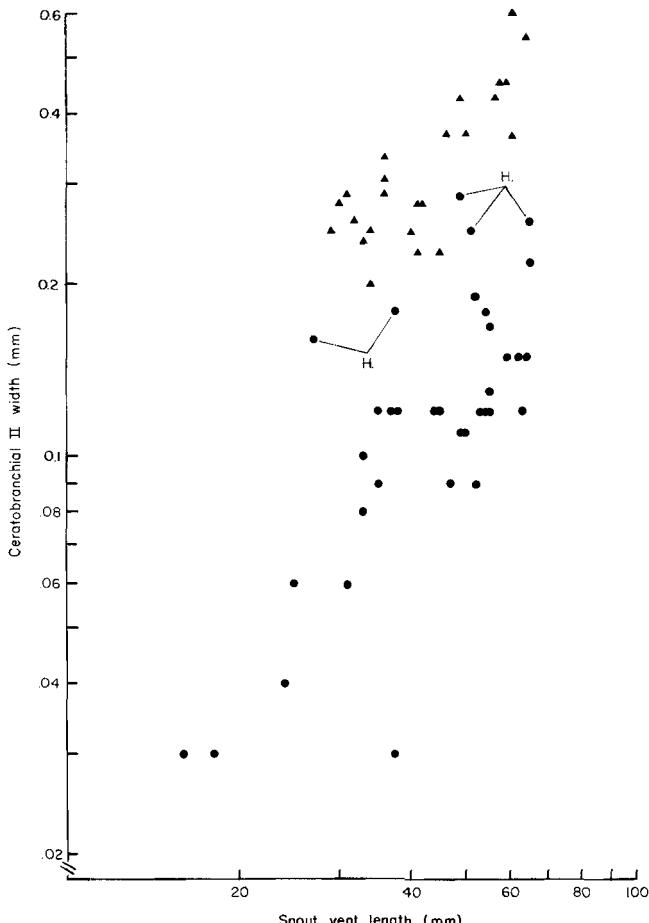


Fig. 14 Relation of the width of CBI to body size (snout-vent length) in some plethodontid salamanders. ● Bolitoglossini, ▲ Hemidactyliini. H indicates the genus *Hydromantes*. Log-log plot.

projection, and the apparatus forms a totally linear array (fig. 15). The glossal ligament retains its attachment to CBI, so the tongue-flipping mechanism operates. This is the most extreme degree of specialization in terms of skeletal elements of the tongue.

Another predicted specialization in the skeleton is increased flexibility of the EB's. This would permit the stalk of the tongue to bend for projection independent of the head. We have as yet been unable to test this prediction, but the relatively great length and slenderness of EB in bolitoglossines suggests that such specialization occurs.

The ceratohyals also would be expected to show modification. These elements are the primary support for the terminal portion of the tractrix and accordingly are expected to

be more flexible in individuals with great directional scope than those with lesser scope. The tongue is projected between the ceratohyals, which remain in the floor of the mouth. Dorsally the ceratohyals are attached to the floor of the mouth by the pharyngeus musculature, and at the anterior edge of this muscular sheet a new muscle, unique to the plethodontids, the suprapeduncularis, extends between the flattened blades of the ceratohyals (Piatt, '35). This short, strap-like muscle forms a short section of a cylinder, through which the hyobranchial apparatus and associated musculature is projected. We have elsewhere (Lombard and Wake, '76) discussed the morphological track formed by the anterior or part of the SARI musculature. This muscle arises on the ventral surface of the ceratohyal

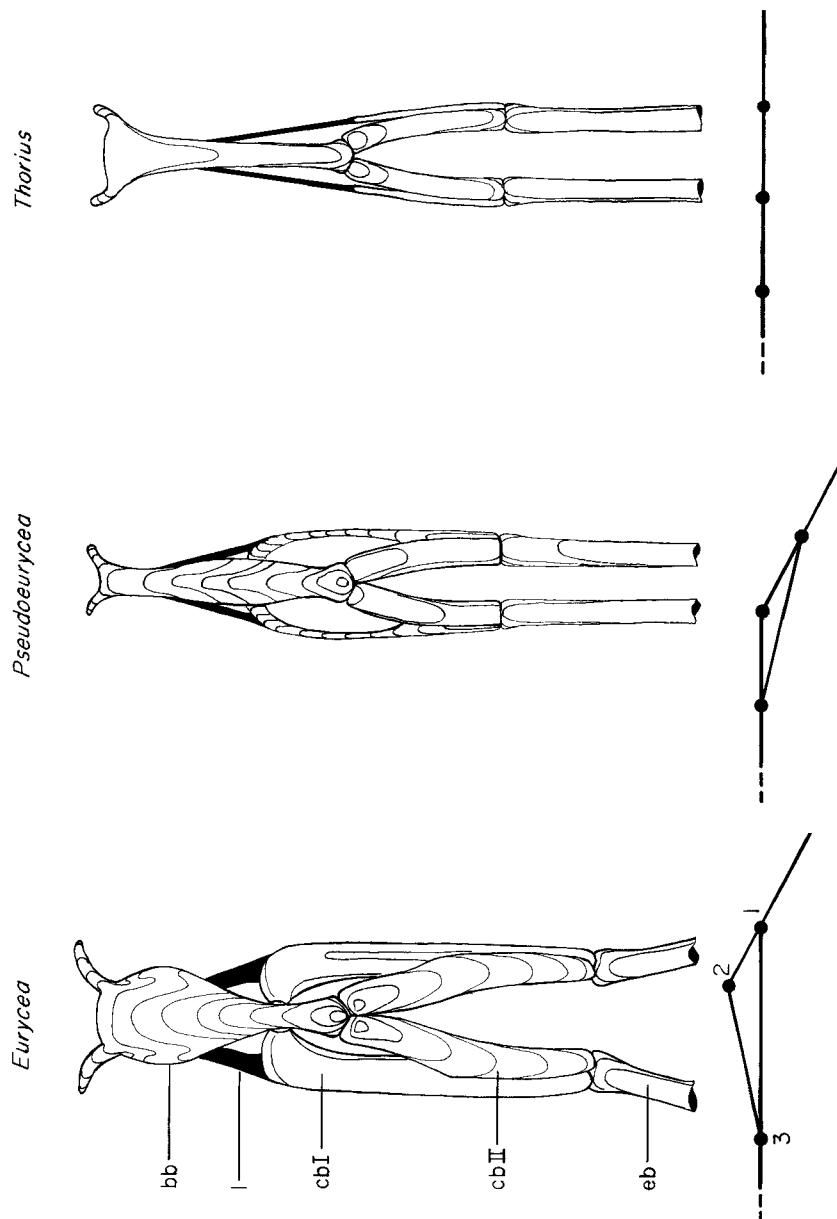


Fig. 15. The articulated hyobranchial elements in three plethodontid genera, nearly fully projected. Serial reconstruction from plastic-embedded material. Contour interval is  $60 \mu$ . Dorsal view. The high point on all reconstructions is the CBII-BB joint. The stick diagrams below each reconstruction illustrate the arrangement of cartilages, viewed laterally. The black dots indicate the sites of joints. Note the "disarticulation" of the CBII-BB joint in *Thorius*, and the near linear array of the cartilages. The specimens are of greatly different size, but have been reconstructed by standardizing to a common BB length. The cartilages are outlined, and the ligaments attaching to the anterior ends of CBII are blackened.

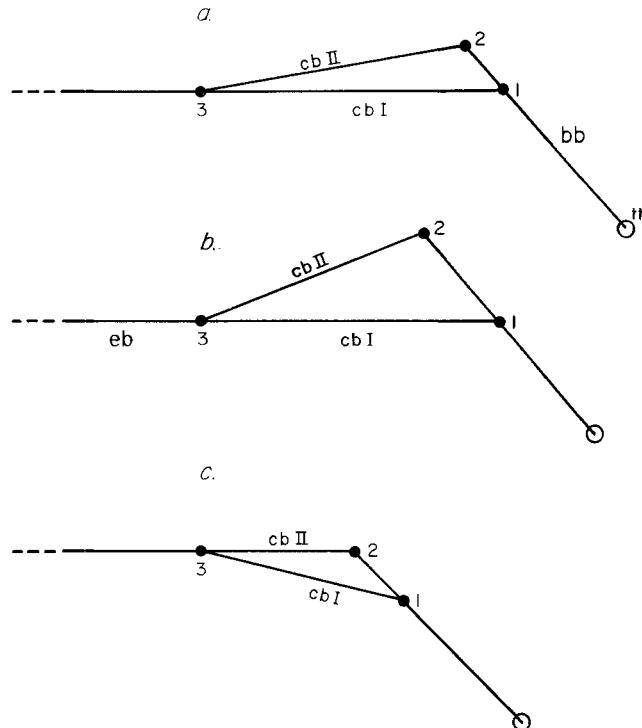


Fig. 16 Various arrangements of articulated hyobranchial cartilages during tongue projection, as seen in lateral view and assuming complete folding. (a) Desmognathinae, Plethodontini, (b) Hemidactyliini, (c) Bolitoglossini.

and extends posterolaterally to wrap around EB. The hyobranchial apparatus folds along the inner margins of this muscle as it is projected forward. Another muscle, the geniohyoideus lateralis, attached to the dorsal and ventral sides of the anterior parts of the ceratohyal, is responsible for controlling lateral excursions of the ceratohyals, and hence of the cylinder, thus directing the tongue (fig. 18). This set of muscles is present in all plethodontids, and all have at least the rudiments of a cylinder. However, in the hemidactyliines and bolitoglossines important modifications occur (cf. a and b: fig. 19; figs. 24, 25). In the hemidactyliines the cylinder is markedly more muscular than in plethodontines and desmognathines, although there are no additional muscles involved. The cylinder is simply more of a morphological and functional entity, and the suprapeduncularis muscle, in particular, is more distinct from the pharyngeus musculature than in more generalized species.

