

# Tongue Evolution in the Lungless Salamanders, Family Plethodontidae

## I. INTRODUCTION, THEORY AND A GENERAL MODEL OF DYNAMICS

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**ABSTRACT** Plethodontid salamanders capture prey by projecting the tongue from the mouth. An analysis of theoretical mechanics of the hyobranchial skeleton is used to formulate a working hypothesis of tongue movements. Predictions that the skeletal elements of the tongue are included in the projectile and that the hyobranchial skeleton is folded during projection are central to the analysis. When decapitated in a particular way, salamanders project the tongue, and it is not retracted. When these heads are fixed and sectioned, examination confirms the predictions. In turn, these observations are used to refine the working hypothesis and to generate a general model of tongue dynamics for plethodontids. Muscles performing the major roles of projection (subarcualis rectus I) and retraction (rectus cervicis profundus) are identified. The skeleton is folded passively along a morphological track having the form of a tractrix. Predictions concerning the shape of the track and the exact configuration of the folded skeleton are confirmed by study of sectioned material. The skeleton unfolds along the track during retraction and is spread into the resting state. The model developed herein will be used as a basis for predictions concerning selection patterns in the family and for analytical purposes in comparative and evolutionary studies.

Terrestrial species of salamanders or urodeles (Order Caudata) are generalized tetrapods that share many common structural features. Yet, among the more than 250 species of the four families (Hynobiidae, Ambystomatidae, Plethodontidae, Salamandridae) that are generally considered to be "terrestrial," remarkable differences are found in behavior, ecology and general way of life. The morphological manifestations of this diversity are most clearly evident in the feeding system.

In nature terrestrial salamanders eat living animals only, principally arthropods. General aspects of ingestion mechanisms have been known for some time, and elaborate descriptions of head morphology are available for many species (e.g., Drüner, '01, '04). Physiological and behavioral studies of feeding (especially the pioneering efforts of Matthes, '34) have tended to emphasize aquatic stages, or to be con-

cerned more with sensory physiology than with jaw and tongue use. Investigations have become more broadly comparative in recent years, but the main emphasis has been on systematics rather than function (Piatt, '35; Tanner, '52; Krogh and Tanner, '72). Interest in functional morphology is only now developing (Regal, '66; Özeti and Wake, '69; Severtsov, '72).

This is the first of three papers dealing with the feeding system of plethodontid salamanders, the largest and most diverse group of urodeles. In this series of papers we limit our analysis to a consideration of feeding in the terrestrial adult. We are interested in the mechanisms associated with seizing and ingesting prey, and the way in which these mechanisms have evolved during the adaptive radiation of the family.

One of the most characteristic features of plethodontid salamanders is their lung-

lessness. The ancestral stock of the family is thought to have inhabited a cool, mountain stream habitat where the buoyancy produced by lungs would be disadvantageous. As all salamanders rely on cutaneous respiration to a large extent, and as the minimum conditions for effective cutaneous respiration were present, it has been suggested that sustained selection led to loss of lungs (Wilder and Dunn, '20). Support for this view includes the fact that many primitive plethodontids live in mountain stream habitats. Further, lung reduction or loss has occurred in certain members of three different families of salamanders that inhabit roughly similar ecological situations: *Rhyacotriton* (Ambystomatidae), *Salamandrina*, *Chioglossa* and *Pachytriton* (Salamandridae) and *Onychodactylus* (Hynobiidae).

Loss of pulmonary respiration has been the most significant factor in the chain of events leading to the specialized method of feeding to be described in this series of papers. In primitive salamanders, and in frogs, the cartilages of the hyobranchial apparatus and their associated musculature, lying predominately ventral to the tongue, are the dominant effectors of pulmonary ventilation (DeJongh and Gans, '69; Severtsov, '72). In lungless forms these elements are a ready source of "raw materials" for a new type of feeding mechanism, associated principally with movement of the tongue out of the mouth.

The animals that we study are small, and the speed of the movements to be analyzed is extremely fast (the feeding sequence may take only 50 msec). This makes direct experimental procedures difficult. We have therefore chosen to use a modeling approach in which we generate specific hypotheses for various experimental and comparative tests.

In this paper we derive and formalize a working hypothesis concerning the dynamics of tongue function in a generalized and unspecified plethodontid. This paper is written in such a way as to expose directly our methodological approach. Starting from theoretical considerations and a few stated assumptions, we first develop a working hypothesis concerning tongue dynamics. Next, where possible, simple tests of various elements of this hypothesis

are performed. As a result of this procedure a model of general tongue dynamics is developed.

We believe that formalization of the steps taken to develop this model leads to the inclusion of non-obvious points of considerable importance which have been overlooked or misinterpreted in the past, and which are unlikely to be discovered by experimental procedures in the future without the general analytical framework provided by the model. In a subsequent pair of papers we will use the hypothetical model generated here as a point of departure for more detailed studies of function and for comparative and evolutionary analysis. Thus, the model developed herein is an essential element of the next two papers and the three papers will form a methodological as well as an analytical treatment.

#### *The feeding apparatus in plethodontid salamanders*

Feeding mechanisms in salamanders involve the combined use of jaws and tongues. In aquatic situations the jaws form circular mouth openings that are used in suction feeding (Özeti and Wake, '69). Some aquatic species have powerful jaws and strong teeth, but they are exceptional (e.g., *Amphiuma*; family Amphiumidae). In species that feed in terrestrial situations the principal prey capturing device is assumed to be the tongue.

The feeding mechanisms of plethodontids have been treated in various degrees of depth by Piatt ('35), Regal ('66) and Wake ('66). The basic method of prey capture is by use of a relatively elaborated tongue. In the most generalized species the tongue pad is a moderately large structure that is richly supplied with mucous glands. It is attached in front and has free lateral and posterior margins. When the hyobranchial apparatus is moved forward, the pad is advanced to or slightly past the anterior margin of the mouth. This movement is frequently accompanied by a forward lunge of the body. Contact of the tongue with the prey and subsequent retraction together with a snapping action of the jaws entraps the prey in the mouth.

In many plethodontid salamanders the tongue pad has either lost the anterior at-

tachment completely or has a rather elastic connection to the lower jaw. The tongue may be extended for relatively great distances from the mouth. It is these species that are of greatest interest in the present work.

In metamorphosed plethodontid salamanders the jaws vary in degree of robustness, but they are invariable in terms of the number and position of bony and muscular components. The premaxillary (paired or single) and maxillary bones form the upper jaw. The dentary is the major element of the lower jaw, with the prearticular and articular located in the posterior portion of each ramus. Jaws are most robust in the genus *Aneides*, a species with exceptionally well developed dentition (Wake, '63, '66) but one which we observe to rely heavily on its tongue for capture of prey. Jaws are most weakly developed in the neotropical species, where there is heavy reliance on highly projectile tongues. Even within this group there are a few species (members of the genus *Pseudoeurycea*) which have relatively strong jaws and teeth. Members of the subfamily Desmognathinae have jaw mechanics that are highly modified, and they differ sharply from other plethodontids in manner of feeding (Wake, '66; Hinderstein, '71).

In addition to the teeth of the jaws, plethodontids characteristically have vomerine teeth. These are arranged in short rows on the roof of the mouth immediately behind the internal nares, and in primitive species they extend posteriorly along the ventral surface of the parasphenoid bone. In most plethodontids the posterior teeth form distinct, paired patches separated from the vomer proper. Each patch forms a shagreen of minute teeth lying directly above the tongue pad. The patches may bear up to 200 teeth in closely packed rows, and they are most extensive in those species that appear to rely almost exclusively on tongue projection mechanisms for prey capture (Wake, '66; Lawson et al., '71).

#### MATERIALS AND METHODS

A total of 344 specimens, prepared either by clearing and staining (241) or sectioning (73), were used in this study.

In addition, at least one specimen of each plethodontid genus except *Haideotriton* and *Typhlomolge* was dissected. Neither of the two mentioned genera (both having larval feeding mechanisms) are represented in the specially prepared material. A total of 72 species of the remaining 21 plethodontid genera were examined. The specially prepared material includes (number of species, number cleared and stained, number sectioned): *Leurognathus* 1, 2, 2; *Desmognathus* 5, 21, 6; *Phaeognathus* 1, 2, 1; *Gyrinophilus* 1, 4, 2; *Pseudotriton* 1, 3, 2; *Stereochilus* 1, 2, 1; *Eurycea* 5, 49, 5; *Typhlotriton* 1, 8, 2; *Hemidactylum* 1, 3, 4; *Plethodon* 7, 27, 6; *Ensatina* 1, 7, 3; *Aneides* 4, 15, 4; *Hydromantes* 5, 14, 3; *Batrachoseps* 6, 15, 8; *Bolitoglossa* 12, 37, 5; *Oedipina* 4, 12, 2; *Pseudoeurycea* 6, 15, 3; *Chiropterotriton* 4, 12, 4; *Lineatriton* 1, 3, 2; *Thorius* 4, 15, 7; *Parvimolge* 1, 5, 3. All measurements and data are on file.

Cleared and stained specimens were prepared following standard techniques and stored for study in glycerine. Sectioned specimens were either embedded in paraffin or epoxy plastic. In both cases the heads were serially sectioned at thicknesses between 5 and 40  $\mu$ . The specimens routinely were sectioned transversely but many of the genera were also sectioned in the frontal and/or sagittal planes as well. Paraffin material was prepared using standard histological techniques and routinely stained with Van Gieson's stain. Those specimens embedded in epoxy plastic were prepared following the technique devised by Lombard ('71) and stained with hematoxylin and safranin O.

Serial reconstructions of both the skeletal and muscular components of the hyobranchial apparatus were done graphically using a Bausch and Lomb microprojector, following the method of Lombard ('71). Only sections embedded in plastic were used for reconstructions. These materials are nearly free of the distortion artifacts often present in material embedded in paraffin.

