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TRENDS IN THE FUNCTIONAL MORPHOLOGY AND SENSORIMOTOR CONTROL OF FEEDING BEHAVIOR IN SALAMANDERS: AN EXAMPLE OF THE ROLE OF INTERNAL DYNAMICS IN EVOLUTION

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ABSTRACT

Organisms are self-producing and self-maintaining, or "autopoietic" systems. Therefore, the course of evolution and adaptation of an organism is strongly determined by its own internal properties, whatever role "external" selection may play. The internal properties may either act as constraints that preclude certain changes or they open new pathways: the organism canalizes its own evolution. As an example the evolution of feeding mechanisms in salamanders, especially in the lungless salamanders of the family Plethodontidae, is discussed. In this family a large variety of different feeding mechanisms is found. The authors reconstruct this evolutionary process as a series of "bifurcation points" of either constraints or opportunities forming a sequence of preconditions for the formation of a high-speed projectile tongue characteristic of tropical salamanders. Furthermore, it is shown how parallel evolution of seemingly unrelated domains within an organism such as respiratory physiology, life history biology and pattern of ontogeny has rather direct relevance to the feeding biology, thus demonstrating that organisms always evolve as wholes.

1. INTRODUCTION

In this article we present and discuss a well understood example of the interplay between structures and functions during phylogenesis. With this example we will show that the course of evolution and adaptation of an organism is strongly determined by internal morphological and physiological properties of the organisms themselves. The internal rearrangements that occur have both positive and negative implications for further evolution: they may either serve as constraints that preclude particular avenues of change, or create new opportunities. As we will see, the latter can be achieved by the formation of a new character or by modification or loss of an already existing character. The organism, therefore, as an "autopoietic", i.e. self-producing and self-maintaining system, canalizes its own evolution [11,16,26 and an der Heiden et al., this volume].

We especially want to show how different morphological and functional parts of an organism are interrelated and how modifications in one part affect other parts that do not seem to be closely connected. In other words: the organism always acts and evolves as a whole [cf. 3,22].

The example we present is the evolution of feeding mechanisms and feeding habits in salamanders, especially in the lungless salamanders of the family Plethodontidae, which is by far the largest, most diverse and most evolved group of urodeles.

This paper is based largely on the studies of R.E. Lombard and D.B. Wake on the functional morphology of the tongues of plethodontid salamanders, on neuroanatomical studies by the present authors on the peripheral innervation of this tongue apparatus as well as its central motor and sensory co-ordination mechanisms, and on neuroanatomical studies on the visual system of salamanders, carried out in the neuroethology research group at Bremen University, done mainly by G. Rettig, W. Grunwald and R. Linke.

2. TONGUE MECHANISMS AND RELATED ADAPTIVE PROCESSES IN SALAMANDERS

Salamanders are predators during larval and adult stages. Prey-catching behavior involves such complex neural and muscular processes as prey recognition and localization, depth perception, motor approach of the prey and final activation of the feeding apparatus and the engulfment of the prey.

In salamanders, as well as in amphibians in general, two distinct types of feeding motor responses are found: one is present in permanently or temporarily aquatic salamanders including larvae, the "Saugschnappen" or suction feeding which consists of a rapid opening of the mouth at the same moment at which the throat is expanded. This results in a rapid inflow of water including the prey item. The tongue plays only a minor role in this feeding sequence. The other type is found in terrestrial salamanders and includes a movement of the tongue out of the mouth such that the prey is caught primarily by gluing it onto the tongue pad. The terrestrial feeding responses of salamanders differ primarily with respect to the mechanisms underlying tongue protrusion and the reach of the tongue.

