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Phylogeny of Plethodontid Salamanders and the Evolution of Feeding
Dynamics**

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TONGUE EVOLUTION IN THE LUNGLESS SALAMANDERS,
FAMILY PLETHODONTIDAE
IV. PHYLOGENY OF PLETHODONTID SALAMANDERS
AND THE EVOLUTION OF FEEDING DYNAMICS

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Abstract.—Plethodontids, a monophyletic group, comprise about 60% of living salamanders. Many have a tongue that may be projected rapidly and for a distance up to half the body length. Previous studies have focused on the functional morphology of the projectile tongue and the comparative morphology of the feeding system in the family. Here we present a working hypothesis for the phylogeny of plethodontids and a scenario for the evolution of tongue feeding based on the phylogenetic hypothesis.

Primitive and derived states are identified and transformation series proposed for 30 characters. Four alternative phylogenetic hypotheses are presented. Our choice of a preferred phylogenetic hypothesis is based on consideration of conflicting characters and tongue projection mechanics. The preferred hypothesis is not the most parsimonious, in a strict technical sense, because several homoplasious characters appear (on functional grounds) to be closely associated with attainment of tongue projectility, which itself has evolved several times. In our hypothesis the bolitoglossines and plethodontines are sister taxa. They in turn are the sister taxon of the hemidactylines, and this grouping is the sister taxon of the desmognathines. Within the bolitoglossines, *Batrachoseps* is the sister taxon of the Neotropical genera (supergen *Bolitoglossa*).

In our scenario for the evolution of tongue feeding, the ancestral plethodontid had an attached protrusible tongue. From this condition attached *projectile* tongues have arisen at least three times within the family: in the ancestors of the hemidactylines; in the ancestors of *Ensatina*; and in the ancestors of the bolitoglossines. In turn, the attached projectile condition has given rise to *free* projectile tongues at least once within the hemidactylines and twice within the bolitoglossines. This scenario tends to maximize the number of times attached projectile and free projectile tongues have evolved in the family. [Plethodontidae; phylogeny; tongue; evolutionary morphology.]

The lungless salamanders, family Plethodontidae, are distributed in North and Central America and northern South America in the New World, and two species of one genus occur in Europe. The family includes over 200 species, currently placed in 27 genera, which comprise about 60% of all salamander species. The family is characterized by a relatively high degree of terrestriality (Dunn, 1926; Wake, 1966) and, in addition, most plethodontids have a highly specialized feeding mechanism, usually extensive tongue projection. Plethodontids are a monophyletic group based on the presence of an opercularis muscle formed entirely or in part from the cucullaris and, in transformed adults, the presence of a nasolabial groove and the

absence of an ossified pterygoid bone. In addition, all are lungless—a condition shared with a few derived species of other families. In this paper we add further synapomorphies from the structure of the feeding apparatus.

For the past 50 years, the hyobranchial skeleton and musculature of the feeding system have been the major structural attributes used in considering plethodontid phylogeny. Thus, it is not surprising that most authors who have considered the phylogeny of plethodontids have also made at least passing reference to feeding evolution, if not considering it in detail. Of particular importance has been the perceived dichotomy “attached tongues” versus “free tongues.” Previous authors either

TABLE 1. Tongue modes and structure/behavior categories in plethodontid salamanders. Letters designating a subfamily or tribe are indicated.

Tongue mode and structure/behavior category		Mode symbol	Genera
Subfamily Desmognathinae – D			
I	Attached protrusible	DES	<i>Desmognathus</i> <i>Leurognathus</i> <i>Phaeognathus</i>
Subfamily Plethodontinae			
Tribe Plethodontini – P			
II	Attached protrusible	PLE	<i>Plethodon</i> <i>Aneides</i>
III	Attached projectile	ENS	<i>Ensatina</i>
Tribe Hemidactyliini – H			
IV	Attached or free projectile	EUR	<i>Stereochilus</i> ^a <i>Typhlomolge</i> ^a <i>Haideotriton</i> ^a <i>Typhlotriton</i> ^a <i>Eurycea</i> ^b <i>Gyrinophilus</i> ^b <i>Pseudotriton</i> ^b
V	Attached projectile	HEM	<i>Hemidactylium</i>
Tribe Bolitoglossini – B			
VI	Free projectile	BOL	<i>Bolitoglossa</i> <i>Nyctanolis</i> <i>Pseudoeurycea</i> <i>Chiropterotriton</i> <i>Lineatriton</i> <i>Parvimolge</i> <i>Thorius</i> <i>Dendrotriton</i> <i>Bradytriton</i> <i>Oedipina</i> <i>Nototriton</i>
VII	Free projectile	HYD	<i>Hydromantes</i>
VIII	Attached projectile	BAT	<i>Batrachoseps</i>

^a Attached projectile tongue, symbolized in paper by EUR¹.^b Free projectile tongue, symbolized in paper by EUR².

have proposed that free tongues have arisen once and that all genera sharing this condition form a monophyletic taxon (Tanner, 1952; von Wahlert, 1957; Regal, 1966), or that free tongues have arisen two or more times in parallel and that certain genera or groups of genera having this condition have closest relatives with attached tongues (Piatt, 1935; Wake, 1966).