Many specimens that were sectioned had been fixed with their tongues partially to completely projected. In order to obtain these important preparations animals were first lightly anesthetized with chloretone. Next, the rectus cervicis profundus muscle

was cut with scissors in the region of the urohyal. The animals were then placed with their venter on a hard surface. A razor blade was then used to sever the head from the body in the region of the anterior trunk vertebrae. This usually caused the tongue to be projected from the mouth. As the *rectus cervicis profundus* had been severed, the tongue remained in a projected state. Fixing, embedding, and sectioning of these specimens were exactly as with more routine preparations.

Linear measurements of in situ skeletal elements of the cleared and stained specimens were made with an ocular micrometer seated in a Wild stereoscopic dissecting microscope. Angular measures between the in situ skeletal elements were made using a goniometer attached to the eyepiece of the microscope. Measurements of CBI, CBII, BB, and EB were made on hyobranchial skeletons that were removed from the cleared and stained specimens. Following extraction, the apparatus was drawn using a camera lucida attached to a Wild compound dissecting scope at magnifications between 10 and 50  $\times$ . The specimens were kept flat for projection and drawing by placing them under a small piece of plate glass on the specimen stage of the microscope. Measurements made directly from the drawings were used to determine proportions of each skeleton. Measurements made on sectioned material were accomplished using an ocular micrometer. All linear measures were made to the nearest 0.01 mm. All angular measures were made to the nearest degree.

## RESULTS

### *Skeletal and muscular structure of the tongue*

Although it has been known that plethodontid salamanders rely mainly on tongue projection to obtain prey, only recently has it been possible to make high speed photographs of the tongue in action (fig. 1). The projectile consists of cartilages as well as muscle, connective tissues, and the moderately complex tongue pad. The skeleton of the tongue develops largely from the skeleton of the hyoid and branchial arches of larvae and is cartilaginous. The

hyoid skeleton has been well described for most plethodontids (Piatt, '35; Tanner, '52; Wake, '66) and its general structure only is reviewed here (fig. 2). A pair of ceratohyals (CH), attached posteriorly by the hyoquadrate ligaments to the suspensoria lie in the floor of the mouth. The ceratohyals do not contact each other nor do they articulate with other elements. The posterior portion of each is cylindrical and hooked, while the anterior portion forms a flattened blade. The cartilages that move out of the mouth with the tongue are articulated to form a single, relatively complex unit. The principal element is the unpaired, median basibranchial (BB). At its anterior end the basibranchial has a projection that may be continuous with the basibranchial or detached and united to it by connective tissue fibers. When detached, the separate portion is called a lingual cartilage (Wake, '66). Also attached to the anterior end of the basibranchial are a pair of radial cartilages. Two pairs of ceratobranchials articulate with the posterior portion of the basibranchial. The first ceratobranchials (CBI) are the longest elements, and they articulate with the basibranchial shortly behind its midpoint. The second ceratobranchials (CBII) articulate with the basibranchial at its posterior end. The first and second ceratobranchial on each side approach each other posteriorly, and together articulate with the epibranchial (EB). The epibranchial is an element of varying length which is tapered from its base, at the articulation with the ceratobranchials, to its posterior tip. The final element of the hyobranchial skeleton is the urohyal (UH, also termed second basibranchial in some works), a bony element which lies at the juncture of the *rectus cervicis superficialis* and *geniohyoideus* muscles. It has no connections to any other elements and is lost in many plethodontid genera (Wake, '66).

The tongue pad is a large element that is supported on the anterior end of the basibranchial. The basibranchial lies in its base and the radial and lingual cartilages extend into the pad. The pad bears a large number of mucous glands, many of which empty into deep crypts on its surface (Seifert, '32). There is a relatively complex intrinsic musculature, most of which takes

## Abbreviations

- BB, Basibranchial  
 CBI, First ceratobranchial  
 CBII, Second ceratobranchial  
 CH, Ceratohyal  
 EB, Epibranchial  
 SARI, Subarcualis rectus I muscle  
 A, Area of hypothetical planar surface  
 F, Force moving hypothetical planar surface  
 L, Separation of two hypothetical surfaces  
 M, Opening of tongue recess  
 Q, Retractive force  
 R, Propelling force  
 S, T, U, Hypothetical forces for folding hyobranchial apparatus  
 W, Hypothetical straight track for folding hyobranchial apparatus  
 X, Hypothetical aperture through which hyobranchial apparatus passes  
 Y, Hypothetical passive device for unfolding hyobranchial apparatus  
 a, b, Ends of rotational arc of joint 3  
 c, d, Ends of alternative rotational arc of joint 3  
 e, f, Orientation points for idealized "average" ceratobranchial  
 a<sub>1</sub>, b<sub>1</sub>, a<sub>2</sub>, b<sub>2</sub>, Alternative positions of basi-branchials and ceratobranchials with different folding positions  
 q, h, i, Alternative vector diagrams at different points on tractrix  
 r, Radius of circle of rotation of hyobranchial elements during folding  
 m, m', Moment arms during folding of hyobranchial apparatus  
 n, n', Moment arms during unfolding of hyobranchial apparatus  
 w, w', Hypothetical compared to real length of CBI.  
 x, y, z, Spatial planes  
 y, y', Axis of projection  
 1, Basibranchial—first ceratobranchial joint  
 2, Basibranchial—second ceratobranchial joint  
 3, Ceratobranchial-epibranchial joint  
 Δ, Field of projection of tongue  
 α, Angle of first ceratobranchial and horizontal  
 γ, Angle between hypothetical passive track for folding hyobranchial apparatus and midline  
 η, Fluid viscosity  
 Θ, Θ', Alternative fields of rotation relating to joint 3.  
 II, Angle between epibranchial and radius of circle of rotation  
 φ, Angle between first and second ceratobranchials

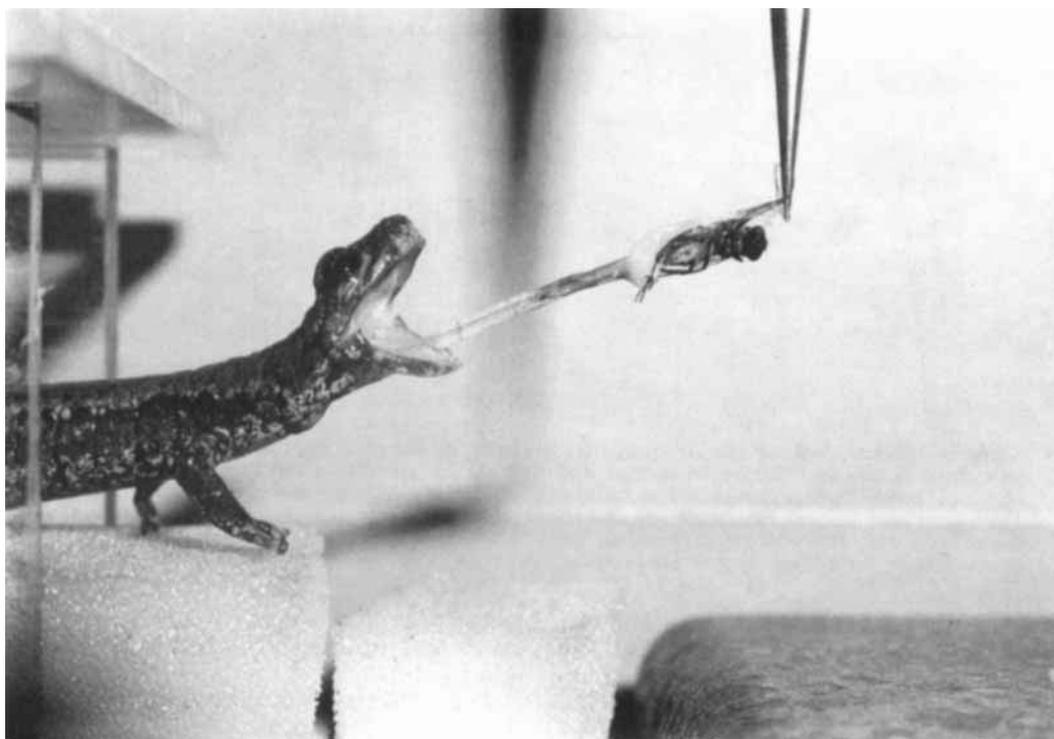


Fig. 1 The tongue in the initial phase of retraction in *Hydromantes italicus*. Photograph by Dr. Gerhard Roth, University of Münster.

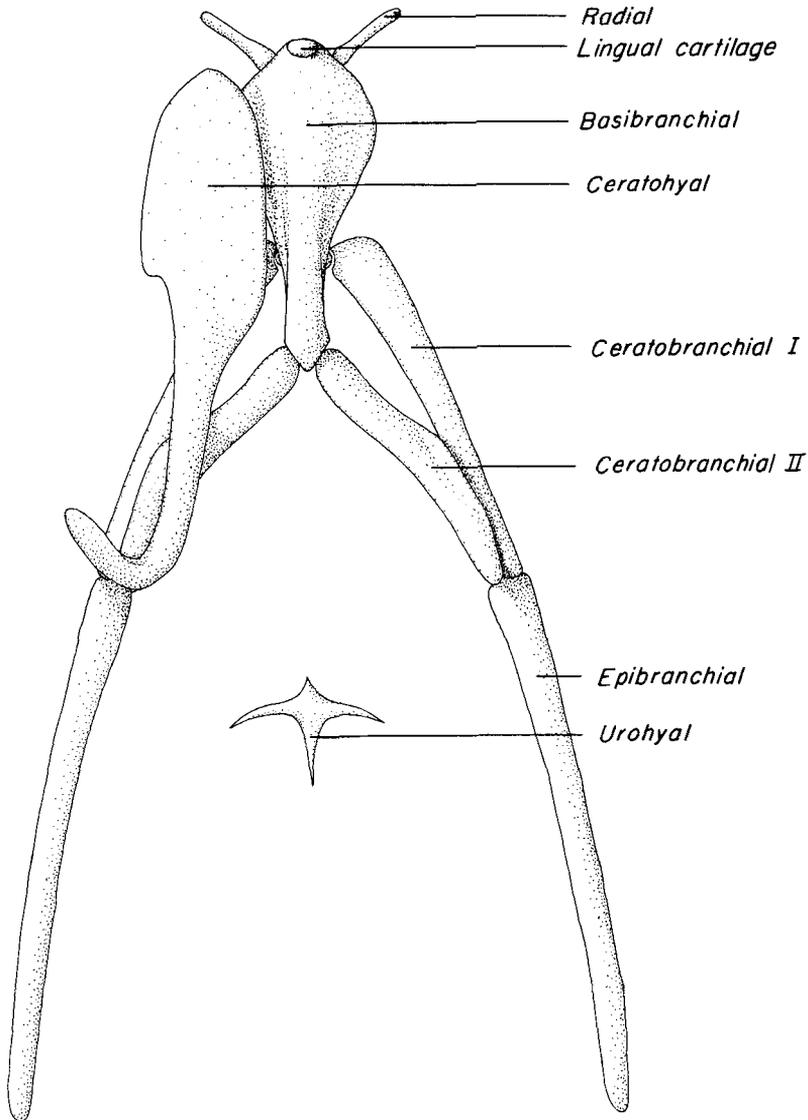


Fig. 2 Dorsal view of the hyobranchial skeleton of *Eurycea bislineata*. Only the left ceratohyal is shown. The basibranchial and urohyal lie approximately in the same plane. The ceratohyals lie just dorsal to and have no articulations with the more ventral structures. The radial and lingual cartilages are embedded along with the tip of the basibranchial in the tongue pad. The urohyal is ossified and all other elements are cartilaginous. Reconstructed from dissections and serial sections. Anterior is to the top of the page.