In most aquatic and terrestrial feeding mechanisms the hyobranchial

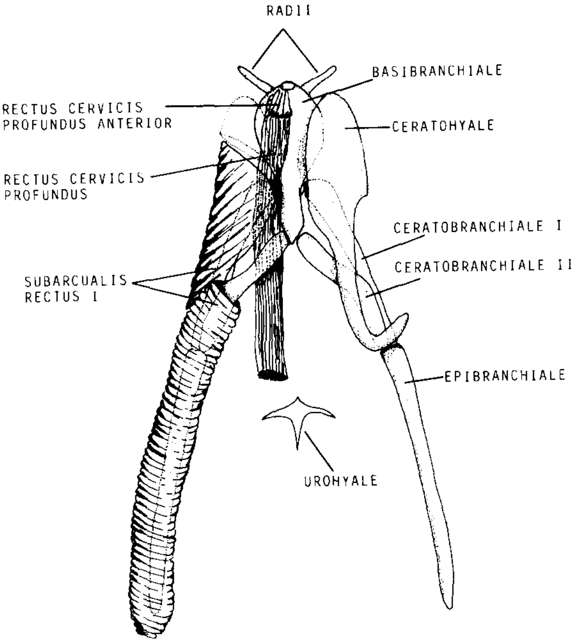

Figure 1. Tongue apparatus of the plethodontid salamander *Eurycea bislineata*. Skeletal elements are presented on the right, the main protractor and retractor muscles on the left. (After Lombard and Wake [8], modified).

apparatus plays a decisive role (cf. Fig. 1). It develops largely from the skeleton of the hyoid and branchial arches of the larvae. In salamanders of the families Plethodontidae, Salamandridae and Ambystomatidae this apparatus consists of an unpaired median basibranchial (BB) which lies in the floor of the mouth and is located far anteriorly, a short distance behind the mandibular symphysis. One to two pairs of radial elements, or radii, are attached to the anterior end of the basibranchial. Two pairs of ceratobranchials (CB) articulate with the posterior part of the BB. The first articulate with the BB near its midpoint, and the second with the BB at its posterior end. The first and second CB on each side extend posteriorly, approaching each other, and together articulate with the epibranchial (EB). The length of this latter element varies greatly among salamanders.

At each side of this apparatus a pair of ceratohyals (CH) lie in the floor of the mouth. They do not make contact with each other or with elements of the remaining hyobranchial apparatus; their posterior end is cylindrical and hooked, while the anterior portion forms a flattened blade. The CH is attached posteriorly by the hyoquadrate ligaments to the suspensorium. The final element of the apparatus is the urohyal which is the remainder of the larval second basibranchial and lies at the juncture of the rectus cervicis superficialis and geniohyoideus muscles. The tongue pad is situated at the anterior end of the BB. The BB lies in its base and the radii extend into the pad. The pad surface is covered by a large number of mucuous glands and with specialized sensory organs.

The main muscles associated with the hyobranchial skeleton are:

1. Subarcualis rectus I (SAR I). This large muscle encircles the caudal end of the EB (or first CB in those species which lack EB; see below) and extends rostrally along this element, forming a muscular sheath. More anteromedially it attaches broadly to the ventral surface of the flattened anterior part of the ceratohyals.

2. Rectus cervicis profundus (RCP). This muscle is a direct continuation of the rectus abdominis muscle and, therefore, originates from the puboischium. The muscle extends forward mediolaterally along the body axis and passes below the second CB and above the first. It enters the tongue pad inserting in various ways dorsal to the apex of the BB.

3. Subhyoideus. This muscle, when present, originates from the prosterior tip of the CH and extends anteriorly, parallel and ventral to the SARI. It inserts near the mandible on the fascia of the m. intermandibularis posterior.

4. Geniohyoideus. The geniohyoideus arises from the vertral surface of the mandible, just lateral to the symphysis, and extends posteriorly, parallel to the body axis, to the urohyal where it inserts.

5. Genioglossus. The genioglossus extends posteriorly from the ventral surface of the mandible on each side of the mandibular symphysis, above the geniohyoideus muscles, and inserts dorsally in the substance of the rostral part of the tongue.

6. Different tongue pad muscles such as the hyoglossus, basiradialis, interradialis [cf. 8].

In all generalized salamanders, the hyobranchial apparatus is involved in a dual function both in larval and metamorphosed animals: respiration and feeding. During the larval stage it serves to move the gill arches for aquatic respiration and to expand the throat during aquatic feeding or "Saugschnappen". After metamorphosis it retains both functions in those salamanders which remain permanently aquatic, or return to water for breeding. In terrestrial salamanders the hyobranchial apparatus develops as a buccal pump for respiration: the medial parts of the apparatus are drawn posteriorly and ventrally to expand the buccal cavity. Then the nostrils are closed, and the buccal cavity is constricted to force air into the lungs.