The greatest development of the muscular sheath is seen in the bolitoglossines. Here the

suprapeduncularis is a very distinct muscle, well separated from the pharyngeus and often extending for a considerable length along the ceratohyals (Tanner, '52). In addition there is a major addition to the musculature of the sheath. The urohyal is absent, and the musculature ordinarily associated with it now attaches to a myocomma on either side of the heart (fig. 9). Thus, at this pair of myocommata the RCS and hebstosteopysiloideus meet the geniohyoideus medialis. The connections immediately in front of this juncture are complex and somewhat variable, and nearly impossible to unravel, for a relatively massive, short muscle extends forward to insert mainly on the dorsal but also on the ventral surface of the ceratohyal blade. Below this muscle, what we have called (above) the geniohyoideus medialis extends to a myocomma lying at about the level of the angle of the jaws. Between this myocomma and the one behind it, fibers either extend directly, or pass dorsally, to join the muscle extending to the ceratohyal. From the more anterior myocomma the geniohyoideus medialis passes unin-

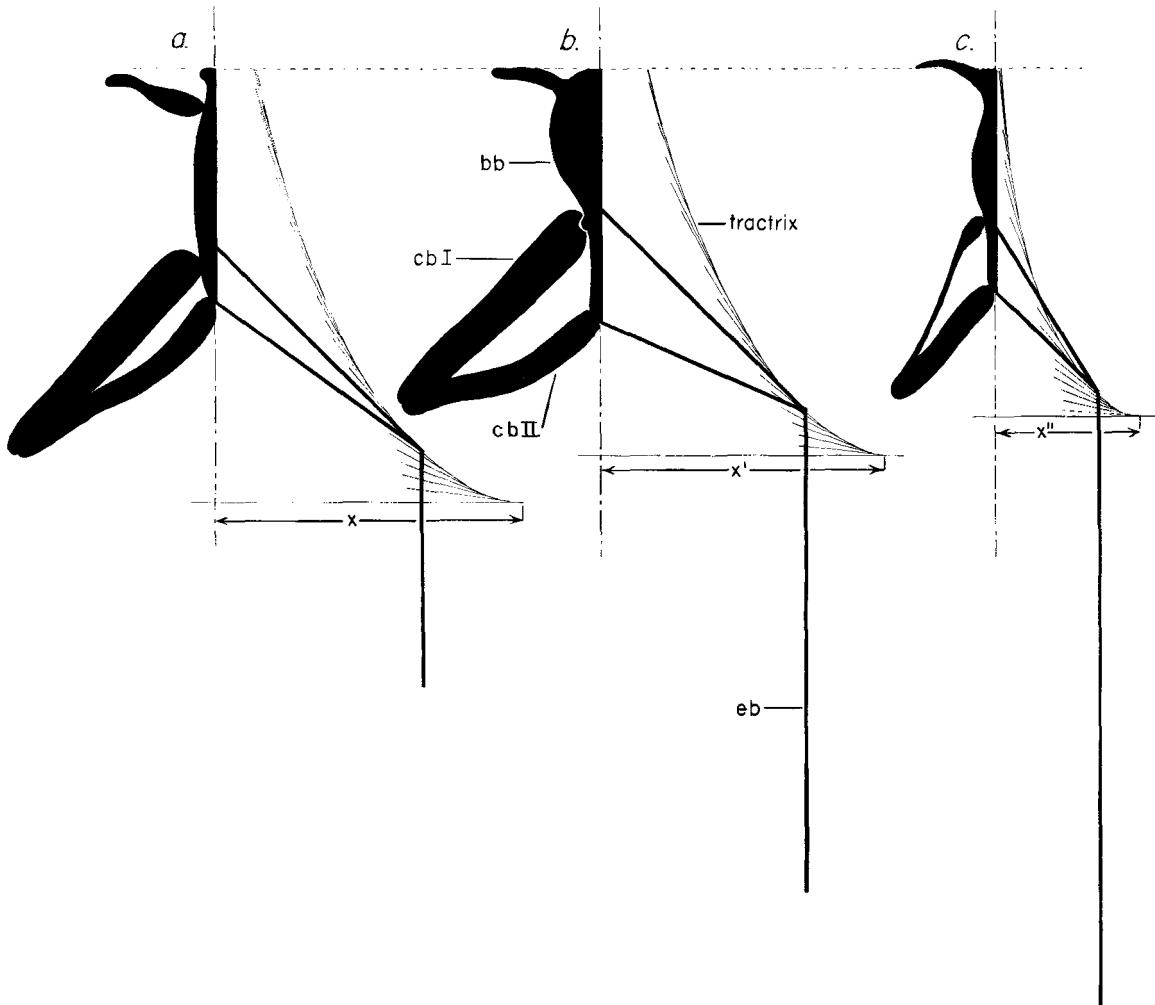


Fig. 17 Generalized arrangement of articulated hyobranchial cartilages in (a) Desmognathinae and Plethodontini, (b) Hemidactyliini, (c) Bolitoglossini, except *Hydromantes*, at rest. The tractrix is constructed in (a) and (b) by the method of Lombard and Wake ('76), in which CBI is moved from horizontal to near vertical, with the distal end always lying tangent to the developing curve. In (c) CBII is used to construct the tractrix. See text for further explanation. Compare with figures 15 and 16.

errupted to the dentary (fig. 9). Since geniohyoideus muscles do not normally have a myocomma, it may be more accurate to refer only to the uninterrupted section by that name, but that would leave the section between the two myocommata without a name, for it is neither hebastoypsiloideus nor rectus cervicis superficialis. As a result of this new organization, the bolitoglossines, and especially members of the Supergenus *Bolitoglossa*, have a relatively massive aiming device in their throats which can best be understood by studying serial sections (figs.

19, 24, 25). In these species the morphological track, along which the hyobranchial apparatus folds during projection, and the cylinder, by means of which the projectile is aimed, reach their highest degree of elaboration within the family.

#### Tongue pad

##### a. Skeletal elements

Features of the skeleton of the anterior tip of the basibranchial, lying in the tongue pad, have been described previously (Wake, '66), and only a summary is presented here. An

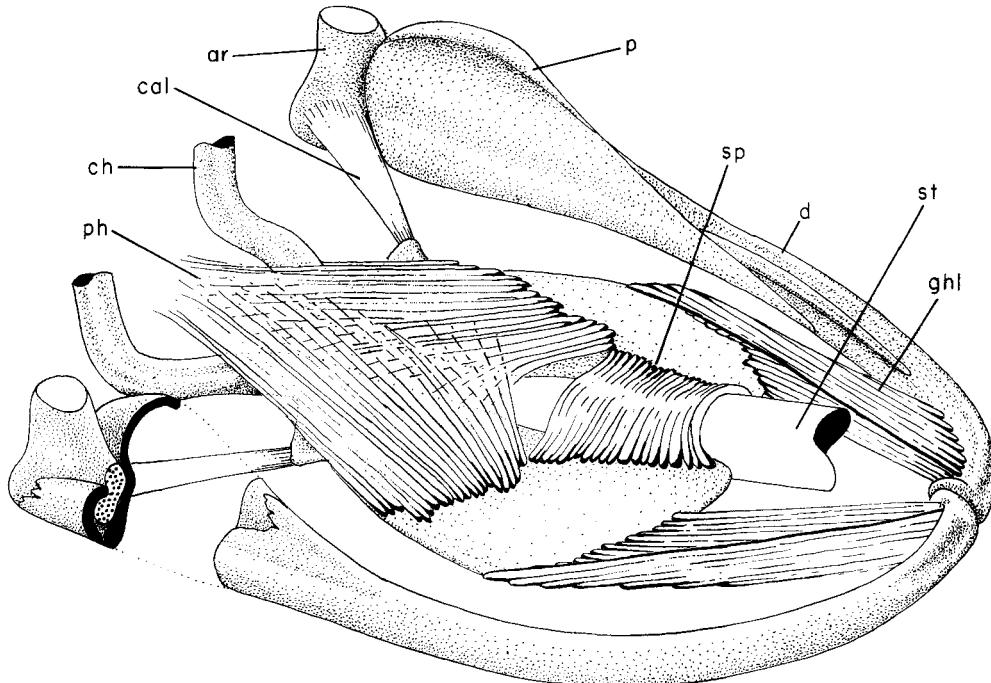


Fig. 18 Generalized view of the intermandibular region in a free-tongued plethodontid salamander. View from above and in front of the lower jaw, with tongue tip and buccal membrane removed. Only some elements are shown. The ceratohyals lie in the floor of the mouth, tied to the lower jaw by the cerato-articular ligament and the geniohyoideus lateralis muscle, and to the quadrate by the hyoquadrate ligament (not shown). The stalk of the tongue passes through a cylinder formed by the ceratohyals, the floor of the mouth, and geniohyoideus medialis and SARI muscles (see also figs. 19, 23, 24). The entire cylinder is directed by the geniohyoideus lateralis muscles working antagonistically with the ligaments. The tongue stalk emerges from a hole in the floor of the mouth, and the anterior margin of the suprapeduncularis muscle, covered by buccal membrane, forms the posterior rim of this orifice.

extension of the BB in front of the attachment of the radii is present in desmognathines, *Plethodon*, and *Aneides*. In all other genera there is some reduction of this process. In *Ensatina* the process is present, but reduced in size, and it is flexibly attached to the main part of the BB. It thus forms a kind of rudimentary lingual cartilage. In all hemidactyliines the process is absent but seems to be represented by what has been called a lingual cartilage. In some species the cartilage is large and well developed. This is especially true of those having tongue projection specializations. In *Hemidactylum* a small pair of cartilaginous projections is present at the anterior end of BB. A small mass of connective tissue seems to represent the lingual cartilage. All bolitoglossines lack an anterior extension of BB, but in some members of the Supergenus *Bolitoglossa* (especially the Mex-

ican group of genera of Wake and Lynch, '76) a well developed lingual cartilage is found. In most bolitoglossine species, including *Batrachoseps* and *Hydromantes*, there is no lingual cartilage. In *Hydromantes* the basibranchial is relatively longer than any other plethodontid (fig. 3). This long basibranchial has an area of flexibility near the tip (1: fig. 21c).

Radii are present in nearly all plethodontids. There is much variation in structure (see Wake, '66, for details). Desmognathines, plethodonines and hemidactyliines have radii that are somewhat more distinctly separated from BB than is true of the bolitoglossines. In the bolitoglossines the radii are so closely connected to the anterior end of BB that they seem to be nearly direct anterior continuations of that element. The radii of desmognathines are cylindrical. Those of pleth-

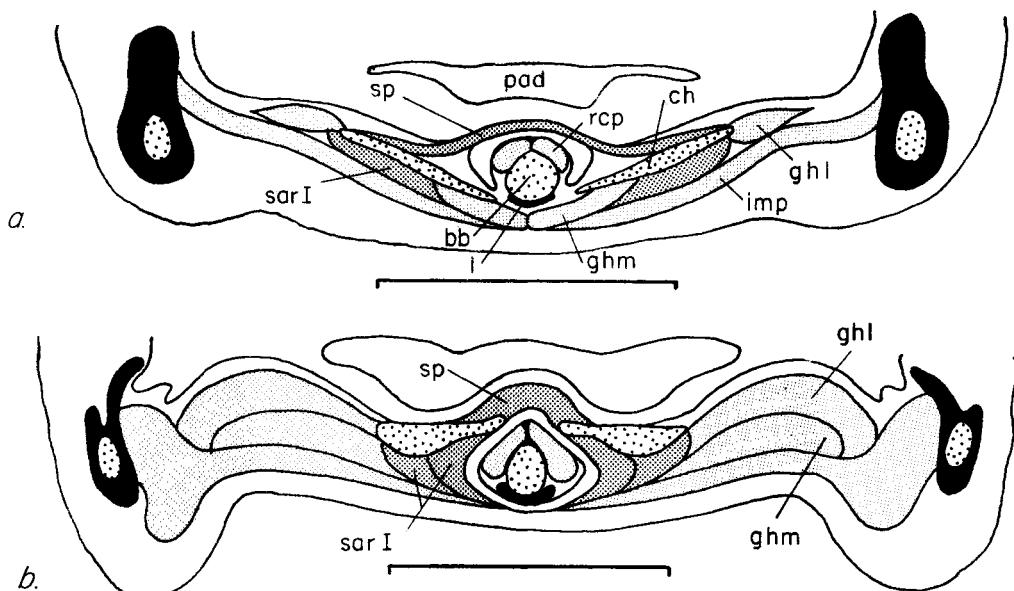


Fig. 19 Semi-diagrammatic drawings of cross-sections through the floor of the mouth in (a) *Desmognathus* and (b) *Lineatrion* illustrating the formation of the projection cylinder (heavy stipple, b) from more generalized muscular arrangements (heavy stipple, a). Scale is 1 mm.

odonines are distally expanded, with the expanded part becoming very thinned. Radii of hemidactyliines are variable in shape, but are generally broad-based and rather narrowly cylindrical, although some distal expansion can be found. Typically plethodontine radii are the longest of this group of genera. In bolitoglossines the radii are highly variable in length, being very long and posteriorly swept in *Batrachoseps* and shorter but typically posteriorly swept in the Supergenus *Bolitoglossa*. The radii in these groups always taper distally, with no expansion.