its origin on the radial cartilages and the tip of the basibranchial (including the lingual cartilage). The pad is richly supplied with specialized sensory organs. The epithelial covering of the pad extends posteriorly around the cartilages and their associated musculature to form a sheath. Far

posteriorly, the sheath doubles back on itself and merges with the floor of the mouth.

The principal muscles associated with the hyobranchial skeleton are the rectus cervicis profundus and the subarcualis rectus I (fig. 3). The former muscle is a di-

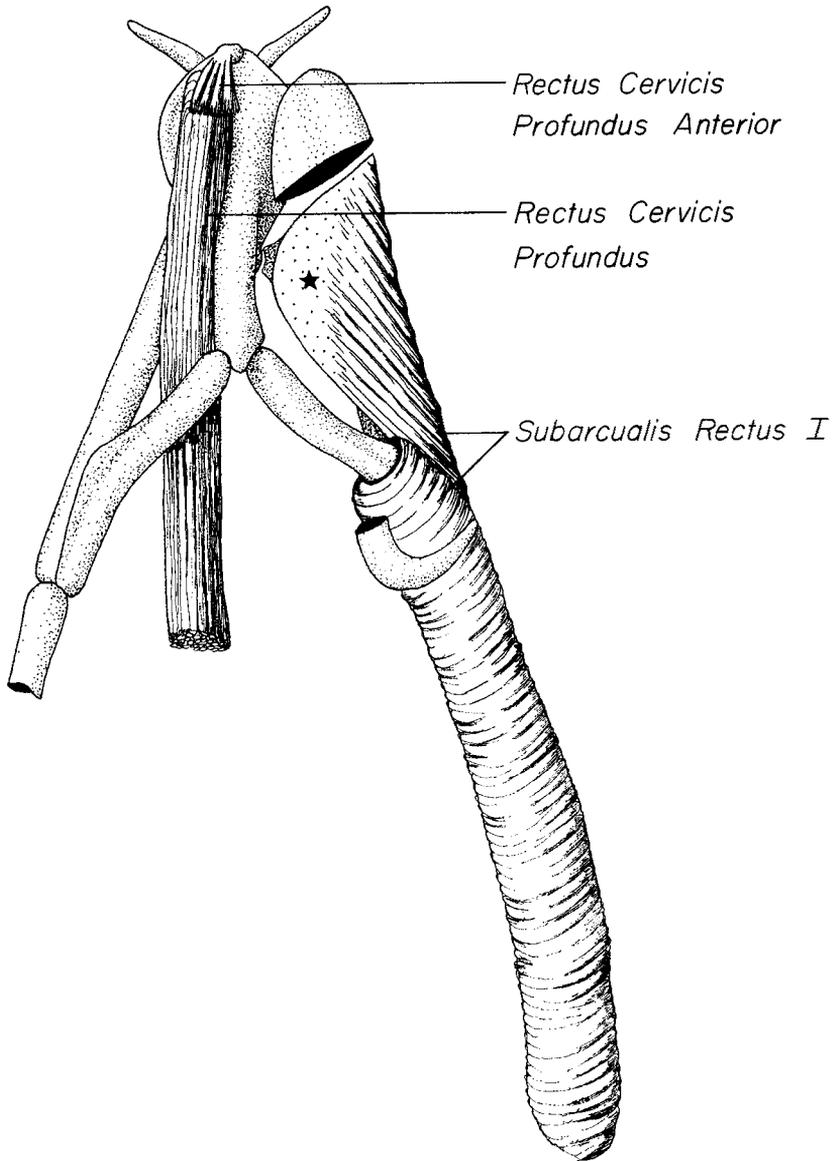


Fig. 3 The principal muscles of the hyobranchial skeleton in *Eurycea bislineata*, viewed dorsally. Part of the right ceratohyal has been removed to show the origin of the subarcualis rectus I muscle (star), on its ventral surface. The muscle fibers sweep posteriorly from the origin to envelop the posterior parts of the ceratobranchials and all of the epibranchials. The rectus cervicis profundus passes anteriorly between the ceratohyals to insert on a common myocomma with the rectus cervicis profundus anterior. The rectus cervicis profundus anterior inserts on the lingual cartilage. Reconstructed from dissection and serial sections. Anterior is to the top of the page.

rect anterior continuation of the muscle that arises on the ischium. It extends past the sternum to the basibranchial region. It passes below CBII and above CBI and has

various connections near the anterior end of the BB. The subarcualis rectus I originates on the ventral surface of the CH and wraps around the EB in a complex spiral,

forming a muscular bulb (fig. 3). There are several additional muscles; most have been described elsewhere (Piatt, '35; Tanner, '52), and we will consider them in detail in later papers.

### *The working hypothesis*

In this section we develop a working hypothesis for the general dynamics of the hyobranchial apparatus. First, hypothetical modes of projection and retraction and methods of attaining them are explored. The possible alternatives are then evaluated to derive an hypothesis concerning dynamics.

### *Theoretical considerations*

An abstraction of the hyobranchial apparatus (fig. 4) forms the basis for our approach. All of the skeletal parts (BB, CBI, CBII and EB) are considered as unidimensional, i.e., having finite length only. Schematics labeled Q through Y represent auxiliary elements and forces, both hypothetical and real, that are explored at appropriate places in the text. The assumed constraints on the apparatus are listed below. References are to figure 4.

1. The apparatus at rest is:
  - a. planar in  $xy$  (frontal plane) and
  - b. bilaterally symmetrical, BB lying on the midline.
2. The sites of joints 1, 2 and 3 are fixed.
3. The cartilaginous elements BB, CBI and CBII react as if they are rigid.
4. The propelling force,  $R$ , is bilaterally symmetrical and is applied along the epibranchials in the  $xy$  plane at joint 3. The direction (parasagittal) is indicated by the arrow at  $R$ .
5. The retractive force,  $Q$ , is applied along the  $y$  axis in plane  $xy$  on the distal tip of BB. The direction of the force is indicated by the arrow at  $Q$ .
6. During projection and retraction the epibranchials remain in the  $xy$  plane.

Constraints 1 and 2 limit the movements the apparatus can make. Both are easily verified by examination of both fresh and fixed material. Both angular and rotational movements are permitted at joints 1, 2 and 3 but there can be no sliding movements. Constraint 3 is qualified; we assume that deformation during propulsion

is negligible. Constraints 4 and 5 are based on the morphology of the epibranchial-subarcualis rectus I and basibranchial-rectus cervicis complexes respectively. Constraint 6 assumes that the subarcualis rectus I muscle does not change position in  $xy$  upon or after contraction. These assumed constraints limit the possible modes of projection and retraction available for the feeding sequence.

### *Hypothetical modes of dynamics*

Two extreme hypothetical modes can be recognized as possible alternatives. Either (i) the skeleton is projected and retracted in the resting position (unfolded mode), or (ii) the ceratobranchials are collapsed to the midline behind BB before or during projection and during or after retraction (folded mode). A continuum of semifolded arrangements between these modes is theoretically possible. Arrangements along this continuum are incomplete representations of the folded mode. Thus all arguments that pertain to the folded mode also pertain to them, variation being only differences in degree. The intermediate possibilities, therefore, are not considered here.

1. *Unfolded mode.* Projection and retraction of the unfolded skeleton appears to be the relatively more simple option. The application of a propelling force at 3 would be transmitted efficiently to the basibranchial by the ceratobranchials. The double triangular arrangement of the apparatus would resist deformation. The length of the elements and the position of the joints are fixed. Therefore, no change in the triangular arrangement is possible. Further, the juncture of the ceratobranchials with the epibranchials (3) lies at the intersection of the arcs of rotation on joints 1 and 2 of each of the ceratobranchial elements (ab, cd, fig. 4), respectively. Thus, a relative displacement of joint 3 anterolaterally in plane  $xy$  would be resisted. Ceratobranchial I is in compression and ceratobranchial II in tension while overcoming the combined inertia of the projected skeletal and soft parts of the tongue, and spreading of the skeleton to the expanded resting position does not occur. The retractive force of the rectus cervicis applied at the distal end of BB is

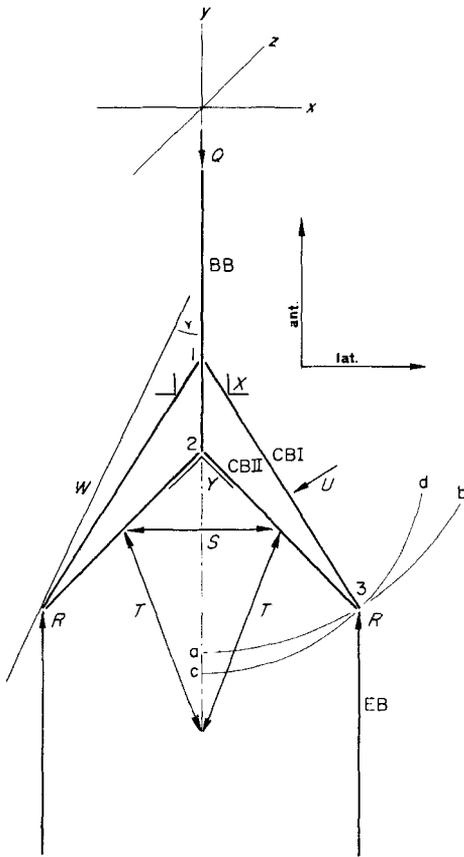


Fig. 4 A schematic diagram of the principal elements of the plethodontid hyobranchial skeleton. The major articulated elements of the skeleton are represented (BB, CBI, CBII and EB; compare with fig. 3). The fixed sites of articulation are numbered (1, 2 and 3). Arrows Q-U represent possible forces of arbitrary magnitude which could effect the dynamics of the skeleton. Schematics W, X and Y represent possible structural features which could affect movement of the skeleton. Arcs *ab* and *cd* are the paths of the tips of CBI and CBII if they are allowed to rotate on their joints with BB (1 and 2). The interactions of these features are explained in the text.

opposed by a certain level of resistance generated by the epibranchials sliding into the subarcualis rectus I muscles. As during projection CBI is in compression and CBII in tension, no spreading in the *xy* plane occurs.