Within the family Salamandridae, three genera, *Salamandra, Chioglossa* and *Salamandrina*, have tongues specialized for feeding in terrestrial situations; all other genera have more generalized tongues, used for apprehending prey in terrestrial situations but with tongue pads that are neither strongly flipped nor projected [cf. 12].

In *Chioglossa* and *Salamandrina* the reach of the tongue is greatly extended by the very long radii and the large tongue with a free posterior flap, and additionally by the long first ceratobranchials. During forward movement of the whole hyobranchial apparatus, through contraction of the subarcualis rectus and subhyoideus muscles, the relatively massive basiradialis muscles situated inside the tongue also contract swinging the elongate radii in 180° acrs and flipping the tongue pad out of the mouth.

Within the family Plethodontidae, the genera *Desmognathus, Phaeognathus* and *Leurognathus* (subfamily Desmognathinae), have the most primitive tongue among plethodontids. Feeding is accomplished mainly by use of the jaws during rapid forward or sideward movement of the head, and only to a lesser degree of the tongue which is only slightly protruded out of the mouth (although, as in all terrestrial urodeles, the tongue makes the first physical contact with the prey). The tongue pad of these genera is relatively large and narrowly attached at its anterior margin to the floor of the mouth. Posteriorly it has a free flap of moderate size.

A more evolved tongue mechanism is found in the genera *Aneides* and *Plethodon* of the tribe Plethodontini whose members are strictly terrestrial They possess a very large tongue pad which fills the whole intermandibular space. Although attached anteriorly, the pad has a large, free posterior flap. The tongue projection mechanisms are basically the same as in the Desmognathinae, only the tongue skeleton moves farther forward. The tongue pad is flipped out of the mouth by a complex interaction between the GG and several tongue pad muscles. The third genus of the tribe, *Ensatina*, has a more loosely attached tongue and can move its tongue skeleton rather far outside of the mouth, though it does not have a genuine projectile tongue.

Most genera of the third group, the Hemidactyliini, rely on tongue projection to capture prey. They all have small tongue pads which either are attached only loosely anteriorly or are totally free. In several genera the EB is much longer than in the previously described plethodontids so that the tongue can be moved much further forward. During forward movement, the tongue skeleton, which at rest lies spread flatly in the mouth is compressed toward the midline by a three-dimensional folding resulting in the formation of a slender, compact projectile which travels about half of its length out of the mouth. The retractor muscle, the rectus cervicis, are slightly folded which increases their length and allows the tongue to protrude out of the mouth before it is retracted by muscle contraction. In addition to the forward movement of the skeleton, the tongue pad is flipped further forward by rotation of the radii and of a lingual cartilage, a disconnected anterior process of the BB.

The most specialized tongue of all salamanders is found in the species of the tribe Bolitoglossini which all have fast, highly protrusible tongues, although the genus *Batrachoseps* has a tongue which retains a loose attachment to the lower jaw.

In the Bolitoglossini the protractor muscle of the apparatus, the SAR, has an especially elaborate form, wrapping around the long EB and forming a complex sheath. The retractor muscle may be strongly folded in the gular region. This muscle here runs uninterrupted by myocommata from the pelvic region to the anterior tip of the basibranchial, thus being greatly extendable.

As the SAR of bolitoglossines and other plethodontids with projectile tongue contracts it pulls the skeleton forward and simultaneously "squeezes" the EB out of the muscular sheath. The skeleton folds completely to a very slender projectile which is fully projected out of the mouth. Retraction is achieved by contraction of the greatly extended rectus cervicis which travels out of the mouth during tongue protraction.