No radii are found in *Hydromantes*, but small remnants are present at the very tip of BB. In some individuals bits of cartilage are found in the region where one would expect bases of radii.

#### b. Musculature

The complex musculature of the tongue pad in the Plethodontidae has not been described previously (the descriptions of Tanner, '52, are inadequate and err in combining several muscles under a single name). There are seven muscles associated with the pad, four of them intrinsic. Not all are found in all species. Some of these muscles are unique to the

Plethodontidae and are described here for the first time. For description the muscles are placed below in three functional groups.

##### 1. Rotators

###### *Genioglossus*

The general comparative features of the genioglossus muscle have been described above. The muscle is absent in all tropical salamanders (Supergenus *Bolitoglossa*), *Hydromantes*, and all Hemidactyliini except *Hemidactylium*. The muscle is present in all other genera. It is rudimentary in *Typhlotriton* (fig. 20e). The paired muscles insert in the connective tissue of the anterior mass of the pad in all animals possessing it.

###### *Circumglossus* (fig. 2a)

This muscle first noted by Magimel-Pelonier ('24), is named here for its orientation. It connects the anterior tips of the ceratohyals and lies ventral to the mass of the tongue. The muscle passes anterior to the genioglossus. This muscle is found in all plethodontids except bolitoglossines.

###### *Basiradialis* (fig. 2a)

The paired basiradialis muscles originate

on the dorsal surface and lateral edges of the tip of BB in the Desmognathinae and Plethodontini. In the hemidactyliines and *Batrachoseps* the muscle arises from the lingual cartilage or connective tissue in a similar position when the cartilage is not present. The muscle is absent in *Hydromantes* and members of the Supergenus *Bolitoglossa* (except *Thorius*). When present, the muscle inserts on the mid to distal shaft of the radius.

#### *Intraglossus* (fig. 2)

The intraglossus muscle has not previously been described for any salamander. All members of the Plethodontidae possess this muscle. In all cases the paired muscle originates on the *Sehnenplatte* (see below). It proceeds antero-ventrally to insert on the lingual cartilage or its connective tissue homolog in bolitoglossines, save *Chiropterotriton*, and hemidactyliines, save *Hemidactylum*. In this genus, the Desmognathinae, and Plethodontini (except *Ensatina*), the muscle inserts on the variously flexible tip of BB. In *Ensatina* and *Chiropterotriton* the muscle wraps over the end of BB and inserts on the glossal ligament (fig. 20c). We earlier referred to this muscle as the RCP anterior (Lombard and Wake, '76), but we have subsequently come to believe that the *Sehnenplatte*, which separates this muscle from the RCP, is an ancient feature which separates very distinct muscles. The likeliest phylogenetic and ontogenetic associates are the anterior and posterior hyoglossus.

#### 2. Molders

##### *Interradialis* (fig. 2b)

The interradialis muscle connects the tips of the radii. It forms a loop encircling the fold of RCP. It is present in all the Bolitoglossini and *Hemidactylum*. In no animal is the muscle robust, and usually it is comprised of only 5 to 15 fibers.

##### *Hyoglossus* (figs. 2b, 20, 21).

The hyoglossus is a complex of muscles. Two major centers of origin are present and at least one of these is present in all plethodontids. In both cases the muscle fibers fan out in several directions (though one direction may predominate) into the substance of the tongue. One center of origin is the region of the BB tip, the lingual cartilage or its connective tissue homologue. These muscle fibers fan out into the anterior mass of the tongue pad, their major direction being antero-dorsal.

This mass of muscle is not present when the genioglossus is present except in the Desmognathinae. It is also lacking in *Hydromantes*. These fibers (anterior hyoglossus) are thus present in the Supergenus *Bolitoglossa* and in the Hemidactyliini (except *Hemidactylum*).

A second center of origin is the *Sehnenplatte*. Muscle fibers arising from this center (posterior hyoglossus) fan out radially into the substance of the pad. A strong mass of laterally and posteriorly directed fibers is present in all plethodontids save in *Plethodon* and *Aneides*. Strong anteriorly directed fibers represent the posterior hyoglossus in these two genera (not illustrated in fig. 2a; see 2, fig. 20b).

#### 3. Restorers

##### *Rectus cervicis profundus* (fig. 2)

The paired RCP is present in the tongue pad of all plethodontids. Two major morphologies are evident. In the first, the muscle lies on the surface of BB so that the series: rectus cervicis profundus—*Sehnenplatte*—intraglossus forms a linear pattern (figs. 2a, 21a,b,c). This arrangement is found in members of the Desmognathinae and Plethodontini. In the second, the muscle is thrown into a fold such that the insertion in the *Sehnenplatte* is removed dorsally from BB (figs. 2b, 20d,e, 21). The fold is concave posteriorly. This pattern is found in the Bolitoglossini and Hemidactyliini. The fold is only slightly developed in *Hemidactylum* (fig. 21a).

#### Connective tissue

The tongue pad is a complex of elongate glands, muscle and a fibrous matrix. One of the most characteristic features of the urodele tongue is a mass of fibrous tissue located at the end of the RCP. This fibrous mass is

Fig. 20 Semi-diagrammatic reconstructions of mid-sagittal sections through the tongues of a group of plethodontid genera having different tongue projection abilities. (a) Mode I, represented by *Desmognathus fuscus*, (b) Mode II, represented by *Plethodon vehiculum*, (c) Mode III, represented by *Ensatina escholtzii*, (d) Mode IV represented by *Pseudotriton ruber*, (e) Mode IV, represented by *Typhlotriton spelaeus*. 1, the well developed aponeurosis lingualis characteristic of Mode I; 2, the unusual posterior hyoglossus of Mode II; 3, the basiradialis muscle can be seen in this view, which is off the midline; 4, the lingual cartilage characteristic of Mode IV; 5, possible remnants of the genioglossal muscle. Note the varying proportions of the muscles shown, especially the large genioglossals of (a), (b), and (c), and the very large suprapenduncularis muscle of the group most specialized for tongue projection (d). Note also the varying arrangement of the RCP-intraglossus complex, from linear (a and b) to folded (d and e). Scale is 1 mm.

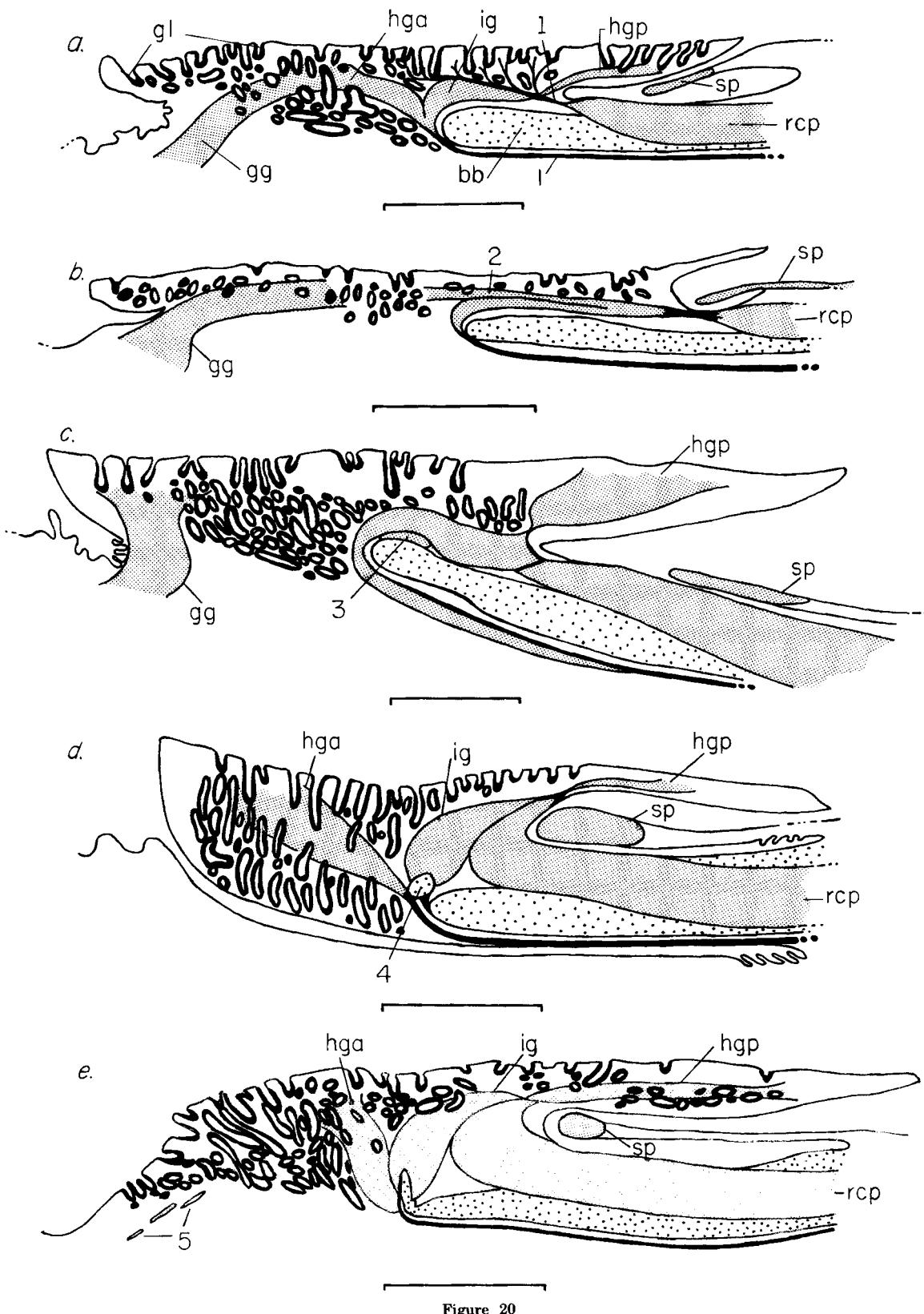


Figure 20

recognized in other urodele groups (Ozeti and Wake, '69), and termed the *Sehnenplatte* by Oppell (1900). In plethodontids it lies in various positions, either in line with the RCP and intraglossus, or dorsally, in the main substance of the tongue pad (figs. 2, 20, 21). The hyoglossus posterior and intraglossus both originate from the *Sehnenplatte*. The *Sehnenplatte* is a major feature of the tongue, and is important as a focal point of antagonistic muscle action. The mass of tissue moves to different positions during tongue protraction and retraction, and mechanical advantage of the attached muscles changes accordingly.