Some additional features are required for this potential mode of projection. The juncture of the ceratobranchials with the epibranchial (joint 3) must resist flexure

in the sagittal plane (*yz*). This becomes important when (i) the tongue is fully extended, i.e., no longer stabilized by the confines of the buccal cavity, and (ii) during retraction. If joint 3 were flexible, flexure of the ceratobranchials in plane *yz* (and, hence, binding of the tongue in a projected position) would occur the moment the retractive force moved out of the *xy* plane. Finally, either (i) one or both of the ceratobranchial-basibranchial joints (1 or 2) must resist flexure in the *xy* plane, or (ii) the epibranchials must behave as if they were rigid. Either prevents folding of the ceratobranchials toward the midline by rotation around the basibranchial at 1 and 2.

2. *Folded mode.* Projection and retraction of the tongue utilizing ceratobranchial folding is the more complex option under the existing constraints. Because of constraint 2 only one means of achieving the folded configuration is possible, however. This involves the movement of joint 3 to the midline. Because of constraint 6, this must take place in plane *xy*. Fortunately, this limits the geometries of folding which must be considered. The configurations that are hypothetically attainable are described below. Figure 5 shows lateral views of the configuration that the apparatus may assume after joint 3 has moved to the midline. There are two possibilities: (i) the second ceratobranchial lies superior in plane *yz* to the first ceratobranchial in the folded state and (ii) the relation is reversed. In both cases a continuum of formations, based on the degree of flexure at joint 3 in the *xy* plane, is evidently possible (circle, radius *r*). We consider here only the two general cases.

The cases illustrated (fig. 5) were achieved by holding the first ceratobranchial in the same plane as the epibranchials (*a*<sub>1</sub> and *b*<sub>1</sub>) and by holding the second ceratobranchial in the same plane as the epibranchials (*a*<sub>2</sub> and *b*<sub>2</sub>). The means of producing these configurations is the same (i.e., moving joint 3 to the midline); therefore the actual folding pattern achieved is a function of the freedom of movement in joints 1, 2 and 3 and forces in the *z* axis on joint 2. The requirements of this mechanical system for each joint are easily derived in the manner discussed

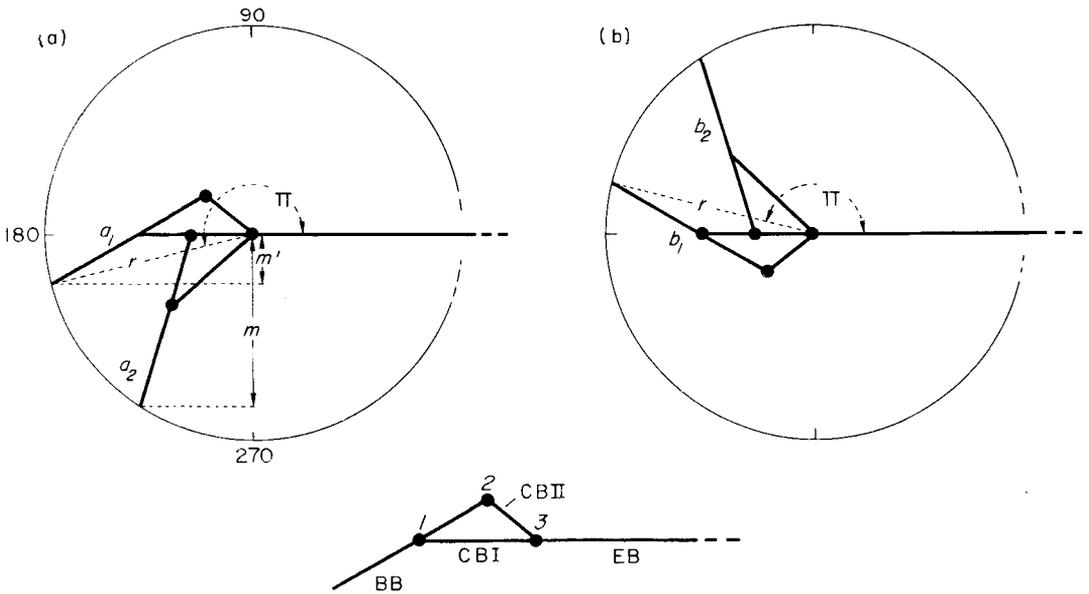


Fig. 5 Schematic diagrams of the articulated hyobranchial elements in possible rotational configurations during folding. The drawings are in the sagittal ( $yz$ ) plane. (a) two configurations possible when CBI is superior in  $z$  to CBII. In  $a_1$ , CBI is in line with EB at joint 3. In  $a_2$  CBII is in line with EB at joint 3. An infinite number of configurations is possible at joint 3, rotating the circle of radius  $r$ .  $\Pi$  is the angle this radius forms with EB at joint 3.  $m'$  and  $m$  are moment arms about joint 3 produced when a force opposite the axis of projection is applied to the tip of the basibranchial in each of the cases illustrated. (b) is similar but CBI is superior in  $z$  to CBII. (c) locates the joints and elements involved.

for the unfolded skeleton. One constraint is operative in all cases. When moving joint 3 to the midline the epibranchials must possess sufficient flexibility to follow. This is necessary to satisfy constraints 2 and 4 (above).

#### *Hypothetical effectors of dynamics*

The process of folding and unfolding the apparatus requires that a force of appropriate magnitude and direction be applied to joint 3. It is impossible to define the magnitude of the force, but limitations can be placed on its direction. First, because of constraint 6, the force must lie in  $xy$ . Further confinements are schematically illustrated in figure 6. Vector 3 ( $V_3$ ) represents a force of an arbitrarily chosen magnitude, the assumption being that it is sufficient to fold the apparatus. It lies normal to a line,  $ef$ , bisecting angle  $\phi$  between the ceratobranchials, representing an "average" ceratobranchial. Further, it

bisects the angle formed by vectors 2 ( $V_2$ ) and 4 ( $V_4$ ), which are tangent to  $ab$  and  $cd$  respectively. Vectors 3 and 4 represent the direction of a force adequate to rotate CBI and CBII, respectively, on joints 1 and 2. Vector 3 represents an "average" force in which the components on CBI and CBII are equal, i.e., the minimum force of the appropriate direction necessary to swing  $ef$  to the midline. Any vector rotation from this position (vector 3) necessitates an increase in the magnitude of force applied in order to produce a resultant equal in magnitude and direction. Further, rotation of the force application would distribute the forces unequally along vectors 2 and 4 on CBI and CBII. A force applied in  $\theta$  produces greater forces on CBI than on CBII. A force applied in  $\theta'$  would produce the reverse. The increase in force necessary would be inversely proportional to sine of the angle in  $\theta$  or  $\theta'$  depending on the direction of rotation. The

absolute limit in the direction a force may be applied to produce a component for folding is asymptotic to  $ef$ . Forces applied along  $ef$  in  $\theta'$  would produce component vectors on CBI and CBII equal in magnitude but of opposite direction, and hence no movement of joint 3 would occur. Vectors 1 and 5 ( $V_1, V_5$ ) represent rotations in the direction of force application, parallel to the  $x$  axis in  $\theta$  and parallel to the  $y$  axis in  $\theta'$  respectively. Their length illustrates the increase in magnitude necessary to produce the appropriate component on joint 3. Unfolding of the apparatus would, of course, require a force equal in magnitude to vector 3 but in the opposite direction.

The hyobranchial skeleton can be folded and unfolded either directly or indirectly. Direct folding and unfolding could involve a muscle or muscles applying force to joint 3. Indirect means of moving joint 3 would

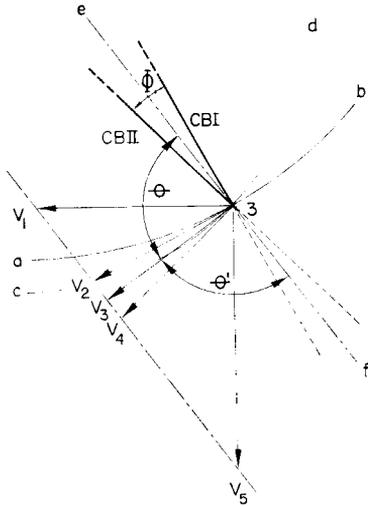


Fig. 6 Schematic diagram of possible forces on joint 3 (first ceratobranchial and second ceratobranchial—epibranchial joint).  $V_3$  is assumed to be the minimum force to move joint 3 to the midline. It is orthogonal to dashed line  $ef$ , the "average" epibranchial.  $V_1$  and  $V_2$  illustrate the increase in force necessary when the direction of force application shifts through field  $\theta$ .  $V_2$  is drawn tangent to  $ab$ , the arc of rotation for the tip of CBI and  $V_1$  is orthogonal to the midline.  $V_4$  and  $V_5$  illustrate the increase in force necessary when the direction of application shifts through  $\theta'$ .  $V_4$  is tangent to  $cd$ , the arc of rotation for the tip of CBII and  $V_5$  is parallel to the midline.  $\phi$  is the angle between the ceratobranchials.

involve the projection and retraction muscles. That is, forces  $R$  and  $Q$  (fig. 4) would by some passive means be made to generate a component force of the appropriate magnitude and direction on joint 3.