In bolitoglossines the feeding apparatus evolved toward an increase in velocity, feeding distance and versatility of the tongue. Increase of velocity of tongue projection was achieved (i) by reduction of mass of the tongue skeleton, (ii) by reduction of the length of the two pairs of CB which considerably shortens the time necessary for folding the skeleton, and by shifting the main line of force transmission from the first to the second pair of CB which optimizes the track of the movable tongue during protraction [8,9] , and (iii) by full elaboration of a complete muscular sheath around the EB by the SAR muscle which wraps around the EB in a spiral way, thus being able to both pull the EB forward and "squeeze" it out.

In such a way, very high tongue protrusion velocities are reached which, as feeding reactions, may be unique among vertebrates. In some species of the genus *Bolitoglossa* the tongue is protruded out of the mouth to its full length of 20-25 mm within 2-4 ms [21]. In *Hydromantes* which possesses by far the longest tongue with a reach of 45-50 mm, the protrusion last 6-8 ms [15].

Tongue-retraction velocity is increased by a unique interaction between the protractor and retractor system. Thexton et al. [21] showed by means of electromyographic studies in *Bolitoglossa occidentalis* that the protractor SAR and the retractor RCP are activated more or less simultaneously. When both muscles contract the SAR has an advantage over RCP due to the differing length tension curves of the two muscles such that the SAR can shoot the tongue out maximally until the RCP is under full tension and draws the tongue back. After Thexton et al. the whole tongue reaction takes place in about 10 ms in *Bolitoglossa occidentalis*. In *Hydromantes* the tongue is considerably slower; it lasts 80-100 ms [15].

The evolution of such a fast, far-reaching tongue has major implications for the feeding behavior of the salamanders and especially for the visual guidance of the feeding reaction. An obvious advantage of such a feeding system is that prey can be captured which have very fast escape velocities and/or are very sensitive to approach movements of predators. The speed of the projectile tongue of most bolitoglossines is such that they can specialize on very fugitive arthropods like collembolans, as is the case in *Thorius* or *Batrachoseps* [10]. In contrast to non-bolitoglossine plethodontids as well as other salamanders which have to come rather close to their prey and have to lunge forward with their whole body to capture it, most bolitoglossini have evolved an "ambush" strategy: they wait until a prey comes within reach of the projectile tongue, and then shoot. They usually do not move their bodies forward during tongue action; they only show slow movements towards the prey before tongue projection if the prey is still out of reach.

Such a feeding strategy requires very precise depth perception. In experiments with *Hydromantes italicus* [15] and *Bolitoglossa occidentalis* [21] in which living prey were very slowly brought to the quietly sitting salamander, it was a question of 1-3 mm of further approach of the prey to elicit tongue projection. The salamanders are highly accurate, even over maximal shooting distance. This means that these animals can estimate prey distance very precisely.

The following results have been obtained concerning the visual guidance system of feeding behavior of plethodontids [14,17]:

1. Those plethodontids which possess projectile tongues have significantly more frontal eyes than those which have a less developed tongue apparatus. The most frontal eyes are found in the Bolitoglossini which also have the most evolved tongue apparatus.

2. The presence of both a projectile tongue and eye frontality is strongly correlated with the amount of so-called ipsilateral retinal input to the visual centers in the diencephalon and the midbrain. The strongest ipsilateral projections of the retina to the visual centers are again found in the Bolitoglossini.

Both features, increased eye frontality and increased number of ipsilateral retinal afferents, are commonly regarded to be prerequisites for good distance estimation. In most non-plethodontids as well as in the plethodontids without tongue specialization we find rather laterally oriented eyes and a restricted binocular visual field. In these salamanders the retina projects mostly to the contralateral visual centers in the brain. There is some ipsilateral input to visual centers in the diencephalon, but little or no ipsilateral retinal input to the main visual center, the optic tectum. In the Bolitoglossini, we not only find a broad binocular visual field, but massive ipsilateral retinal projections to the thalamus and the optic tectum. In some parts that are related to the binocular visual field, the ipsilateral retinal input equals the contralateral one.

This situation creates a complete dual projection of the binocular visual fields in both hemispheres of the brain, which can be used for very exact and fast estimation of object distance. This may be of great importance for these salamanders, because due to the relatively enormous size of the eye lenses distance estimation by means of eye accomodation seems to be difficult and/or very slow.