Another dominant feature of the tongue is the glossal ligament, extending from each CBI to attach to the tip of the BB or its homologue (fig. 23). It plays an important role in flipping the tongue pad into a position where the sticky surface meets the prey as an automatic consequence of folding of the hyobranchial skeleton during tongue projection (see below).

#### DISCUSSION

Data presented above make clear the diversity of structure among the plethodontid genera. In order to examine the relevance of this diversity to evolution of these salamanders, it is necessary to find some structure to the pattern of variation presented. We have chosen to work at the generic level and this reduces our number of units from over 200 to 23. We choose to ignore the permanently larval genera *Typhlomolge* and *Haideotriton*, but 21 groups are still unwieldy. Accordingly we have grouped the genera into eight functional modes based on structure and function in relation to behavior and ecology. The structural basis of the groupings is considered in detail by Wake ('66), and it will be recognized that the modes correspond to subfamilial, tribal, or suprageneric groupings recognized in that work. The exceptions are modes 2 and 3, which simply represent a division of the Tribe Plethodontini and modes 4 and 5 which subdivide the Hemidactyliini. The reality of these modes and a formal consideration of characters used in their recognition are the subject of the final paper in this series. Here we stress only functional aspects of this work.

In this section we also develop a series of hypotheses for the functions of the components in each of the modes. In all cases the general projection and retraction dynamics

developed by Lombard and Wake ('76) are assumed. Thus, during projection the hyoid skeletons are assumed to be folded, whatever the degree, by use of a morphological track, having the shape of a tractrix. We are concerned here with the functions, within the general framework previously developed, of those structures showing significant variation.

#### *Functional modes*

*Mode I:* *Desmognathus*, *Phaeognathus*, *Leurognathus* (figs. 2, 20, 23)

#### Behavioral and ecological correlates

These genera comprise the Subfamily Desmognathinae, a group restricted to eastern North America and concentrated in the southern Appalachian Mountains. *Leurognathus* and some species of *Desmognathus* are highly aquatic, stream and stream-side dwellers. These large salamanders eat mainly aquatic prey, including larvae and small salamanders of related species. Some species of *Desmognathus* are semi-aquatic to largely terrestrial, and terrestriality is correlated with reduction in size (Organ, '61). *Phaeognathus*, however, is both the largest and the most terrestrial of the group. The terrestrial species mainly eat terrestrial arthropods. The desmognathine feeding mechanism has been discussed by Wake ('66) and Hinderstein ('71). The tongue is used as a part of a "snap" which delivers prey to the mouth. The most distinctive aspect of feeding by these salamanders is extensive use of skull movement in feeding. We give little attention to this group, for we are interested in tongue specialization. In terms of tongue structure and function this is the most generalized in the family.

Species comprising this mode mostly have aquatic larval stages, but some species of *Desmognathus* have greatly abbreviated larval stages and one (*D. wrighti*) is considered to have essentially direct development. Larvae

Fig. 21 Reconstructions as in figure 20. (a) Mode V, *Hemidactylum scutatum*, (b) Mode VI, represented by *Bolitoglossa adspersa*, (c) Mode VII, represented by *Hydromantes brunus*, (d) Mode VIII, *Batrachoseps pacificus*. 1, the point of flexion in BB; 2, the site of attachment of CBI (diagonal lines indicate sectioned CBI). Note the positioning of the tongue pad above the anterior end of BB in (c). The elongated genioglossal muscles of *Batrachoseps* are surrounded by a pleated sheath (d). Massive amounts of glandular tissue are present in the tongue and along the stalk of the tongue in (b), and the sheath of the tongue stalk is strongly pleated. Scale is 1 mm.

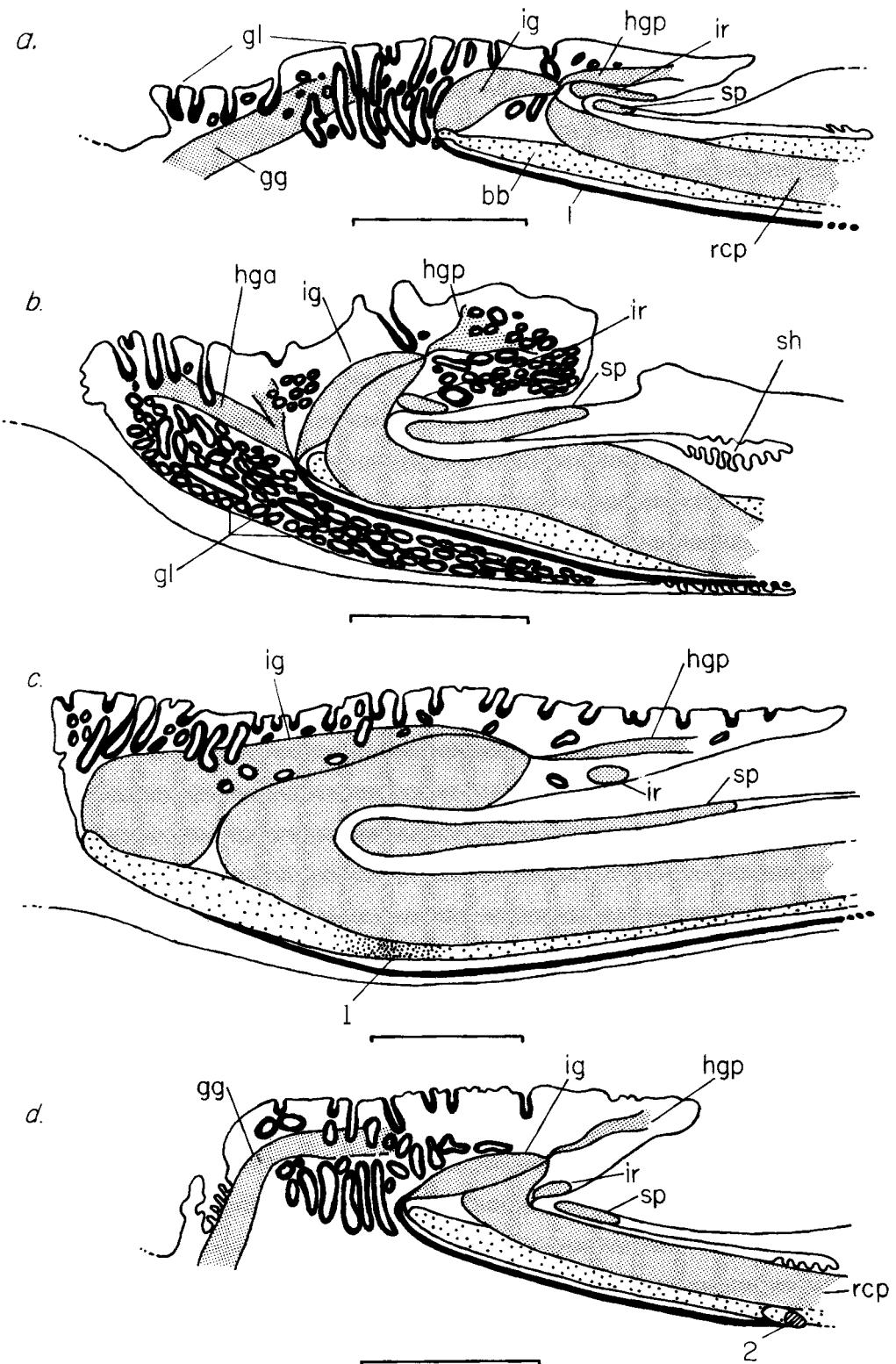


Figure 21

of *Phaeognathus* are unknown, and it is presumed that the single species has direct development.

### Morphological features

The tongue pad of desmognathines is a relatively large structure, narrowly attached at its anterior margin to the floor of the mouth (fig. 12a). Posteriorly the pad broadens and there is a relatively large, free flap.

BB, CBII and EB are roughly of the same length (fig. 5). The basibranchial is rod shaped. The shafts of BB, CBII and EB have similar diameters. The flattened CBI is much larger and has a greater cross section than CBII. The anterior projection of BB in front of the radii is stiff, and the radii show a distinct joint with BB. The glossal ligament runs from the tip of the BB projection to the distal tips of CBI. A mineralized urohyal is present. Mineralization may be present in BB, CBI, and EB.

The origin of the SARI muscle is unspecialized. The RCP lies flat against the dorsum of BB and inserts in the *Sehnenplatte*. There is no interradialis, and the suprapeduncularis is not differentiated from the pharyngeus muscle. The genioglossus is well developed, as are the circumglossus and basiradialis. Both an anterior and posterior hyoglossus are present. The lateral slip of RCS and the omohyoideus are relatively well developed, and the hebstoeypiloideus attaches to the urohyal (fig. 8).

### Proposed mechanical events

When SARI contracts, the force generated on the EB's is transferred to the BB by CBI. Thus, during forward movement of the hyoid, CBI is the element fitted to the tractrix formed by the sheath of SARI (fig. 17). Projection is not great, and the hyoid skeleton is probably only slightly folded at full projection. Support for these notions comes from the fact that CBI is the stouter ceratobranchial and often shows partial calcification indicating compressive stress. Further, graphic reconstruction of partially or completely projected tongues in modes II-V indicates that CBI lies directly in line with EB in the projected state (fig. 16). Finally, behavioral observation indicates that tongue projection is a limited aspect of the feeding sequence.

As the hyoid moves forward, the tip of BB over-rides the insertion of the genioglossus muscle. Contraction of the genioglossus pulls

the anterior mass of the pad to a vertical position, the basiradialis muscles contract, pulling the radii down and forward, spreading the pad, and the intraglossus contracts, pulling the posterior mass of the pad forward. The circumglossus forms a sling which gives the genioglossus the appropriate direction (down and back) to pull the anterior segment of the pad ventrally. These events are hypothesized from the location of the muscles involved and their probable relations to one another as the hyoid moves. The pad is molded by contraction of the posterior hyoglossus.