The direct and indirect methods of folding and unfolding can be subdivided into three classes in which the effector: (i) is internal to the apparatus, connecting one part to another; (ii) is connected to both the apparatus and some structure in its surroundings; and (iii) is external to the apparatus.

Examples of three classes of direct methods for folding the skeleton are schematically represented by  $S, T$  and  $U$  in figure 4. A muscle, represented by  $S$ , connecting two points on the apparatus would create, upon contraction, a force on joint 3 in the direction of vector 1 (fig. 6), thus folding the ceratobranchials. A bilateral muscle, represented by  $T$ , connecting the apparatus to an external structure, would create an initial force on joint 3 in the direction of vector 4 (fig. 6). During contraction the force direction on joint 3 would rotate in  $\theta'$  from that of vector 4 to that of vector 5. Finally, a muscle, represented by  $U$ , external to the apparatus and bilaterally symmetrical, would create a force on joint 3 in the direction of vector 2 (fig. 6).  $U$  could be, for example, a sphincter muscle surrounding the ceratobranchials. It is also possible that several muscles acting indirectly might produce this force. It is unproductive to consider all, or even part, of their full range. For the purposes of this discussion it is important only to acknowledge the possibility of existence for future reference.

The first class of indirect methods of folding the skeleton involves a passive effector internal to the apparatus, but no such arrangement is possible. Creation of a component force along vector 3 on joint 3 from  $R$  requires the connection of some point on an element forming joint 3 to a point on a structure of the apparatus which is: (i) parallel or posterior to it in  $x$  (ii) on or across the midline,  $y$ , and (iii) stable, or moving at a relatively slower rate on  $y$  than joint 3. Though the first two criteria can be met, the third cannot. With the bilateral application of  $R$  (constraint 4) all parts of the structure

would be moving at the same rate. Unfolding the apparatus by internal, indirect means is impossible for similar reasons.

Examples of the remaining two of the three classes using indirect means of folding joint 4 are represented by *T* and *W* (fig. 4). Schematic *T*, a bilateral effector, represents a connection of the apparatus to an external structure. It might represent an elastic ligament, for instance, that would create a force on joint 3 along vector 3 (fig. 6) with the application of *R*. Assuming the external structure of insertion is stable, relative to joint 3, the force created would rotate in  $\theta'$  from vector 4 to vector 5 as the apparatus is propelled along *y*. An analogous situation could be constructed to unfold the ceratobranchials.

Schematic *W* (fig. 4) represents a track in *xy* along which joint 3 could move as the apparatus is propelled from or retracted to the mouth. One requirement of the track is that it be unmoving. The requirement that the track be stable enforces another condition upon it. Because of constraint 3, the ceratobranchials must at all times clear the track as they are folded to the midline during propulsion. A track in the shape *W* (fig. 4) does not fulfill this requirement. The first ceratobranchial would cross through the track when the angle it forms at joint 1 with *BB* equals angle  $\gamma$ . The only shape the track may have and fulfill the clearance criterion is the curve, a tractrix<sup>1</sup>, shown in figure 7. This curve was derived by construction. The light lines, equal in length to *CBI*, between the midline and the curve demonstrate the method. Construction started at the bottom of the curve with the line normal to the midline. The line was moved a finite distance on *y* and the distal end dropped to the previous line. This process was repeated to produce the curve. This curve permits *CBI* to be tangent at all times as angle  $\alpha$  goes from  $0^\circ$  to  $90^\circ$  thus permitting continuous clearance. Mathematically, a tractrix can be described by the equation:

$$y = a \log \frac{(a \pm \sqrt{a^2 - x^2})}{x} \pm \sqrt{a^2 - x^2}. \quad (1)$$

where *a* equals the length of *CBI* in figure 7.

The tractrix fulfills the requirement of producing a continuous component force on joint 3. In fact, such a curved track is the only wholly external, passive means of creating such a force.<sup>2</sup> Application of *R* to the tractrix would create a component force on the track opposite the direction of vector 2 in figure 6. The track would oppose this with an equal force on joint 3 along vector 2. Further, this force would remain tangent to arc *ab* (fig. 6) as the ceratobranchials are folded to the midline. The vector diagrams *g*, *h*, and *i* in figure 7 illustrate this point at three selected positions on the curve. The vectors parallel to the *y* axis are instantaneous representations of an arbitrary *R* of constant magnitude. The tractrix resolves these vectors into the two components shown, one tangent and the other normal to the curve. The force exerted by the track opposite in direction to the normal component is tangent to arc *ab* and is responsible for folding the ceratobranchials.

As the retractive force *Q* (fig. 4) is applied along *y*, the tractrix cannot be used for unfolding the apparatus under the given constraints. Another external structure, generalized by *Y* (fig. 3) could exert a force on joint 3 for unfolding. Minimally it must be a point of finite dimension in *x*, but it might extend from joint 2 to joint 3, coinciding with *CBII* at rest.

A further requirement is necessary. In the folded state the apparatus could be subject to premature spreading. This problem would arise (i) during the period of deceleration as the tongue contacts the prey, and (ii) during retraction, especially

<sup>1</sup> The tractrix is also known as the *tractorie von Huygens* after its discoverer (Mathematisches Wörterbuch, Vol. II, p. 739. J. Naas and H. L. Schmid, eds., Pergamon Press, 1962). The curve was originally described as the path followed by a weight attached to one end of a wire when the other end was accelerated upwards on a straight line. The essential features are that the wire is tangent at all times to the curve at one end, abuts on a straight line on the other and does not change length. The role of the wire is played by *CBI* in our model. Modern usage of the tractrix seems restricted to differential geometers who use it as an example problem of transcendental curves for students.

<sup>2</sup> At first glance one might consider an aperture generalized by *X* (fig. 3), as an indirect means of folding. Analysis of the forces involved shows, however, that such an aperture would act as a fulcrum, reversing *R* on *y*. To escape this problem, *R* would need be applied on joint 3 in  $\theta$  or  $\theta'$ . In addition to being contrary to constraint 4, this would obviate the necessity for an aperture. The propellant force would no longer be directed to the aperture and would act to fold the joint of its own accord.

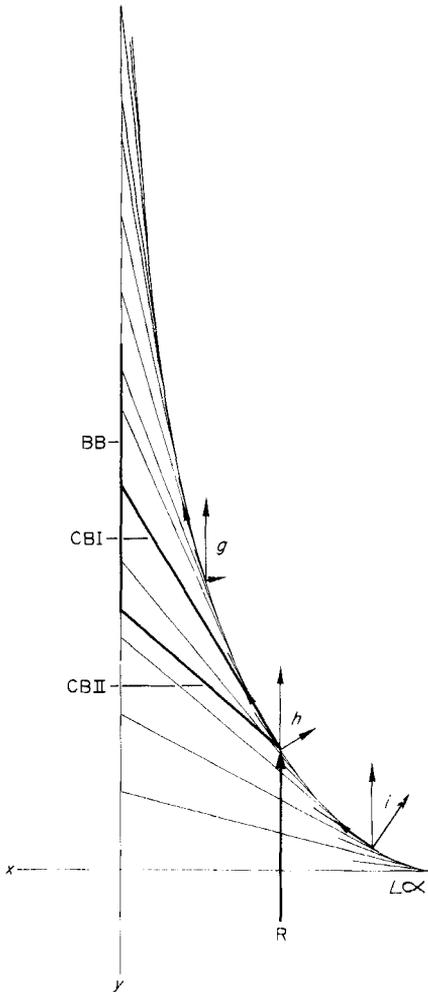


Fig. 7 Diagram of a tractrix and method of construction. The light construction lines are of equal length and are always tangent to the curve. The heavy lines represent elements of the hyobranchial skeleton placed in proper relation to the tractrix (BB, CBI, CBII). CBI is equal in length to one of the construction lines and is tangent to the tractrix.  $R$  represents the direction of the projecting force. Vector diagrams  $g$ ,  $h$  and  $i$  show the magnitude of forces normal and tangent to the tractrix at different points given a propelling force of constant magnitude and direction.

as the apparatus is rapidly accelerated by the retractor muscles.

In both situations the forces for spreading are the same, but their causes are different. The forces involved are shown in figure 4. In the first case  $Q$  would represent

the forces exerted by the prey on the tip of BB and  $R$  the momentum or driving force of the apparatus. In the second case  $Q$  is the retractive force and  $R$  represents the inertia of the apparatus or the resistance of the subarcualis rectus I sheath to the epibranchials. In either case, if joint 3 were not exactly on the midline a force opposite in direction to vector 3 (fig. 6) would be created and spreading could occur. In the abstract model, joint 3 would be on the midline if the apparatus were fully folded. In reality, however, the ceratobranchials have a finite thickness and joint 3 could not be on the midline in the folded state. Thus the apparatus requires some mechanism to eliminate or change this force on joint 3 to prevent premature spreading.

#### *Derivation of working hypotheses*

##### *Mode of dynamics*

1. *Folding.* Projection of a folded skeleton appears to be the more complex mode of dynamics. However, it could offer two important advantages resulting from linear compactness (the collapsed, rigid distal parts of the apparatus are trailed by their flexible epibranchials, all lying on the midline). First, a folded projectile could be aligned over a much wider field than an unfolded one. This point is schematically illustrated in figure 8.  $Z$  represents an aligning device that would bring joint 3 to the margin of the jaw. In  $a$ , the unfolded condition, it must act through a much smaller distance than in  $b$ , the folded condition. Assuming, for the moment, that epibranchials have infinite flexibility in both cases, the field of projection ( $\Delta$ ) in  $b$  is much greater than in  $a$ .