A final internal adaptive phenomenon related to feeding is the reorganization of the peripheral innervation of the projectile tongue. The peripheral nerves serving the tongue muscles, especially those of the tongue pad, must differ in their pathways among species having different patterns of tongue use, for biomechanical reasons, and they do [25]. For example, in the case of tongue pad flipping, where the tongue pad is fixed to the mouth and the skeleton is moved forward only slightly, there must be coiling of the nerves supplying the tongue pad, in order to supply sufficient length of the inflexible nerve to accomodate tongue pad flipping. But there is no special requirement for additional length of the nerves to accomodate the slight hyobranchial protraction. In contrast, in those species with tongue projection, where the tongue pad travels out of the mouth together with the skeleton, sometimes over a considerable distance, there must be a provision for extension of the nerves both to the tongue pad and to the projectile as a whole. The sites of coiling of the relevant nerves differ in the two groups with free tongues - Hemidactyliini and Bolitoglossini. In the former the coiling is in an anterior position, suggesting that hemidactyliines evolved from an ancestor that practiced tongue flipping. In contrast, the bolitoglossines have a posterior coiling, and the group may have evolved very early as tongue projectors from an ancestral stock which utilized only modest tongue flipping. In this regard it is interesting to recall that Wake [23] suggested that the bolitoglossines were the earliest plethodontid lineage to evolve direct development and complete terrestriality during phylogenesis (note that the question of whether direct development evolved separately in the Plethodontini and Bolitoglossini is undecided, cf. [6]).

In contrast to the situation in the periphery of the nervous system, central motor components are apparently conservative among the plethodontids. The same central coordination pattern has different effects due to differences in the biomechanically important geometry of peripheral structures having biomechanical importance (Roth and Wake, in preparation).

Finally, the development of a slender, rapid and far-reaching tongue restricts the range of possible prey types, especially because bolitoglossini usually make little use of their poorly developed jaws. While many non-bolitoglossine plethodontids and other salamanders are able to feed on large and elongate prey item like worms with the help of their large tongue and their jaws, most bolitoglossini are restricted to rather small, compact prey. This disadvantage seems to be fully compesated by the ability to feed on fast-moving prey which usually escape other salamanders, or by the possibility to invade habitats in which these types of prey are dominant, as may be the case in arboreal microhabitats.

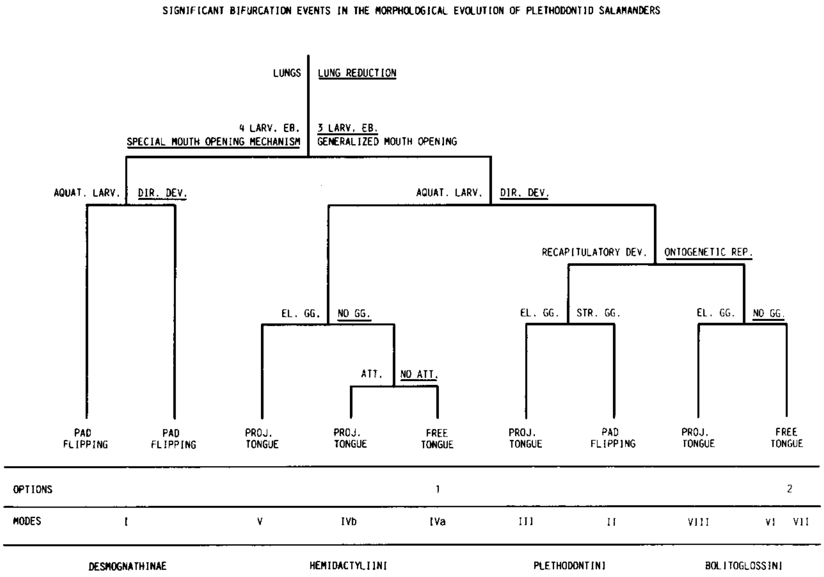

Figure 2. Schematic reconstruction of the morphological evolution of plethodontid salamanders related to feeding. All ancestral evolutionary steps are underlined. Abbreviations: LARV. EB: larval epibranchials; AQUAT. LARV.: aquatic larvae; DIR. DEV.: direct development; RECAPITULATORY DEV.: recapitulatory development; ONTOGENETIC REP.: ontogenetic repatterning; EL. GG.: elongated genioglossus muscle; NO GG.: no genioglossus; STR. GG.: strong genioglossus; ATT.: attached tongue; NO ATT.: no attached tongue; PROJ. TONGUE: projectile tongue. Numbers of "OPTIONS" and "MODES" refer to functional types of plethodontid tongues described in Lombard and Wake [9].