Retraction of the tongue pad to the mouth is accomplished by contraction of the RCP and RCS (lateral slip)—omohyoideus complex. As they contract, the hyoid moves backward and the ceratohyals are spread to the resting position. RCP inserts in the *Sehnenplatte*, which in turn is bound to the radii (by fibers of the aponeurosis lingualis). Contraction of the RCP thus restores the radii and the pad to the resting position (1: fig. 21a). The system contains a coupled tongue retraction-pad restoration system with the retractor muscle performing both functions by a combination of direct and indirect action.

### Mode II: *Aneides*, *Plethodon* (figs. 2, 5, 20, 23, 29)

#### Behavioral and ecological correlates

These two genera include terrestrial, mainly woodland species of eastern and western North America, with three species in relatively restricted parts of the Rocky Mountains. *Plethodon* is a very generalized feeder, using a short tongue thrust to seize prey and following with a slight forward lunge and jaw snap. *Aneides* includes species that have the most highly developed jaws in the family, with heavy, reinforced maxillary, premaxillary, and mandibular bones, large, long, flattened teeth, and hypertrophied adductor muscles (Wake, '63, '66). Nevertheless, some use is made of the tongue even in the species with the highest degree of jaw development, *A. lugubris*. *Plethodon* and *Aneides* are known to feed primarily on arthropods, and Lynch ('74) has shown that size of prey is correlated with size of salamander. *Aneides* will eat small salamanders of other species. In terms of tongue structure and function, both genera are relatively generalized. They are of special interest in this study because all species have direct development, and the hyoid apparatus never functions in feeding in aquatic situa-

tions. The species thus form something of a base line for analysis of terrestrial feeding specialization, for they are freed from at least that ontogenetic constraint.

#### Morphological features

The pad of these genera is very large, essentially filling the intermandibular area (fig. 12). There is a broad anterior attachment. Posteriorly the large flap is extended into paired posterior extensions.

Mode II BB, CBII and EB are approximately of the same length (fig. 5). The BB is rod shaped. The shaft of BB, CBII and EB is nearly equal in diameter. CBI is relatively flattened and has a greater cross section than CBII (figs. 2a,b). The anterior projection of BB is flexible. The radii are spatulate and have a distinct joint with BB. The glossal ligament runs from the tip of BB to the distal end of CBI. A mineralized urohyal is present. Mineralization may be found in BB, CBI and EB.

The origin of the SARI is unspecialized. The RCP lies flat against the dorsum of BB and inserts into the *Sehnenplatte*. The intraglossus arises from the *Sehnenplatte* and inserts on the BB projection. The RCP, *Sehnenplatte* and intraglossus all lie in a linear array (fig. 20b). There is no interradialis, and the suprapeduncularis is not differentiated from the pharyngeus musculature. The genioglossus, circumglossus and basiradialis are well developed (fig. 2a). Only a posterior hyoglossus is present and it is directed anteriorly. The lateral slip of RCS and the omohyoideus are relatively well developed, and the hebosteopysiloideus attaches to the urohyal.

#### Proposed mechanical events

The projection mechanics and pattern of force transmission is the hyoid cartilages are similar to those in Mode I. The tongue can be projected for a greater distance from the mouth, but folding of the hyoid is still incomplete. In the most folded state, CBI is in line with EB, as in Mode I.

Flipping and spreading the tongue pad is more complex in animals of this group than in those in Mode I. This is the result of a flexible BB tip. The BB over-rides the insertion of the genioglossus, and the genioglossus contracts through the loop of the circumglossus to pull the anterior mass of the pad down, as in Mode I. Contraction of the basiradialis pulls the radii down and spreads the pad. The glossal

ligament pulls the flexible tip of BB down as the skeleton folds, thus giving the basiradialis muscles a favorable orientation for spreading the pad, in contrast to Mode I (cf. figs. 20a,b). The insertion of the intraglossus muscle is also pulled down as the tip of BB is bent, and contraction of the muscle pulls the posterior mass of the tongue pad forward. The sequence of these actions is unknown, but it is likely that they are simultaneous, or nearly so. Flipping the pad is a complex action, involving four muscles—genioglossus, circumglossus, basiradialis and intraglossus—and relative movement of the BB, its anterior projection, CBI (through the glossal ligament), and the radii. The hyoglossus posterior molds the tongue surface.

Retraction of the tongue to the mouth is accomplished by RCP and RCS (lateral slip)–omohyoideus as in Mode I. As retraction proceeds the ceratobrachials are spread, thus allowing the tip of BB (through the glossal ligament) to return to the resting position. This event is aided by the force exerted by the RCP through the *Sehnenplatte* and intraglossus on the tip. Restoration of the BB tip to the resting position and the posterior movement of the *Sehnenplatte* under the action of RCP return the tongue pad to the resting position. No special muscular acts are required to restore the pad, in contrast to the relatively complex arrangement necessary for flipping the pad during projection. The retractor muscle both retracts the tongue and returns the pad, but this is accomplished by a somewhat different mechanism than in Mode I.

#### Mode III: *Ensatina* (figs. 12, 20c)

#### Behavioral and ecological correlates

This monotypic genus of western North America is a terrestrial inhabitant of wooded to somewhat open areas. It is a generalized feeder, distinguished from *Aneides* and *Plethodon*, its closest relatives, by its broader head and more numerous, smaller teeth. It seems to be more reliant on tongue projection than are its relatives, and general attributes of the use of its tongue (Regal, '66) and its prey (Lynch, '74) have been described. Like its relatives, it has direct terrestrial development.

#### Morphological features

The tongue pad of *Ensatina* is smaller than that characteristic of Mode II (fig. 12). The

anterior attachment is narrower and less restrictive, and the flap portion lacks posterior extensions.

The morphological attributes which differentiate it from Mode II are as follows: the genioglossus inserts on the middle of the mandibular ramus on both sides, thus providing more freedom of movement of the tongue pad (fig. 7). In addition the muscle and its investing connective tissue are pleated at rest, suggesting that much stretching can occur. The intraglossus inserts on the glossal ligament. The muscle wraps over the end of a jointed basibranchial projection (fig. 20c). The epibranchial is slightly lengthened relative to BB and CBII. As in Mode II, the RCP, the *Sehnenplatte*, and intraglossus form a linear array (fig. 20c). These features in combination with a generalized jaw mechanism form the major attributes of this relatively specialized representative of the salamanders with a tongue attached at the front.

#### Proposed mechanical events

The projection mechanics and force transmission in the hyoid are similar to those in Modes I and II. However, the tongue can be projected for a considerable distance from the mouth, and folding of the hyoid skeleton is thought to be complete in the fully projected state. When fully projected, CBI is in line with EB.

Flipping and spreading the tongue pad are similar to the Mode II system. The major morphological differences in this mode—the elongate genioglossus and the unusually extended intraglossus insertion—are related to long distance projection of an attached tongue. These modifications of the generalized morphology of Mode II allow both (1) a retention of the original functions performed as in Mode II, and (2) a new general behavior (long distance projection). Presumably the elongate genioglossus can be stretched further than a short one, thus both allowing long distance projection, generally, and pulling the anterior pad down, specifically. Elongation of the intraglossus permits the muscle to shorten over a greater distance, counteracting the tendency of the *Sehnenplatte* to be pulled posteriorly by the drag from RCP as the tongue is projected.

Retraction of the tongue to the mouth is accomplished by contraction of the RCP and RCS (lateral slip)-omohyoideus complex, as in Modes I and II. The tongue pad is restored to the resting position as in Mode II.

**Mode IV:** (a) *Eurycea*, *Gyrinophilus*,  
*Pseudotriton*, (b) *Stereochilus*,  
*Typhlotriton* (figs. 6, 15, 16, 20, 22, 23)

#### Behavioral and ecological correlates

These five genera are characteristically found in aquatic or semiaquatic situations. All are found principally in southeastern to south-central United States. *Gyrinophilus* is a large and relatively voracious genus, known to feed on other salamanders. Its primary food consists of arthropods, as does that of the other genera. Adult *Typhlotriton* are restricted to caves in the Ozark highlands of south central United States. While it and *Stereochilus* have incompletely freed tongues, they rely heavily on tongue projection to capture prey, as do the other three genera. All species of these genera have an aquatic larval stage of considerable duration.

#### Morphological features

The genera of group (a) have a small pad, free all around (fig. 12) with a small posterior flap. The genera of group (b) have a small pad that is loosely attached at the front.

In Mode IV, CBII is relatively shorter and EB relatively longer than in the previous modes (fig. 6). The BB is spatulate. The BB shaft, CBII, and EB are of approximately equal diameters. CBI has a greater cross section diameter than CBII, and is relatively flattened anteriorly. There is no anterior projection of BB, but it is usually replaced by a lingual cartilage. The radii show a distinct joint with BB, and they are typically broad-based, tapering toward the tip. The glossal ligament runs from the lingual cartilage to the distal tips of CBI. A mineralized urohyal is present. Calcified cartilage may be present in BB and CBI.

The RCP is folded anteriorly, rising dorsally and extending posteriorly to its insertion in the *Sehnenplatte*, well above the dorsal surface of BB (fig. 21). The intraglossus extends anteroventrally from the *Sehnenplatte* to insert on the lingual cartilage. The interradialis is absent. The genioglossus is absent (a) or vestigial (b). Both circumglossus and basiradialis are present. A distinct supraperduncularis and both an anterior and posterior hyoglossus are present. The lateral slip of RCS and the omohyoideus are well developed, and the hebstoeypsiloideus attaches to the urohyal.

Generic groups (a) and (b) differ in that (b) has an anterior connective tissue connection

between the floor of the mouth and the tongue pad, and is not truly "free tongued."

#### Proposed mechanical events

The projection mechanics and force transmission pattern in Mode IV are similar to those in Modes I, II, and III. However, in group (a) the tongue is free of attachments to the buccal floor and can be projected for large distances. In *Typhlotriton* and *Stereochilus* only small amounts of tissue connect the tongue to the buccal floor. This restricts projection only slightly. The hyoid in all genera of this mode is folded through most of the projection sequence, probably before the pad passes the margin of the jaw. When folded, CBI is in line with EB (figs. 15, 16b). Projection for a relatively great distance is a function of the elongate EB's and rapid folding of the shortened CB's.

During the folding sequence the lingual cartilage is rotated around the end of BB from its dorsal resting position to a location ventral to the BB tip (fig. 22). During folding of the hyoid, the glossal ligament is drawn posteriorly as CBI rotates about its joint with BB. This pulls the cartilage to its new position. The three muscles which insert on the cartilage—the basiradialis, anterior hyoglossus, and intraglossus—are thus in a position of maximal mechanical advantage. The anterior hyoglossus pulls the anterior portion of the pad down (a function of the genioglossus in Modes I-III). The basiradialis pulls the radii down and forward, thus spreading the pad, and the intraglossus pulls the posterior portion of the pad forward to complete the pad flip.