A second advantage of folding is the possibility of reducing viscous friction. On the assumption that the greatest speed with the least force would be of selective advantage, a reduction in resistance due to viscous friction would be of great significance. The pertinent parameters concerning this problem are illustrated in figure 9 and can be related by:

$$v = \frac{FL}{A\eta}, \quad (2)$$

where  $v$  is the velocity of one surface in

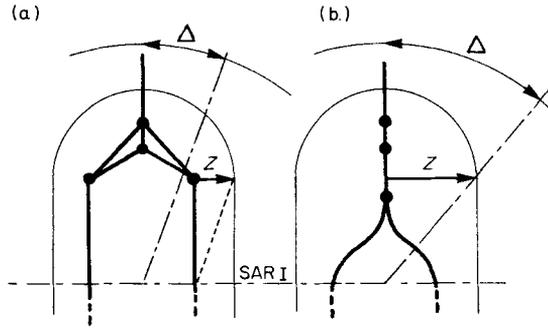


Fig. 8 A hypothetical construct of possible methods of aligning the tongue independently of head position in (a) the unfolded mode and in (b) the folded mode. Z is a device for aligning the projection to an off-center direction.  $\Delta$  is the field through which Z is effective. SARI represents the end of the subarcualis rectus I sheath. This is taken as the point at which the epibranchials can exhibit flexibility and is identical in both (a) and (b). The skeletons are depicted in a partially projected state.

relation to the other;  $F$  is moving force;  $L$  is the separation between the surfaces;  $\eta$  is the fluid viscosity; and  $A$  is the surface area. Figure 9a represents a section through the sheath surrounding the projected elements (solid line) as shown in 9b, a sagittal section through the tongue. Dorsal perspectives of the shape of the tongue recess (dotted line) in the unfolded (fig. 9c) and folded (fig. 9d) conditions in partially projected states clarify the problem. The skeletal elements are disposed so that the ceratobranchials are clear of the recess. Taking the schematics as instantaneous representations in the projection sequence and assuming (i) equal projection force in both cases, (ii) equal surface separation, and (iii) equal fluid viscosity the velocity of the apparatus is then inversely proportional to the surface area of the recess in each instance, i.e.,

$$v \sim \frac{1}{A} \quad (3)$$

The pertinent surface area in 9c is about 62 units<sup>2</sup> and in 9d 4 units<sup>2</sup> (using 1 unit as the depth of the square in c and the diameter of the cylinders in d). Thus, the unfolded condition presents about 15 times the surface area for viscous friction as that of the folded mode, requiring a corresponding increase in force to give an equivalent velocity. We assume, of course, that the properties of the fluids do not change under varying dynamic conditions.

Folding the hyobranchial skeleton would

appear to confer to the system the two distinct advantages outlined above. Both bear directly on efficiency of feeding in an animal using a projectile tongue. For these reasons the folded mode is chosen as the foundation of the working hypothesis.

2. *Relations of CBI and CBII.* Assuming that the folded condition prevails, the more detailed relations of the distal elements of the hypobranchial skeleton must be specified. Folding joint 3 to the midline must of necessity cause the rotation of BB about joint 1 in plane  $yz$  (fig. 4). The direction of rotation would depend on whether CBI or CBII were uppermost after folding (fig. 5). With CBI uppermost, rotation would be clockwise (as drawn) and BB would be oriented such that its distal tip is directed dorsally. With CBII uppermost, rotation would be counterclockwise (as drawn) and BB would be oriented such that its distal tip is directed ventrally. The tip of BB bears the tongue pad, which is supplied with mucous glands on its dorsal surface. Therefore, a ventrally directed BB would direct the pad toward the substrate. This orientation is not an absolute requirement. However, in generalized feeding situations (where the prey rests on the substrate) we assume it would be preferred. Having CBII superior to CBI would also offer the rectus cervicis profundus muscle a more direct line of action for retraction. The rectus cervicis profundus muscle lies ventral to CBII and dorsal to CBI (fig. 3). Folding of the apparatus such that CBI

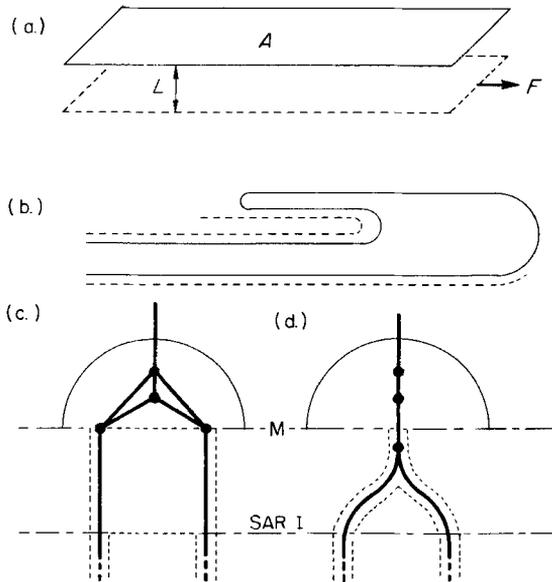


Fig. 9 Factors considered in determining the possible role of viscous friction in tongue projection. (a) is the general case and (b) is its relation to the tongue sheath shown in sagittal section.  $A$  is the area of the opposed surfaces,  $L$  is the separation distance between the surfaces and  $F$  is the force moving one surface past the other. In (b) anterior is to the right and the tongue is in the resting state. The dashed line represents the buccal epithelium, the solid line the epithelial surface of the tongue and the sheath surrounding the hyobranchial skeleton. (c) and (d) are representations of partial projections in the unfolded and folded modes seen from above. The semicircles represent the margins of the jaws.  $M$  locates the opening of the tongue recess to the buccal cavity. SARI locates the end of the SARI sheath (as in X-sec *a*, fig. 12). The dashed line outlines the surface areas between  $M$  and SARI where viscous frictions would affect movement. The surface area in (c) is much greater than in (d).

is superior to CBII would necessitate a rather abrupt fold in the muscle. After passing ventral to CBII it would then proceed dorsally at an acute angle to pass dorsal to CBI. In the reverse situation the muscle could proceed between the ceratobranchials without a bend being necessary. For these two reasons (especially the morphological one) a folded condition in which CBII is superior to CBI is chosen for formulation of the working hypothesis.

3. *Angles of CB's with EB.* The angles which the ceratobranchials form with the epibranchial at joint 3 in  $yz$  must have some limitations. The circle of radius  $r$ , shown in figure 5a (the preferred relations of CBI and CBII), includes all possible positions of the distal tip of BB and, hence, of the tongue pad. At values of angle II [formed by the epibranchial and the radius,  $r$ ] greater than 270 degrees or less than 90 degrees, the tongue tip no longer

would be the leading element during projection. When angle II is (i) greater than 90 degrees but less than 180 degrees, and (ii) greater than 180 degrees but less than 270 degrees, a moment arm,  $m$ , (fig. 5a) is created about joint 3 for forces parallel to the axis of projection acting on the tongue pad. Such forces are expected to occur with contact of the prey. The tendency in these situations would be to collapse the structure back on the epibranchials by buckling joint 3. As angle II approaches 180 degrees, the moment arm decreases as in  $m'$  (fig. 5). The moment arm is 0 when the tongue tip is in line with joint 3, with  $r$  on the axis of projection. To achieve this situation, the angle of the ceratobranchials must be between about 170 and 135 degrees, with respect to the epibranchials. The exact angles of the ceratobranchials with the epibranchial which are necessary to eliminate the mo-

ment arm depend on the proportions of the elements involved and the distances between joints 1, 2, and 3.

Further support for our argument that an angle of about 135 to 170 degrees must obtain for a joint 3 is gained from consideration of the rectus cervicis profundus muscle. At angles within this range the muscle approaches linearity (again, the precise angles depend on the proportions of the skeletal elements). Linearity of the muscle provides maximal efficiency during retraction of the apparatus to the mouth. At angles outside those specified, the muscle would bend in order to achieve insertion on the tongue tip. For these reasons an angle of between 135 and 170 degrees for the ceratobranchials with EB is chosen for the working hypothesis.

#### *Effectors of tongue dynamics*

1. *Projection.* Only the subarcualis rectus I muscle has an arrangement suitable to project the tongue from the mouth (fig. 12). For this reason the subarcualis rectus I muscle is incorporated as the method of projection in the working hypothesis.

2. *Folding.* No morphological evidence can be found for a direct effector of folding. For this reason, an indirect means of folding, i.e., one in which the force on joint 3 for folding is derived from the projective force, is expected. There are two possibilities: (i) an effector connecting the hyobranchial apparatus to some non-projectile portion of the head (*T*, fig. 4), and (ii) a track, wholly external to the apparatus *W* (fig. 4). The latter is preferred because an effector such as *T* in figure 4 would ultimately limit the distance the tongue could be projected. In addition it would increase the mass of the projectile. These problems would be avoided if folding occurred along a track. We have shown that the track must have the properties of a tractrix. The concept of a tractrix, therefore, is incorporated into the working hypothesis.

3. *Retraction.* The rectus cervicis profundus muscle has an arrangement suitable to retract the hyobranchial apparatus to the mouth. For this reason the rectus cervicis profundus muscle is incorporated

as the means of retraction in the working hypothesis.

4. *Unfolding.* No direct means of unfolding the hyobranchial skeleton upon return to the mouth is evident at a gross level of examination. Of possible indirect means, one wholly external to the apparatus would be preferred for reasons similar to those given above for folding. A complete or partial track approximating *Y* in figure 4 would be expected on arguments presented above. Unfolding of the apparatus by use of a track is thus incorporated into the working hypothesis.

#### *Summary of hypothesis*

##### *Mode of dynamics*

1. The hyobranchial skeleton is folded during the feeding sequence. Folding is achieved by apposition of joint 3 to the midline.

2. In the folded state CBII is superior to CBI in plane *yz*. Accordingly, during folding BB is rotated about joint 1 such that the distal tip is directed ventrally.