3. DISCUSSION

Plethodontid salamanders are an ancient group and we cannot hope to reconstruct the environments in which evolutionary processes led to the establishment of particular feeding mechanics. But we can take advantage of the diversity of living lineages and the apparently stable systems which exist today to establish a logical chain of events involving organismal-wide phenomena that have given directionality to the pattern of phylogenesis. We argue that certain historical events unrelated to feeding have had profound impact in channeling the evolution of morphology and function.

We envisage a series of bifurcations during the evolution of the family

Plethodontidae, as shown in figure 2. For the sake of argument imagine that ancient populations faced a limited set of options in confronting provincial environments. We avoid speculation as to what specific selection or other pressures might have been involved, and concentrate only on the role "decisions" made at bifurcation points have as they relate to future contingencies.

We have one bias: as phylogenesis proceeded, plethodontids generally diverged from feeding systems characteristic of generalized members of the families Salamandridae and Ambystomatidae in the directions of increase in terrestriality, and in speed, reach and mobility of the tongue.

The initial bifurcation in our scheme involves loss of lungs. The hyobranchial skeleton acts as a force pump to fill the lungs of generalized urodeles, and this imposes a powerful functional constraint on patterns of change in tongue function [24] . All terrestrial urodeles employ modest tongue projection during feeding [2,5,19] , but among the more than 325 species of urodeles there are none that have both lungs and highly projectile tongues. In contrast all species with biomechanical specialization for tongue projection either have greatly reduced and largely nonfunctional lungs, or no lungs at all.

But surely lung reduction is only a necessary, and not a sufficient, condition for the evolution of projectile tongues. There are, for example, even among the exclusively lungless plethodontids such genera as *Desmognathus* and *Aneides*, in which tongue projection is modest. While such nonplethodontids as *Salamandrina* and *Chioglossa* have highly specialized projectile tongues and greatly reduced lungs, the genera *Pachytriton* and *Rhyacotriton* also have reduced lungs but have no appreciable biomechanical specializations for tongue projection. In fact, *Pachytriton* appears to have a reduced tongue pad and to be specialized for aquatic feeding [12] . Furthermore, lung loss is not a sufficient condition for determining what particular pattern of tongue projection is produced. In the most biomechanically specialized plethodontids hyobranchial projection is featured, but in *Salamandrina* tongue pad rotation is used. Both are used by *Chioglossa*, and we speculate that lung loss in this genus might have occurred earlier during the evolution of biomechanical specialization than in *Salamandrina*, which already might have experienced a substantial reduction in the epibranchials (on which hyobranchial projection depends) by the time lung reduction commenced (it is the basibranchials and ceratobranchials that function in the air force pump).

But, for whatever reason lungs were lost in early stages of plethodontid evolution [27] , this event opened an evolutionary channel leading to tongue projection that has remained open throughout plethodontid history.

The second bifurcation involves loss of a pair of epibranchials in aquatic larvae, and a probably independently derived specialization of head structure. Higher numbers of epibranchials represents the primitive condition in salamanders, and only desmognathines among plethodontids retain as many as 4 epibranchials. The extreme reduction of epibranchials has eventual important implications (see below), but the initial reduction from 4 to 3 is perhaps of little immediate functional or evolutionary significance. As with many other factors in our scheme, reduction is a necessary precondition for what later happens, and is not sufficient to force a biomechanical response. While all plethodontids with high specialization for tongue projection have 3 or fewer larval epibranchials, such genera as *Plethodon* and *Aneides* have retained rather generalized tongues. But for the desmognathines the existence of 4 larval epibranchials acts in no particularly limiting way, for very early in the history of this group the lineage became biomechanically specialized for using their heads as wedges in rocky streambeds. This specialization, which involves elaboration of bony parts, ligaments, tendons and muscles of the head and neck region, has major implications for patterns of head evolution and function [4,23] . We suspect that these changes largely preclude elaboration of morphological modifications for more than modest tongue projection.