**Retraction of the tongue** is accomplished by contraction of RCP, RCS (lateral slip), and omohyoideus. The slightly folded nature of the muscles when at rest suggests a storage specialization for the long muscle. The increased length allows increased projection distance. With contraction of the RCP, the *Sehnenplatte* is pulled down and back to its resting position. The posteriorly directed force generated on the lingual cartilage through the intraglossus muscle by this event, coupled with the relaxation of the tension in the glossal ligament as the hyoid unfolds, restores the anterior portion of the pad to the rest position. Restoration of the pad to the resting position is an automatic function of the general retraction musculature, as in Modes II and III.

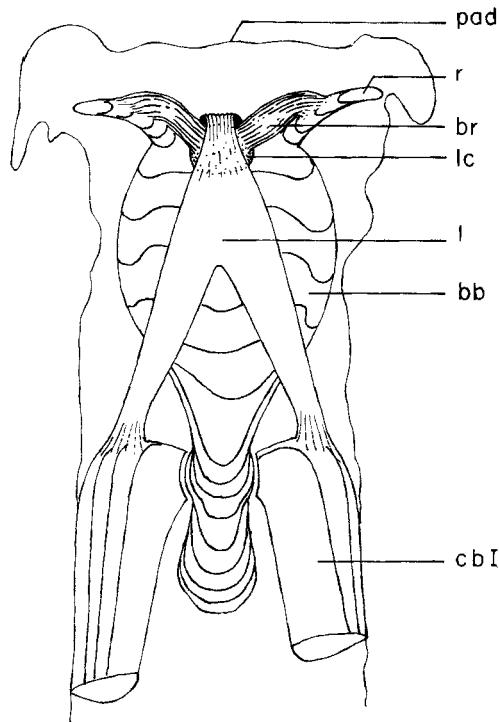


Fig. 22 Schematic reconstruction of the tip of the projected tongue in *Eurycea bislineata*, ventral view. The glossal ligament has pulled the lingual cartilage from the dorsal to the ventral side of the BB. The basiradialis muscles pass from the lingual cartilage to the radii. The radii point downward and support the pad. The glossal ligament has become taut as a result of folding of CBI during protraction.

#### Mode V: Hemidactylum (figs. 7, 12, 21a)

##### Behavioral and ecological correlates

*Hemidactylum* includes one small species of wooded areas bordering shallow ponds and, frequently, sphagnum bogs in eastern North America. Extensive use of the tongue is made to obtain small arthropod prey. There is a relatively short-lived larval state.

##### Morphological features

The pad of *Hemidactylum* (fig. 12) is small and similar to that in *Eurycea*. There is a narrow attachment at the front. The posterior flap is relatively small.

Hyoid proportions and BB shape are similar to Mode IV. There is a pair of small bilateral projections on the tip of the BB. The radii, ceratohyal, and pattern of hyoid mineralization are as in Mode IV. The glossal ligament connects the small BB projections to the distal tips of CBI. The origin of SARI and the

*suprapeduncularis*, *basiradialis*, *circumglossus*, *RCS*, *omohyoideus*, and *hebosteoypsilosoides* are as in Mode IV. The RCP is less folded than in Mode IV, and the *intraglossus* inserts into the BB projections (fig. 21a). Both the *interradialis* and *genioglossus* are present. Only a posterior *hyoglossus* is present.

#### Proposed mechanical events

The projection mechanics and force transmission pattern in Mode V are the same as in the modes discussed so far. The dynamics of folding the hyoid are like those in Mode IV, since the skeletal proportions are similar.

Both a *genioglossus* muscle and rudimentary structures that represent a projection of the BB are present. Consequently, pad flipping is similar to that in Modes II and III rather than IV. The *genioglossus* is specialized in a manner very similar to that in Mode III, and presumably for the same reasons. Thus, the *genioglossus*, acting with the *circumglossus*, pulls the anterior portion of the tongue pad down. The elongate *genioglossus* facilitates the extended projection seen in this group with attached tongues. The small BB projections are pulled ventrally by the *glossal ligament*, and the *basiradialis* contracts from this new position, pulling the radii down and forward, and simultaneously spreading the pad. The *intraglossus* completes the flip as before.

The *interradialis* muscle is present in Mode V. Its function is not clear, but may be similar to that in Mode VI (see below).

Retraction of the tongue and restoration of the pad to the resting position are accomplished as in Mode II.

**Mode VI:** *Bolitoglossa*, *Chiropterotriton*, *Lineatriton*, *Oedipina*, *Parvimolge*, *Pseudoeurycea*, *Thorius* (figs. 2, 6, 11, 13, 15, 16, 21, 23)

#### Behavioral and ecological correlates

These seven genera include all of the plethodontid species that occur in the New World tropics. All are fundamentally terrestrial in habits, but a great diversity of habitats and microhabitats is utilized (Wake and Lynch, '76). Development is direct in all genera. As in other plethodontids, arthropods are the principal prey. Tongue projection is the exclusive feeding mechanism, and jaws are relatively poorly developed. The tongue is free in front and is capable of extensive and very rapid projection.

#### Morphological features

Tongue pads are relatively small, and lack anterior attachments. They have a circular to oval form, with little development of a posterior flap (figs. 2, 13).

The hyobranchial apparatus is greatly elongated, and the proportions of the elements are unequal. The EB's are very long, and CBII very short. The BB has slight lateral flanges. The BB shaft, CBII, and EB are of approximately equal diameter (figs. 3, 6). CBII is larger in diameter than CBI (fig. 2b). A lingual cartilage is usually present, but a connective tissue mass may take its place. The radii show no discrete joint with BB. The *glossal ligament* runs from the lingual cartilage or its equivalent to the distal tips of CBI (fig. 21b). There is no *urohyal*. Mineralization may be found in BB, CBII, and EB.

The origin of SARI is specialized to form an elaborate muscular sheath around the projected hyoid elements. The RCP is folded as in Mode IV. The *intraglossus* connects the *Sehnenplatte* to the lingual cartilage or its connective tissue equivalent. An *interradialis* and *suprapeduncularis* are present. The *genioglossus*, *basiradialis*, *circumglossus* and *omohyoideus* are absent. All genera except *Thorius* lack a *basiradialis*, and the muscle is minute in that genus. Both *hyoglossus* muscles are present. The lateral slip of the RCS is absent, and the main part of this muscle joins the *geniohyoideus medialis*. The *hebosteoypsilosoides* joins the complex muscular sheath of the tongue.

#### Proposed mechanical events

Upon contraction of the SARI muscles, the force generated on the EB's is transferred to BB by the CBII. Thus, during forward movement of the hyoid, CBII is the element fitted to the tractrix formed by the SARI sheath. CBI is very attenuate and conforms to the curve of the tractiform projection track (fig. 6). CBII is thus in line with EB, as compared with CBI in all previous modes (figs. 15, 16). Projection in this mode is great and the hyoid is completely folded before the pad leaves the margin of the jaw (fig. 1). In *Thorius* the hyoid is entirely linear (see above; fig. 15). Support for this hypothesis comes from the fact that CBII is the stouter CB and often shows partial calcification, thus indicating compressive stress (Uzzell, '61; Wake, '66). Graphic reconstructions of projected tongues indicate that CBII is in the same plane as EB (figs. 11, 15,

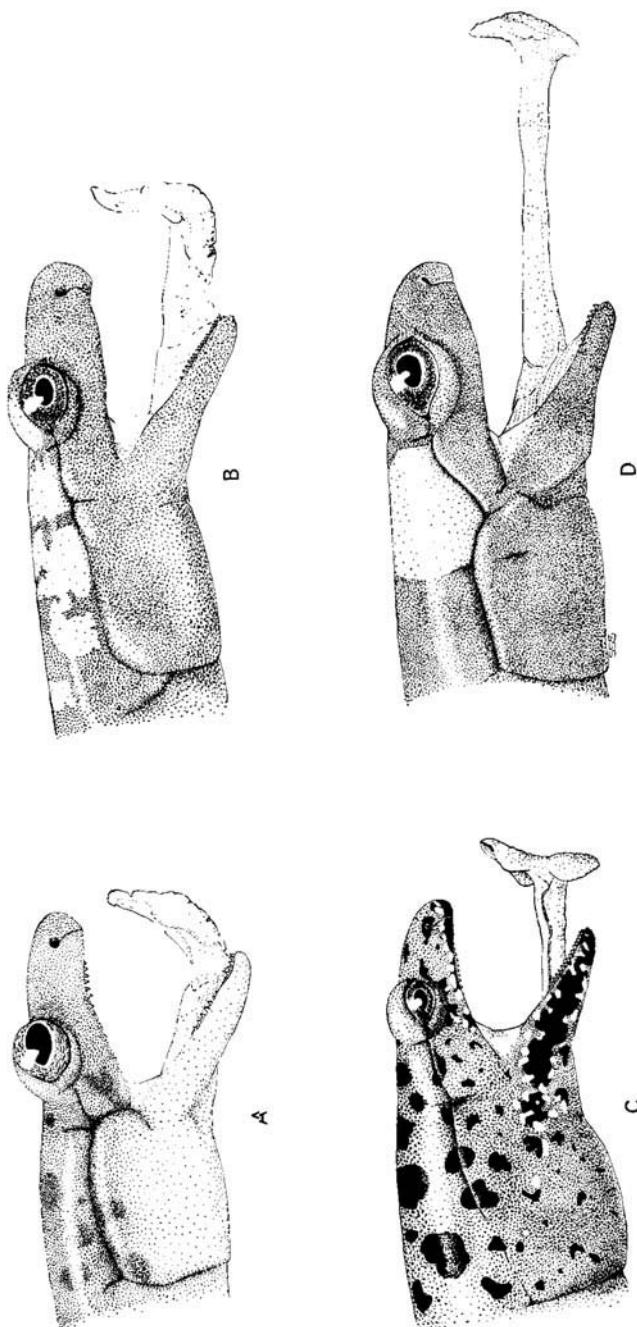


Fig. 23 Heads of salamanders during tongue projection. (A) *Desmognathus monticola*, (B) *Ensatina escholtzii*, (C) *Pseudoeurycea bellii*. These drawings are based on preserved specimens, living specimens, photographs and motion pictures. They depict the tongue during projection, but not yet fully projected. The heads surely raise more than is illustrated, but the degree of mouth opening has been impossible to determine precisely. The mouth is opened maximally both by head elevation and jaw lowering just as tongue retraction begins (cf. fig. 1 in Lombard and Wake, '76).

16). Finally, behavioral observation indicates a remarkable ability to project the tongue.