3. In the completely folded state the ceratobranchials form an angle of between 135 and 170 degrees with the epibranchials at joint 3 in plane *yz*. The precise angles necessary to place the distal tip of BB on the axis of projection are determined by the proportions of the skeletal elements and the relationships of their joints with one another.

##### *Effectors of tongue dynamics*

1. Projection of the tongue is accomplished by the subarcualis rectus I muscle acting on the epibranchials.

2. The skeleton is folded as the ceratobranchials move forward along bilateral tracks. The tracks have the form of a tractrix.

3. Retraction of the tongue is accomplished by the rectus cervicis profundus muscle acting on the basibranchial.

4. Unfolding is accomplished along a complete or partial bilateral track that is coincident with the second ceratobranchials when the hyobranchial skeleton is at rest.

A Problem: In the folded state there must be a mechanism to prevent premature spreading, which would result from

the forces generated both by prey contact and by acceleration for retraction.

#### FUNCTIONAL OBSERVATIONS AND DISCUSSION

In this paper we present only a limited number of observations which support crucial elements of the working hypothesis. Phylogenetic diversity complicates the picture. The results of a detailed comparative study will be published shortly; these extend and reinforce the limited data presented here.

#### Mode of dynamics

The distal elements of the hyobranchial skeleton are folded during the feeding sequence (figs. 10, 11). Figure 10 is a reconstruction of the skeleton of *Eurycea bislineata* in a partially projected condition. Figure 11 shows the skeleton of *Pseudoeurycea nigromaculata* when the tongue is fully projected. In both instances, joint 3 has been moved toward the midline relative to its position at rest (fig. 2). Movement of joint 3 to the midline is nearly complete in the early projection stage in *Eurycea*. Apposition is as complete as possible in the presumed terminal stage shown in *Pseudoeurycea*. We have confirmed these observations in many additional species and the phenomenon is general in plethodontids. During projection CBII is superior to CBI in the sagittal plane,  $yz$  (figs. 10, 11). The contour lines fall away from the starred high point, and in both instances the distal tip of BB is directed ventrally. This condition was found in all other partially or completely projected tongues studied. It was not observed in the skeleton of tongues at rest.

In *Eurycea* (fig. 10), the first ceratobranchial lies in the horizontal plane,  $xy$ . Thus it forms an angle of 180 degrees with the epibranchial at joint 3 in  $yz$ . The second ceratobranchial obviously forms a lesser angle with the epibranchial. Rough calculation, based on the contour intervals, indicates the angle is about 160 degrees. In *Pseudoeurycea* (fig. 11), the second ceratobranchial forms an angle of approximately 180 degrees with the epibranchial at joint 3. The first ceratobranchial forms an angle greater than 180 degrees. Again, calculation from the contour intervals in-

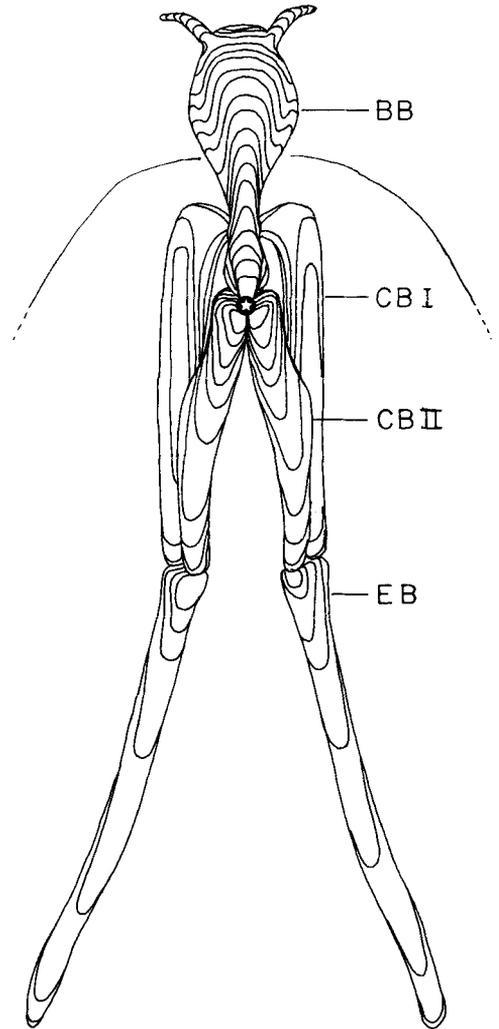


Fig. 10 The articulated elements of the hyobranchial skeleton of *Eurycea bislineata* in a partially projected state. Serial reconstruction from plastic-embedded material. Contour interval is  $30 \mu$ . Dorsal view. The curved line represents the margin of the jaw. The star represents the most dorsal point on the reconstruction.

dicates that the angle is about 205 degrees. This difference in the relations of the ceratobranchials with the epibranchial has phylogenetic significance and will be discussed in greater detail in a subsequent paper. In both cases illustrated, the distal tip of BB lies slightly below the axis of projection, which is assumed to lie in a plane containing CBI and EB in *Eurycea* and CBII and EB in *Pseudoeurycea*.

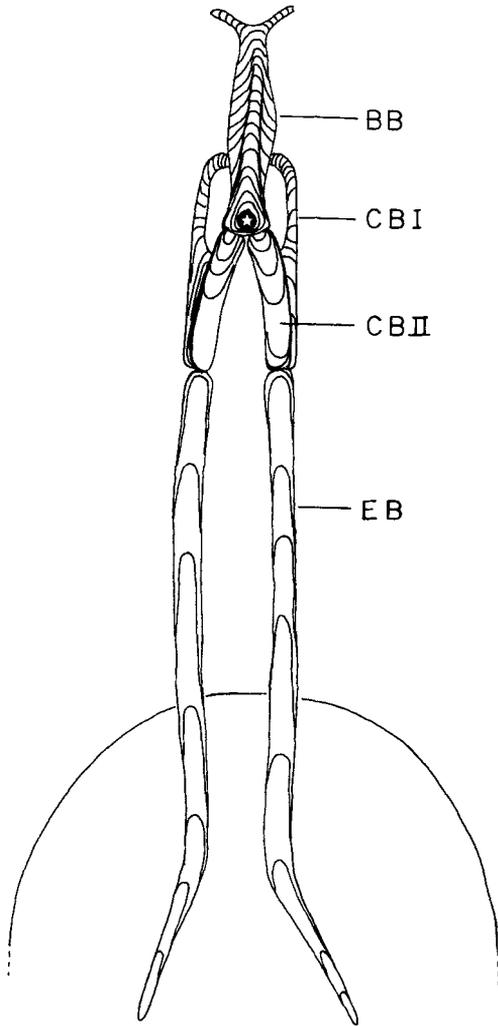


Fig. 11 The articulated elements of the hyobranchial skeleton of *Pseudoeurycea nigromaculata* in a completely projected state. Serial reconstruction from plastic embedded material. Contour interval is  $50 \mu$ . Dorsal view. The curved line represents the margin of the jaw. The star represents the most dorsal joint on the drawing.

The hypothesis concerning the mode of dynamics as derived from geometric considerations is generally supported by the observations made above. In all specimens in which the tongue is partially or completely projected, the hyobranchial skeleton is folded in the predicted manner: joint 3 is shifted from its resting position toward the midline and CBI is superior to CBI II with BB directed ventrally. Devia-

tion from the expected mode is evident in the relation of the distal tip of BB to the axis of projection. In both instances that are illustrated (figs. 10, 11) and in other specimens the distal tip of BB lies below the axis of projection. This is demonstrated by measurement of the angles that are formed by the ceratobranchials with the epibranchials in the  $yz$  plane. In all instances one or the other, or both, of the ceratobranchials form an angle with the epibranchial that is greater than predicted ( $> 170$  degrees).

The arrangement of the soft parts of the tongue, particularly the tongue pad, suggests a possible explanation for this observation. Figure 1 is a photograph of *Hydromantes italicus* taken during the initial stages of retraction in the feeding sequence. The bulk of the tongue pad lies above the axis of projection. The distal tip of BB lies in the extreme ventral portion of the pad. It is clear in the photograph that the prey is not taken on the tip of the basibranchial but more or less on the center of the pad proper. Contact with the prey occurs on the axis of projection but not on the basibranchial tip, as predicted. Centering the prey on the flexible tongue pad which is anchored ventrally to the basibranchial circumvents the problem of creating a moment arm in  $yz$  about joint 3 during prey contact. Reconstructions of the tongue pad in partially projected tongues confirm the morphological observations made here. In all cases the distal tip of BB lies in the ventral portion of the pad and the center of the pad lies more or less on the axis of projection. Representatives of these reconstructions will be published in a subsequent paper, in the context of a detailed treatment of the arrangement of the tongue pad.

A final consideration of the mode of dynamics involves the epibranchials. Both figures 10 and 11 illustrate that these elements are flexible, in contrast to the ceratobranchials. Epibranchial flexibility was a condition ultimately assumed in determining our working hypothesis (see above).

#### *Projection and retraction of the tongue*

The subarcualis rectus I muscle is depicted in schematic section in *a* and *b*,

figure 12. These schemata are taken from the subarcualis rectus I muscle of *Eurycea bislineata* while the tongue is at rest (as in fig. 3). Sectioned material from all other species that have been examined shows a similar pattern. The fibers of the muscle are arranged in a complex spiral pattern about the epibranchial sheath. The precise courses of the individual fibers were not determined. The arrangement of the SARI fibers suggests contractions of this bulb-like muscle serve to propel the tapered epibranchial from its inner recess. Comparison of the subarcualis rectus I muscle in figure 3, where the apparatus is at rest, and figure 12, where the tongue is in projection, indicates that the muscle also contracts along its long axis to propel the epibranchial. The muscle is much shorter in figure 12 than in figure 3. Most of this shortening takes place in the more posterior part of the muscle.

Figure 12 is constructed from serial sections of the subarcualis rectus I muscle and pertinent parts of the hyobranchial skeleton. The projection is greater than is shown in figure 10 in the same species. The heavy solid line traces the extent of the cavity occupied by the skeletal elements within the muscles when the apparatus is at rest. As indicated by these lines and shown in schematic section (fig. 12a) the lateral portions of the muscular sheath extend much further anteriorly than other parts of the muscle directly related to the skeleton. The lateral fibers are cut in transverse section in figure 12a.