The next major bifurcation involves evolution of direct development and it occurs in both branches of our scheme - that leading to the Desmognathinae and that leading to the Plethodontini plus Bolitoglossini. Here, again, is an event apparently unrelated to feeding which has far-reaching consequences. Surely direct development is not a sufficient condition for tongue specialization, because the direct developing species of desmognathines have not evolved beyond a stage of modest tongue projection (pad flipping) characteristic of the group as a whole. And, in contrast, the hemidactyliines, which retain aquatic larvae, include such biomechanically specialized tongue projectionists as *Eurycea*.

But, direct development is a necessary precondition for certain patterns of biomechanical evolution [9,24] . In larvae there is a strong gradient from anterior to posterior in degree of development of the ceratobranchials and epibranchials. These elements are linked by ligaments and muscles, and act as a unit in gill ventilation and suction feeding. The largest muscles attach to the largest (most anterior) skeletal elements, and forces are transmitted in chain-like fashion to the more posterior units. Furthermore, during metamorphosis feeding continues by generation of buccal suction which requires hyobranchial function. The adult epibranchial develops as a de-novo structure while the larval epibranchials are retained [20] , and during this period the ceratobranchials are the primary functional components of buccal expansion.

So in the newly metamorphosed animals life on land commences with a strong disparity in size of the ceratobranchials that is simply carried over from the larval state. Throughout life the first ceratobranchial remains the larger element and the primary force transmitter. The folding of the hyobranchial apparatus during tongue projection is determined by this size disparity [8,9] .

At first there is no biomechanical limit on tongue projection in the species with aquatic larvae, but countervening forces eventually do limit the extent to which this system evolves. The large first ceratobranchial has important implications for the efficiency of force transmission, and the hyobranchial apparatus remains relatively massive, even in highly specialized forms. So, relative to some other plethodontids, there is an eventual limitation on speed, directional versatility, and reach of the tongue tip, and the extremes achieved elsewhere are not attained.

But achievement of direct development is not a sufficient condition to overcome the limitations mentioned above, for as has been shown, direct developing desmognathines are far less specialized for tongue projection than are hemidactyliines. Further, the direct developing Plethodontini never achieve high levels of biomechanical specialization. But without loss of aquatic larvae, the opportunity for important ontogenetic alterations is limited.

The next bifurcation in our scheme separates largely recapitulative ontogenies from those in which extensive ontogenetic repatterning, including paedomorphosis in several lineages, occurs. The most evident outcome of significance for tongue evolution of following the more derived pathway is the mixing up of developmental events (what Wake [23] called differential metamorphosis, and is now generally known as dissociation), which leads in the bolitoglossines to new structural arrangements including the most elongate but also the most compact and biomechanically efficient hyobranchial apparatus. Whereas the more recapitulatory Plethodontini follow a relatively conservative ontogeny, including, for example, three developmental epibranchials of graded size despite no direct functional role for them, the bolitoglossines are freed from this apparent developmental constraint. There is a strong suggestion [23] that this group never passes through the stage of three-graded epibranchials, and the outcome is that the second ceratobranchial, when it appears during ontogeny, is larger than the first, which is reduced in size to the point that it no longer plays an important biomechanical role in tongue projection [9].

There is a second possible implication of ontogenetic repatterning, or at least of direct development (on which the possibility of ontogenetic repatterning itself depends). Plethodontids as a group differ from other salamanders that have been studied in the degree of eye frontality and the presence of ipsilateral projections from the retina to the optic tectum. However, within plethodontids there is a clear association between the elaboration of these factors and the loss of aquatic larvae. In larvae the eyes have a strongly lateral orientation and almost no ipsilateral fibers to the central visual system are present. During metamorphosis, as in amphibians in general, the eyes undergo some forward migration, and a few ipsilateral fibers are established, mostly to the diencephalon rather than to the tectum. However, in the bolitoglossines eye frontality is pronounced, and the degree of ipsilaterality is greatly increased [14]. These factors, which are of considerable significance in the achievement of binocularity, which in turn has obvious relevance to feeding by tongue projection, do not become well developed without the loss of larvae, but since they are no better developed in the Plethodontini than in the Hemidactyliini, we suspect that the more general level of ontogenetic repatterning achieved by the bolitoglossines is a necessary precondition.