As the tongue is projected it passes through an extremely well developed muscular sheath at the level of the anterior tips of the ceratohyals (fig. 19). Extreme development of the sheath is achieved in *Oedipina*. Orientation of this sheath by movement of the ceratohyals allows the animal to direct projection of the tongue largely independent of head position.

As the hyoid is folded the lingual cartilage or its connective tissue equivalent is rotated about the tip of BB from dorsal to ventral, as in Mode IV. This is accomplished by the glossal ligament as it is pulled posteriorly by the folding CBI's.

With this new orientation of its origin the anterior hyoglossus pulls the anterior part of the pad ventrally (fig. 11). Similarly the intraglossus pulls the posterior portion of the pad forward, completing the pad flip. The tongue pads in this mode are relatively small (figs. 2b, 13). The radii are not jointed as in previous modes and there are no basiradialis muscles in most species. Our hypothesis is that these morphological attributes are related. There is no need to spread and support the small pad in this mode, and the structural correlates of this action are lost.

In some members of this mode the connective tissue of the glossal ligament inserts on the radii as well as to the lingual cartilage. It is possible that in these animals the ligament pulls the radii down as it rotates the lingual cartilage. This condition was noted in *Thorius* and *Oedipina*. It may be present in other animals in Mode VI but was not clearly evident in our material.

Retraction of the tongue to the mouth is accomplished by the RCP alone, for the RCS (lateral slip)-omohyoideus complex is not present. The long length of this muscle, the excess of which is coiled at rest, permits retention of the retraction function in the behavioral extreme characteristic of this mode.

*Thorius*, which is special in many ways, has an unusual arrangement of the RCP. The muscle terminates in a connective tissue net about two-thirds the distance along the BB. This connective tissue forms a kind of tendon which passes along the BB and, at the anterior end of BB, extends dorsally and then immediately posteriorly into the pad. The tendon becomes continuous with the *Sehnenplatte*.

The arrangement conforms to the folded pattern, discussed above, even though it is the tendon, and not the muscle, that is folded. Functionally, the systems are identical.

As the RCP contracts, it pulls the *Sehnenplatte* (into which it inserts) posteriorly through a hoop formed by the surface of the basibranchial, the radii and the interradialis muscle. This gives the pad surface a conical form. The prey item is thus surrounded by parts of the tongue pad as it is retracted to the mouth. This method of molding the tongue is viewed as a necessary correlate of the relatively small pad present in this group, which moves at high speed over relatively great distances.

The pad is restored to the resting position as the ceratobrachials are spread, thus allowing the lingual cartilage to flip back to the dorsum of BB.

*Mode VII: Hydromantes* (figs. 9, 13, 21; see also Lombard and Wake, '76: fig. 1)

#### Behavioral and ecological correlates

The genus *Hydromantes* includes two species of European salamanders and three in California. The species are found in areas where underground retreats can be utilized; several species are commonly found in caves. It has long been known that *Hydromantes* uses its long, highly projectile tongue to capture its prey, which are always obtained in terrestrial situations. All species have direct development of eggs laid in terrestrial sites.

#### Morphological features

*Hydromantes* has a larger pad than is found in Mode VI. There is a distinct posterior flap. In addition, a bulge at the anterior margin of the pad marks the tip of the relatively long BB characteristic of this mode (fig. 13).

Mode VII shows extreme development of the hyoid length assymetry noted in Modes IV and VI. Mode VII also differs from Mode VI in having no lingual cartilage, but instead having a small projection of the BB. There are no radii and no urohyal. The interradialis muscle originates from the distal sides of BB. There is no geniglossus, anterior hyoglossus, or circumglossus. The suprapeduncularis is very well developed. There is no lateral slip of RCS or omohyoideus. The hebstoeypsiloideus and RCS (fig. 9) insert into the complex muscular sheath which has been described in Mode VI.

### Proposed mechanical events

The dynamics of projection in Mode VII are equivalent to those in Mode VI. There is no free lingual cartilage as in Mode VI, but the flexible anterior projection of BB serves an equivalent function. This projection has connections similar to a lingual cartilage (glossal ligament, intraglossus). When this cartilage is pulled ventrally by the glossal ligament during folding, the anterior part of the tongue pad is pulled to the vertical position. The intraglossus pulls the posterior part of the pad forward to complete the pad flip. The relation of the pad to the BB tip permits this unique anterior pad flipping mechanism (no muscular effort). At rest the tip of BB is in the extreme anterior part of the pad (fig. 21c).

Retraction of the tongue to the mouth is accomplished by the RCP as in Mode VI. The *Sehnenplatte* is pulled through the hoop formed by the interradialis as in Mode VI. The *Sehnenplatte* is connected to the BB tip by the intraglossus to couple the RCP to the skeleton. A photograph of the fully projected tongue in *Hydromantes* at the start of the retraction is found in Lombard and Wake ('76).

### Mode VIII: Batrachoseps (figs. 7, 11, 13, 21)

#### Behavioral and ecological correlates

*Batrachoseps* is a diverse genus including at least eight species with a distribution centered in California. The strictly terrestrial species all have direct development of eggs. These slender salamanders have projectile tongues which are used to capture food, principally small arthropods.

#### Morphological features

The tongue pad in this mode is very similar to that in Mode VI, but a narrow, loose anterior attachment is present. The posterior flap is relatively small (fig. 13).

Mode VIII differs from Mode VI in that the tongue is attached and genioglossus, lateral slips of RCS, and omohyoideus muscles are present. There is no circumglossus. Only the posterior hyoglossus is present. The interradialis is present, but the basiradialis is reduced to a few fibers. The genioglossus muscles attach proximally on the rami of the mandibles, near the articular joint, and both the muscle and its sheath are pleated in the resting condition. No lingual cartilage is evident. There is no urohyal. The hyoid assymmetry is

less pronounced than in the members of Mode VI and Mode VII. There is no anterior hyoglossus.

### Proposed mechanical events

The dynamics of projection in Mode VIII are generally equivalent to those in Mode VI. However, a genioglossus is present, so flipping the tongue pad to the vertical position is achieved as in Modes II, III, and V. The genioglossus pulls the anterior portion of the pad ventrally, and the intraglossus pulls the posterior portion forward. The genioglossus can perform this function because of excessive length (fig. 7) and unique orientation. The pad develops a cone shape during restoration as in Modes VI and VIII.

Retraction of the tongue is accomplished by RCP and the lateral slip of RCS-omohyoideus complex. These muscles are of excessive length at rest, and this extra length is stored by pleating within an enveloping connective tissue sheath, in contrast to the coiling seen in Modes VI and VII.

### CONCLUSIONS

Salamanders are a conservative group with an ancient heritage. To a surprising degree generalized structure is present even in the most derived family, the Plethodontidae. Yet, within this single family a great deal of differentiation has occurred in the feeding system of different species. Use of our general model has enabled us to analyze this diversity in terms of its probable biomechanical significance. We now can recognize eight discrete modes in terms of biomechanics. These conform to a large degree with current views of phylogeny, and this gives us confidence that our approach is "robust." For example, the most generalized tongue function is found in the genera of Mode I, which comprise the Subfamily Desmognathinae, a group thought to be derived early in the history of the family. While this group has a generalized tongue, it has highly specialized jaw mechanics (Wake, '66; Hinderstein, '71). All of the specialized tongue projection systems occur in the Subfamily Plethodontinae, a group that includes both generalized and the most specialized and derived plethodontids. Modes II and III are found in genera of the Tribe Plethodontini, Modes IV and V in the Hemidactyliini, and Modes VI, VII, and VIII in the three supergenera of the Tribe Bolitoglossini.

Specializations for tongue projection and features associated with it (distance, speed, directional versatility) have involved three very distinct (Modes IV, VI, VII) complexes of muscles, cartilages and connective tissue. In addition, Modes III, V, and VIII show strong and unique tendencies in the same direction of tongue specialization. Clearly specialization for tongue projection in this family has been a dominant theme in its evolution. Species comprising the three most specialized modes account for about two-thirds of living urodele species.

In other families of salamanders there are also tendencies in the direction of freeing the tongue for projection. For example, two distinct patterns of tongue projection have appeared in the family Salamandridae (Özeti and Wake, '69). In neither instance (*Chioglossa*, *Salamandrina*), however, is there as much specialization for projection as is seen in the three most specialized modes of plethodontids; rather, both genera use mainly pad flipping.

Perhaps what is most important in the evolution of tongue projection specializations is the nature of the constraints within which they evolve. Plethodontids, with the most specialized projection systems, are lungless. Possibly the role of the hyobranchial apparatus in buccal pumping imposes constraints on specialization in groups with lungs. It may be significant that both *Chioglossa* and *Salamandrina* have greatly reduced lungs, and they have the most specialized tongues among the salamandrids.

Another constraint is the presence of an aquatic larval stage in many salamanders. The hyobranchial apparatus has many functions in larvae, including feeding and respiration. The plethodontids with the most extremely specialized tongues (Modes VI and VII) lack larval stages. Mode IV species, on the other hand, also have highly projectile tongues but have larval stages. It is appropriate to examine these three modes in more detail to determine what role is played by the system of constraints characteristic of the species involved.

Species with generalized tongues (Modes I, II) use them in a variety of aquatic and terrestrial sites, depending on the particular species under consideration, but tongue projection is slight. The pads are large and the elements which contribute most to increased

distance of projection (EB) are short. The anterior attachment of the pad is strong, and acts as a pad rotator.

Species with Modes III, V, and VIII all show derived features which are best interpreted as specializations associated with increased tongue projection. The pads are relatively small, their anterior attachment is "loosened," and the cartilages of the tongue tip are modified in ways that can be interpreted in terms of biomechanical advantage, in comparison with the more generalized modes. Yet, each of these three modes is uniquely specialized, and differs in important ways from the three most specialized groups. Adults of all genera feed away from the water, and *Ensatina* and *Batrachoseps* are strictly terrestrial.