The lateral margins of the SARI form a curve that conforms to a portion of the postulated tractrix. The dotted line in figure 12 is a constructed continuation of the tractrix. If (i) the lateral wall of the cavity is part of a tractrix, and (ii) the dashed line is a good fit to the portion of the tractrix not represented morphologically, then  $w$  (arrow-headed line, figure 12) should equal CBI in length if the scale of the tractrix is appropriate to CBI. Line  $w'$  represents CBII mapped onto line  $w$ . Lines  $w'$  and  $w$  are approximately equal in length.

The rectus cervicis profundus muscle is the only structure with an anatomical orientation suitable to retract the tongue skeleton to the resting position (fig. 3).

This conclusion is supported by experimental evidence. When the rectus cervicis profundus muscle is severed (see MATERIALS AND METHODS), the projected tongue is not retracted.

The inner margins of the recess of the SARI provide a track that approximates the shape hypothesized as necessary to unfold the hyobranchial skeleton. However, we know from serial reconstructions of projected tongues that the epibranchials may actually evacuate these recesses. Following this evacuation, the epibranchials move into apposition on the midline. Thus, some feature has been sought which could perform the function postulated for Y in figure 4. The heart and associated more anterior mass of connective tissue have a position sufficient to play such a role. These structural elements would serve to force the projected epibranchials into the cavity of the SARI muscle as the tongue is retracted. As the epibranchials diverge, the hyobranchial skeleton is unfolded. A second means of unfolding could involve the use of restoring forces inherent in the deformed elastic epibranchials. In this situation unfolding would occur along the tractrix.

#### *The problem of a folded condition during projection and early retraction*

A possible mechanism for maintaining the integrity of the folded skeleton in the face of forces tending to spread it is partly indicated in figure 13. The illustration represents the completely folded distal elements of the hyobranchial skeleton of *Eurycea* during the feeding sequence. The dashed line  $yy'$  represents the axis of projection. The arrows Q and R represent the forces, of unspecified magnitude, which would tend to induce spreading in the folded skeleton. This combination of forces would occur (i) with contact with the prey (Q) while the apparatus was still in motion (R), and (ii) during retraction by the rectus cervicis profundus muscle (Q) when the epibranchial is being forced into the subarcualis rectus I sheath (R). Since R, in contrast to Q, does not lie on the axis of projection, the possibility of premature spreading to the resting condition is present. The folded state reduces the moment arm  $n$  for R acting through CBI on joint

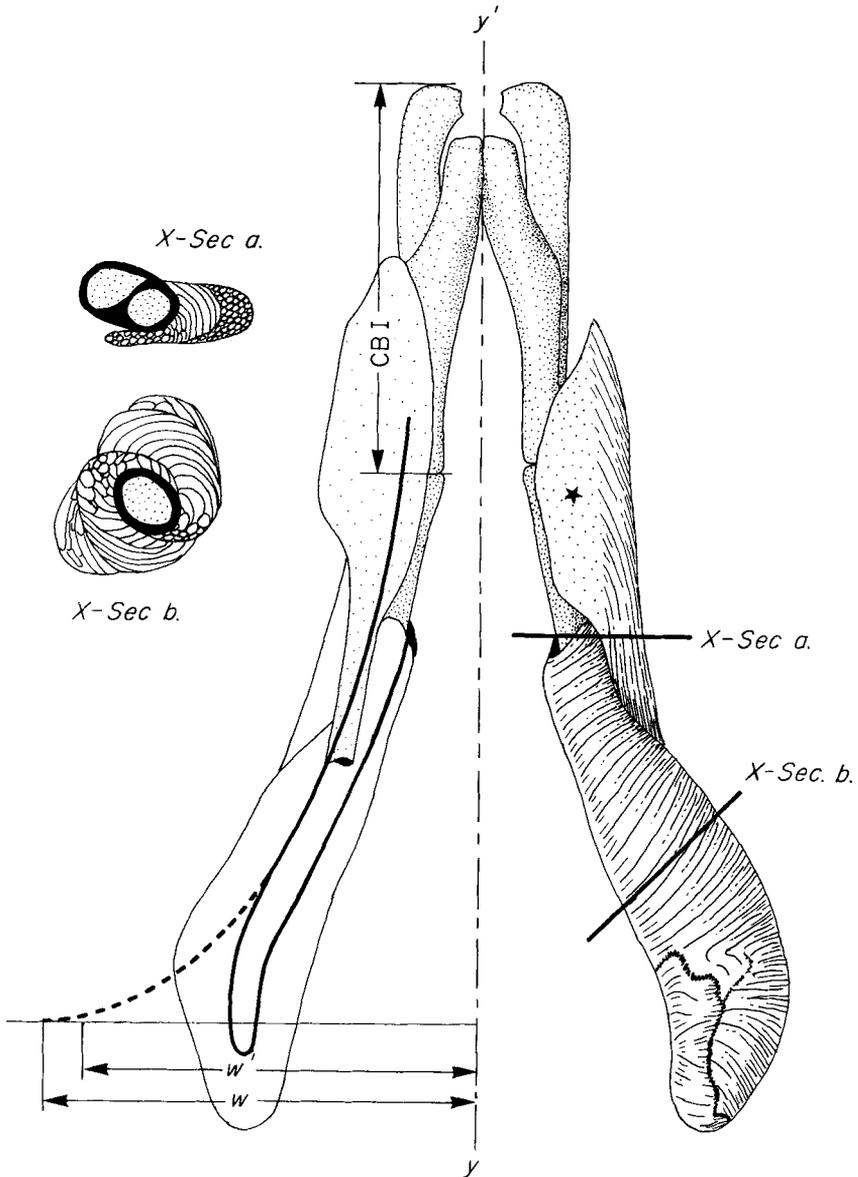


Fig. 12 The subarcualis rectus I muscle cavity as a part of a tractrix in *Eurycea bislineata*, viewed dorsally. The tongue is partially projected (compare with fig. 3). The right ceratohyal is not shown. The stippled area (star) is the insertion of SARI on the ventral surface of the ceratohyal. The heavy line delineates the extent of the cavity within the muscle which receives the epibranchial. Representative cross sections through the muscle are shown in (a) and (b). These cross sections were taken from a SARI muscle where the tongue was at rest. Lines (a) and (b) indicate the approximate locations of these sections. CRI shows the length of ceratobranchial I and is equal to  $w'$ .  $w$  was used to construct the tractrix fitted to the lateral wall of the SARI cavity (heavy line plus dashed line).  $w$  and  $w'$  are approximately the same length as would be expected if the tractrix were the mechanism used in folding the skeleton. From a graphic reconstruction of plastic-embedded material.

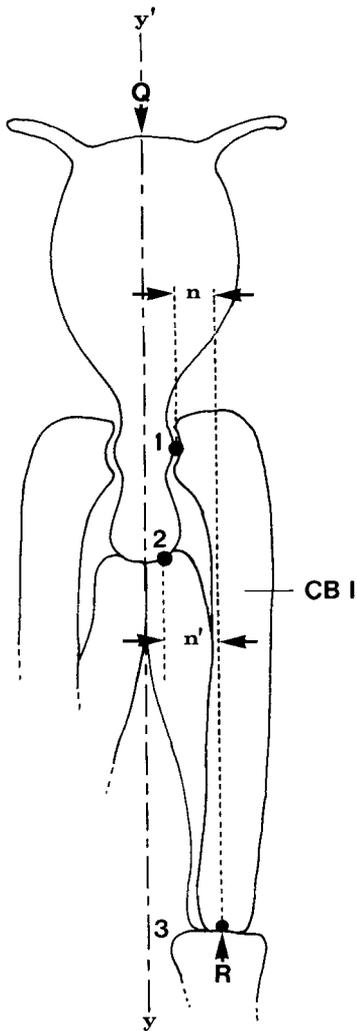


Fig. 13 The distal elements of the hyobranchial skeleton at full projection in *Eurycea bislineata*.  $Q$  and  $R$  are forces on the skeleton during projection and retraction.  $n$  and  $n'$  are the moment arms about joints 1 and 2 created by  $R$ . Ventral view from graphic reconstruction of plastic-embedded material.

1. In fact, with only a slight increase in inclination of CBI, the moment arm would reduce to zero as  $R$  passes through the joint. When this occurs there would be no forces promoting spreading. The moment arm of  $R$  through CBII acting on joint 2 is also illustrated ( $n'$ , fig. 13). The moment arm is slightly larger than  $n$  but is still small.

In all the skeletons studied the moment arms described are very small. It may be that complete elimination of the moment arms is not necessary. All that may be required is a reduction of the forces tending to spread the skeleton such that they can be counteracted by the epithelial sheath investing the elements in this region.

#### The model

1. The mouth opens.
2. The subarcualis rectus I muscle contracts, both squeezing and thrusting the epibranchial cartilages forward to propel the tongue from the mouth.
3. The ceratobranchial - epibranchial joints on each side ride along a morphological track formed by the lateral wall of the cavity of the subarcualis rectus I muscle. This track has the shape of a segment of a tractrix. Movement along the track forces the joints toward the midline. The distal elements of the apparatus are folded in three dimensions during this process.
4. While folding, CBI comes to lie superior to CBII and BB rotates about joint 1 so that its distal tip is directed ventrally. This occurs before the tip of the tongue has passed the margin of the jaw.
5. Contact is made with the prey on the axis of projection. Capture is accomplished by a mucous coating on the tongue pad.

6. The rectus cervicis profundus muscle contracts, returning the apparatus with the captured prey to the mouth. Integrity of the folded skeleton is maintained by the investing epithelial sheath which reduces disruptive forces.

7. During retraction, the epibranchials are separated and directed into the cavity of the subarcualis rectus I muscle either by a mass of connective tissue associated with the heart, or elastic recoil of the epibranchials themselves, or both.

8. The distal, folded elements of the skeleton are forced apart to the resting position by the same process.

9. The forces generated while bringing the apparatus to a complete stop are absorbed by the connective tissue mass and the heart.

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