The final level of bifurcation in our scheme is the only one that has an apparent direct relevance to tongue projection. The genioglossus muscles attach the anterior part of the tongue to the lower jaw at the mandibular symphysis, and so long as they are present the tongue cannot be truly free. But even in this case there are important contingencies. Thus, in three entirely separate lineages (represented by the genera *Hemidactylium*-Hemidactyliini, *Ensatina*-Plethodontini, and *Batrachoseps*-Bolitoglossini the genioglossus has undergone a shift in orientation and a modification in structure which permits but does not facilitate substantially more tongue projection than occurs in other plethodontids which retain the muscles.

An extreme is reached in *Batrachoseps* in which the muscle is so slender and elongated that it inserts near the posterior end of the mandible [13]. Alternatively, in the hemydactyliine genera *Typhlotriton* and *Stereochilus* the genioglossus is reduced to a few fibers or is absent, but a fleshy (fibrous connective tissue and epithelium) attachment connects the tongue to the anterior floor of the mouth. Nevertheless, in order to attain a truly free and projectile tongue, the genioglossus muscles and the fleshy attachments both must disappear.

The options taken at this final bifurcation have implications, and each has an apparent stopping point imposed either by this event or some prior one. Thus *Batrachoseps* entered a channel which led to very great specialization of the genioglossus and substantial projectile capacity, but nevertheless left it with an attached tongue and an apparently closed evolutionary channel. We have already discussed the stopping point reached by the hemidactyliines. The stopping point of the two free-tongued bolitoglossine supergenera (*Hydromantes, Bolitoglossa*) is more speculative because of our knowledge of the existence of two morphological states which we could not have predicted from biomechanical considerations related to the theoretical model of Lombard and Wake [8].

First, in *Hydromantes* an unexpected lengthening of the basibranchial occurred in conjunction with a very great lengthening of the epibranchials, associated with increased reach of the tongue. Basibranchial length bears a near isometric relationship to body length in all other plethodontids, and this new relationship could not be predicted. Secondly, in *Thorius* and possibly some other tiny members of the supergenus *Bolitoglossa* the first ceratobranchial is so reduced in size that the anterior attachment is weakened and the normally articulated hyobranchial apparatus disarticulates during projection, thus at least in theory increasing the mechanical efficiency of the system. Again, this was not predictable, and in fact Lombard and Wake [8] accepted articulation as a premise in developing their biomechanical model. The occurrence of these two extremes of specialization should caution against further prediction that bolitoglossines have reached a morphological stopping point, although we think it likely (but we could be accused of failure of imagination!).

4. CONCLUSIONS

Our goal for this essay has been to demonstrate with an empirical example what we believe to be a principle of phylogenesis. There is an unfortunate modern tendency to ignore what we consider to be internal factors in evolution, such as the various constraints that restrict phylogenetic diversification, and the factors which, in contrast, open what are essentially organismal (i.e., developmental, morphological, physiological, behavioral) channels along which evolution appears to move with directionality, following avenues of least resistance. But the existence of such channels does not ensure a particular pathway. Rather, some organismal phenomenon is a necessary precondition for a particular pattern, or subpattern within an overall pattern of parallel evolution. In the case we have chosen, the parallel evolution of feeding systems utilizing projection of free tongues in plethodontid salamanders, such seemingly remote phenomena as respiratory physiology, life history biology, and pattern of ontogeny have been shown to have rather direct relevance to the feeding biology, including such diverse components as sensory perception and biomechanics. This paper is an attempt to reintroduce a strongly organismal component to considerations of evolution and phylogeny, such as we have advocated elsewhere [7,26] .

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