The three most specialized modes include genera with tongues that lack anterior muscular attachment of the tongue pad, and usually lack all anterior attachment. The pads are small, and the cartilages and muscles structured in ways that are interpretable in terms of biomechanical advantage for projection. The genera of Mode IV have aquatic larvae and are at least semiaquatic as adults, while those of Modes VI and VII lack larvae and are strictly terrestrial throughout life. The skeleton of Modes VI and VII are structured differently from those of Mode IV, which has a skeleton that is relatively little derived in comparison with Modes I and II (fig. 6). In generalized salamanders CBI is large and stouter than CBII (Özeti and Wake, '69; Krogh and Tanner '72). It is the principal element in transmission of projectile force from EB to BB. In generalized salamanders the projection distances are thought to be so short that relatively little folding of the hyobranchial apparatus occurs. In such a situation little movement of the force transmitting element along the tractrix occurs (fig. 17). As the EB lengthens and projection distance increases, movement along the tractrix assumes increasingly great biomechanical significance, for the hyobranchial apparatus must fold. As we have shown, either CBI or CBII can "ride" the tractrix. We have reported (Lombard and Wake, '76) that in *Eurycea* CBI and EB are coplanar during projection, while in *Pseudoeurycea* CBII and EB are coplanar during projection. We now know that the first condition is characteristic of the projection patterns of species in Modes I, II, III, IV, and V, while the second is characteris-

tic of species in Modes VI, VII, and VIII (figs. 15-17). This means that CBI moves along the tractrix in the most generalized species as well as in one group of specialized tongue projectors, but that CBII moves along the tractrix in different groups of tongue projection specialists. These are, in fact, the two possible options that could be selected for extremes of projection. We have shown earlier that arcs of rotation for the CB-EB joint during folding of the hyobranchial apparatus will be determined by which CB is coplanar with BB (Lombard and Wake, '76: fig. 6). These folding patterns have important implications for the degree of specialization that can occur. Apparently the options represent ancient adaptive "choices," and we believe that once specialization proceeds to a certain, undetermined degree, no switching to the other projection system is possible. We suggest that these options were exercised very early in the history of the lineages which show extreme tongue projection. Mode IV simply retained the generalized option and specialization has been constrained as a result. Possibly the fact that this group has retained aquatic larvae was an important factor in retention of this option. The ceratobranchials play important functional roles in larvae and CBI is larger and has more generalized functions than does CBII. At metamorphosis EB is formed essentially *de novo*, but CBI and CBII undergo only relatively minor adjustment and remodeling (Smith, '20). It seems likely that important larval functions are simply slightly reorganized in the metamorphosed animals, and it is thus not surprising that the first option was retained. Presumably the ancestor of Modes VI, VII, and VIII (collectively the Tribe Bolitoglossini) had already lost the larval stage and adopted direct terrestrial development before any significant degree of tongue specialization occurred (Wake, '66). Mode VIII, which still retains an anterior attachment and a genioglossus muscle, clearly has adopted the second option of folding patterns, and this suggests that the option was adopted early in the history of the bolitoglossines, before much tongue specialization had occurred. Even *Batrachoseps* (Mode VIII) is rather highly specialized in terms of tongue projection abilities, and it is unlikely that we will ever know the matrix in which the second option was first adopted. We believe that the second option is the more suitable for extreme

tongue projection specialization, on biomechanical grounds. So long as CBI is the principal force-transmitting element it must remain relatively stout. Because of its placement during projection, against the sides of BB, the projectile must be relatively stout. Further, shortening of the CBI will have only a slight, if any, effect on its movement along the tractrix. We have shown that both of these features are important in speed of tongue projection.

In contrast, when CBII is the principal force-transmitting member the projectile can be far more compact, and, on strictly theoretical grounds, more efficient. CBII abuts directly against the posterior end of BB and so long as the two elements are coplanar, efficiency of force transmission should be maximal. Further, this option permits packaging in a highly efficient manner. Note that in species of Mode VI and VII the epibranchials are longer and the ceratobranchials shorter relative to BB length than in species of Mode IV (figs. 5, 6, 15, 17). Further, CBI is much smaller in Modes VI and VII than in Mode IV, and typically its attachment to BB is relatively more posterior. This means that the projectile is slimmer, and that it folds more rapidly, thus gaining maximal advantage of the biomechanical attributes of the tractrix. CBI in Modes VI and VII has a shape at rest that conforms to the outline of the tractrix. In these modes a projection cylinder is very well developed. This cylinder has the shape of a three-dimensional expansion of a tractrix (technically known as a "bugle body"), and in cross-section it appears circular (figs. 9, 24, 25). The hyobranchial apparatus in this structure lies in a position ideal for instantaneous folding and projection. This is not possible in Mode IV, even though it is remarkably specialized in its own right.

The extremes that are possible in exercise of the second option can be illustrated by two examples. Since force transmission is transferred from CBI to CBII and because the lateral slip of RCS is lost, the only remaining function of CBI in Modes VI and VII is associated with flipping the tongue pad. Theoretically the element could be lost completely and be replaced by a glossal ligament that extended to the EB. In fact, this has very nearly been accomplished in *Thorius* and some other genera of Mode VI, in which CBI has lost any articulation with BB. The advantage

of this situation is that folding of the hyobranchial apparatus can now occur in a single plane, and the projected bundle is concomitantly reduced in size (fig. 15). The other example is the unique pad-flipping arrangement which has evolved in *Hydromantes* (Mode VII). This new arrangement has permitted shortening of CBI and associated posterior movement of the attachment to BB. This, again, has implications associated with rapid folding and relative reduction in movement out of one plane during folding.

In our verbal explanation of our model we presented a series of nine statements concerning tongue action in plethodontids and intimated that these occurred in the sequence of presentation. In particular, we argued that SARI first contracted to protract the tongue, and that RCP later contracted to retract the tongue. In fact we know now that contraction of these muscles is simultaneous (Thexton et al., '77). Nevertheless, their mechanical expression is determined by the geometry of the muscles and as a result of biomechanical factors. The importance of this discovery is that it heightens our interest in detailed biomechanical considerations from our general model, for it shows the significance of particular form in analysis of function. The hyobranchial apparatus is, in effect, "cocked," so that triggering the muscles results in instantaneous forward motion because of the circular arrangement of the posterior fibers and taut arrangement of the anterior fibers of SARI. On the other hand, the lax RCP does not become effective immediately, and when it does it is at first unable to counteract the forward moving projectile. When RCP gains mechanical advantage over SARI, the tongue returns to the mouth even though both muscles continue to "fire." As we gain further physiological information it will be increasingly important to understand the detailed structure of the tongue, so that biomechanical interpretation of the physiological result can be accomplished.

At a more general level, we hope that we have demonstrated the utility of an approach to comparative morphology. By proceeding from theory to model to comparative analysis we have shown that it is possible to make predictions and test hypotheses, rather than simply to seek order and arrangement. Our general model forces into consideration data that we might otherwise consider trivial. The result of our work to date has been formula-

tion of theory and production of a model (Lombard and Wake, '76), and formulation of predictions which we have explored by comparative methods (present paper). In a future paper we will explore the uses of the data we have generated for analysis of the phylogenetic history of the family.

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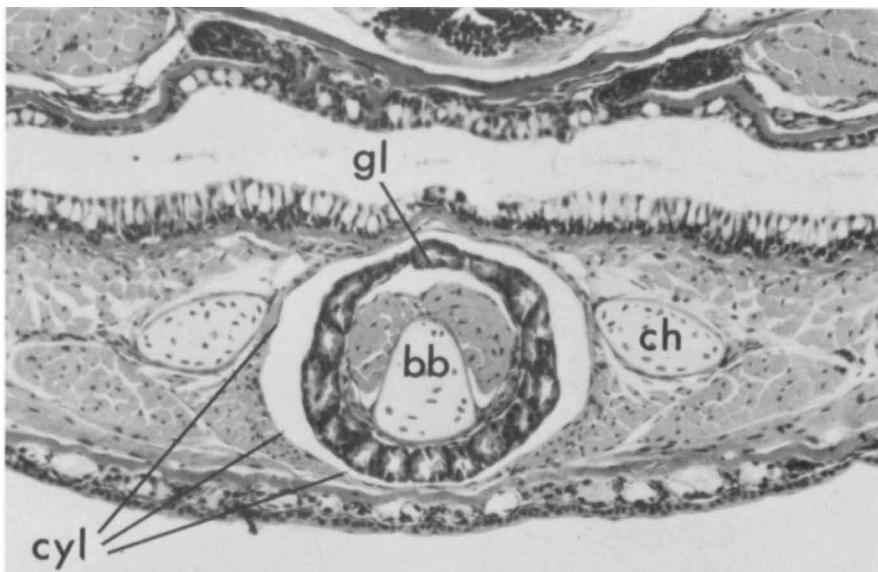
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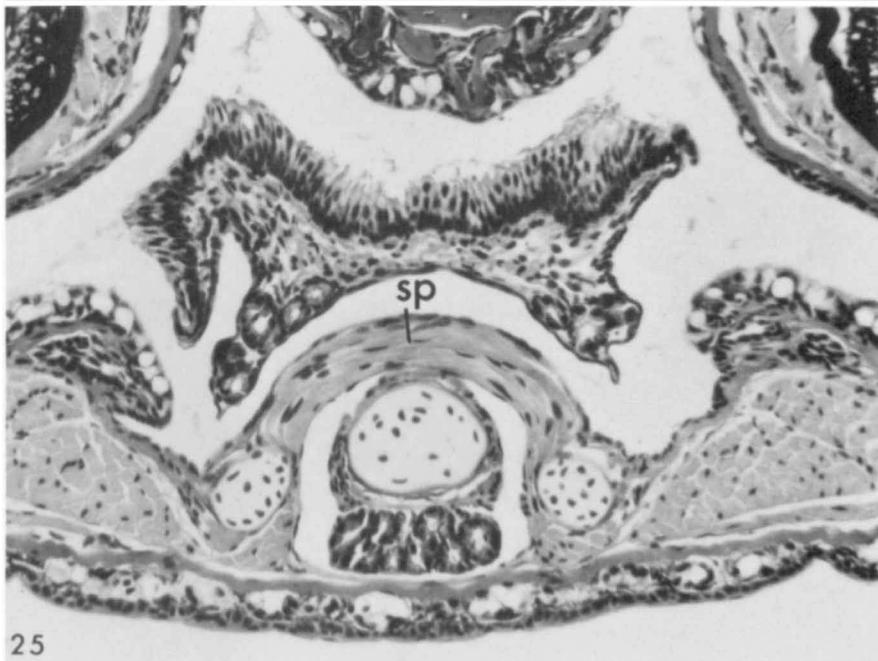
PLATE 1

EXPLANATION OF FIGURES

- 24 Transverse section through the floor of the mouth of a 20.4-mm snout-vent length *Thorius dubitus*. There has been some shrinkage of this paraffin-embedded specimen, which accentuates the tongue stalk lying within the cylinder formed at this level by the floor of the mouth, the gular skin, the ceratohyals, and SARI muscles. Note especially BB and two RCP muscles that are surrounded by a band of glandular tissue. This glandular tissue expands within the cylinder and may act as a lubricant. The designated section of the cylinder is also the morphological part of the tractrix, described in Lombard and Wake, '76. Compare with figures 18 and 19.  $\times 97$ .
- 25 Same specimen as figure 24, but much farther anterior. The posterior part of the tongue pad appears in this section. At this level the somewhat flattened ceratohyals of figure 24 have become rounded. The suprapeduncularis is the dominant element of the bugle body, the three dimensional expansion of the tractrix through which the tongue stalk will move on projection. No muscle is seen surrounding BB at this level in *Thorius*, in which the tendinous material lying between BB and the glandular tissue extends from the anterior end of RCP into the tongue pad. Compare with figures 18 and 19.  $\times 125$ .



24



25