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Feeding mechanisms and the evolution of plethodontid salamanders.

The tongue pad of plethodontid salamanders lies at the anterior tip of the cartilaginous hyobranchial skeleton. The skeleton consists of a median basibranchial and bilateral radial cartilages, first and second ceratobranchials, epibranchials and ceratohyals. A median lingual cartilage may also be present. Movement of these elements, save the ceratohyals, effects projection and retraction of the pad during the feeding sequence.

Projection is accomplished by contraction of the paired subarcualis rectus I muscles. These muscles are spirally wound about the tapered epibranchials. On contraction, a force is generated on the epibranchials to propel the skeleton from the mouth. Retraction is accomplished by the paired rectus cervicus profundus muscles. These muscles run uninterrupted in the ventral body wall from the pelvis to the anterior tip of the basibranchial. At rest they are coiled or pleated in the gular region. During projection, they uncoil and, when extended, contract to return the tongue to the mouth.

Although the skeletal elements could be projected in the rest position, theoretical advantages are gained by folding the ceratobranchials and epibranchials to the midline during projection. These include a greater efficiency in aiming, a larger field of projection, and a decrease in surface area subject to viscous friction. Serial reconstructions of tongues in various stages of projection show that the skeleton is indeed folded. During projection, the ceratobranchials are moved to the midline behind the basibranchial. The flexible epibranchials follow. The result is a linearly compact projectile with the tongue pad at its anterior tip.

The arrangement and numbers of muscles and relations of the skeletal elements place limitations on the skeleton for movement. Analysis of these limitations indicates that the skeleton can be folded only by indirectly forcing the ceratobranchials to the midline on a rigid track. Further analysis shows the track would need to be in the form of a tractrix:

$$y = \int \frac{a}{x} \sqrt{1 - \frac{x^2}{a^2}}\, dx$$

where (a) is the length of the ceratobranchial riding on the tractrix. Measurements on partially to completely projected tongues validated this concept. Serial reconstructions show that the anterior slips of the subarcualis rectus I muscles form the track as they proceed antero-medially from their spiral insertions to their origin on the ceratohyals. Using a tractrix for folding theoretically gains the animal the ability to move the tongue pad at a constant velocity during the acceleration and deceleration phases of projection and retraction.

Premature unfolding of the ceratobranchials during the feeding sequence is prevented by a simple locking mechanism. A ligament running from the anterior tip of ceratobranchial I to the lingual cartilage acts in a manner analogous to the radius lever in a vice grip, preventing spreading.

Specializations for increased projection distance include loss of the genioglossus muscle and loss of integumentary attachments. The length of the basibranchial and diameter of the subarcualis rectus I muscle are comparable in all animals regardless of the projection distance. Increased projection distance is gained by lengthening the epibranchials.

Certain features of the system involve specializations for increased efficiency. As epibranchials increase in length in a lineage, second ceratobranchials tend to shorten. This can be explained by analysis of movements along the track. The system should fold rapidly, for folding places the major elements in a position of maximum efficiency for force transmission. In addition, these proportional changes theoretically increase projection speed.

Comparative studies permit sorting of the plethodontid genera into functional and phylogenetic groups. This sorting is based on detailed analysis of structure and relative proportions of skeletal elements, presence and absence of skeletal elements and muscles, and structure and arrangement of muscles. Various arrangements of skeletal elements and muscles are interpreted in functional terms, and common patterns of function and organization emerge.

Theoretically, the movable portions of the hyobranchial apparatus can fold in two ways. In one the first ceratobranchial moves along the track in a more or less planar path, and the second ceratobranchial and basibranchial buckle. This is found in hemidactyliine genera. The other pattern is for the second ceratobranchial to move along the track in a planar path, in which case the first ceratobranchial and basibranchial buckle. This occurs in bolitoglossine genera. A number of proportional and muscular changes characterize these alternative adaptive pathways.

Tongue freedom (loss of anterior muscular and cutaneous attachments) has evolved independently in groups having the distinctive folding patterns. In both groups there are forms which have the characteristic folding pattern of that group, but which retain an anterior attachment. The folding patterns are fundamental differences between the groups and evolved prior to the acquisition of tongue freedom.

Tongue pad structure and function is also subject to variation that is of phylogenetic significance. For example, in the hemidactyliine genera with free tongues the basiradialis is a dominant pad muscle, and the interradialis is absent, while the reverse is true in bolitoglossines.

Hemidactylium possesses a combination of characters which suggests that it has the most generalized tongue in the subfamily Plethodontinae. It retains an aquatic larval stage and has a distinct larval hyobranchial apparatus, in contrast to the situation in members of the tribes Plethodontini and Bolitoglossini. It is the only plethodontid genus which has both a basiradialis and an interradialis muscle, and it has a relatively generalized anterior basibranchial. Its tongue is sufficiently different from that of other hemidactyliines as to raise questions concerning the current tribal level taxonomy of the family. Perhaps _Hemidactylium_ should be placed in a separate tribe, with the remaining members of the currently recognized Tribe Hemidactyliini being transferred to a new Tribe Euryclini. This transfer would make possible a phylogeny of the Subfamily Plethodontinae in which free tongues evolved twice, and direct development only once.

Lunglessness has been a key factor in the evolution of extreme tongue projection specializations in salamanders. The use of the hyobranchial apparatus as a force pump, to fill the lungs, imposes design constraints that keep the system relatively generalized in most salamanders. Those species with tongues specialized for projection (for example, _Rhyacotriton_, _Salamandrina_, _Chioglossa_ and many plethodontids) have without exception "escaped" this constraint by becoming lungless, and this event has been highly significant in the evolution of tongue specialization and terrestriality in salamanders. (Supported by National Science Foundation Grant GB 17112).