In a previous paper (Lombard and Wake, 1976), we described the general morphology of the skeleton, musculature, and connective tissue of the feeding apparatus, and formulated a hypothesis of biomechanical function for tongue movement. In a second paper (Lombard and Wake, 1977), we

described the diversity of morphology found in the skeleton, musculature, and soft tissues of the tongue in plethodontids. For each element we proposed functional roles and summarized our findings by identifying eight tongue feeding modes that are listed in Table 1 (which also contains explicit reference to the acronyms used in this paper) and are based on unique combinations of tongue structures.

Members of modes I and II have *attached protrusible* tongues. In these two modes, the tongue is attached anteriorly to the jaw by a short genioglossus muscle, connective, and mucosal tissue, yet the tongue is protrusible a moderate distance beyond the

TABLE 2. Character-state distribution for eight tongue-mode OTUs.

Characters	OTU							
	DES	PLE	ENS	EUR	HEM	BOL	HYD	BAT
1 Urohyal	1	1	1	1	1	1a	1a	1a
2 Basibranchial	2	2	2	2a	2a	2a	2a	2a
3 Radii	3a'	3a''	3a''	3	3	3a	3b	3a
4 Hyobranchial proportions	4	4	4	4a	4a	4b	4b	4b
5 Ceratobranchial function	5	5	5	5	5	5a	5a	5a
6 Rectus cervicis profundus	6	6	6	6a	6a	6a	6a	6a
7 Rectus cervicis superficialis	7	7	7	7	7	7a	7a	7
8 Omohyoideus	8	8	8	8	8	8a	8a	8
9 Muscular cylinder	9	9	9	9	9	9a	9a	9a
10 Genioglossus	10	10	10a	10a'	10a	10a'	10a'	10a
11 Circumglossus	11	11	11	11	11	11a	11a	11a
12 Intraglossus	12	12	12a	12	12	12/12a	12	12
13 Basiradialis	13	13	13	13	13	13/13a	13a	13
14 Hyoglossus anterior	14	14a	14a	14	14a	14	14a	14a
15 Hyoglossus posterior	15	15a	15	15	15	15	15	15
16 Suprapeduncularis	16	16	16	16a	16a	16a	16a	16a
17 Tongue attachment	17	17	17	17/17a	17	17a	17a	17
18 Tongue nerves	18	18	18a	18	18	18a	18b	18a
19 Epibranchial number	19	19a	19a	19a	19a	19b	19b	19b
20 Tail breakage	20a	20a'	20b'	20	20a''	20b'''	20a'	20b''
21 Jaws	21a	21	21	21	21	21	21	21
22 Brainstem	22	22	22	22	22	22a	22a	22a
23 Vomer	23	23a	23a	23	23	23a	23a	23a
24 Parietal	24a''	24	24	24a	24a	24a'	24	24a'
25 Maxilla	25a'	25a''	25a''	25	25	25	25	25a
26 Premaxilla	26a	26	26	26/26a	26	26a'	26	26/26a'
27 Chromosome number	27	27	27	27	27	27a	27	27a
28 Development	28/28a	28a	28a	28	28	28a	28a	28a
29 Amphibian periotic canal	29a'	29a'	29a'	29a'	29a'	29/29a	29a	29
30 Otic semicircular canal	30	30	30a	30	30	30b	30b	30b

margin of the jaw. Members of modes III, V, and VIII have *attached projectile* tongues. The tongue is attached to the jaw by an elongated genioglossus plus connective and mucosal tissue. The tongue is capable of rapid projection well beyond the margin of the jaw. Members of modes VI and VII and some members of mode IV have *free projectile* tongues. The genioglossus muscle and anterior connective tissue are absent (free tongue). The tongue is capable of rapid projection for a considerable distance beyond the margin of the jaw.

These three structure/behavior categories—attached protrusible, attached projectile, and free projectile—represent a partitioning of the attached-tongue condition not explicitly recognized by previous authors. Von Wahlert (1957), Regal (1966), and Wake (1966) referenced some genera possessing the attached projectile

condition as perhaps “tending towards” the free projectile state, but did not discuss all genera with this condition, nor consider them explicitly in their ideas of tongue evolution. The attached projectile tongue is in its own way as specialized as the free projectile tongue and deserves explicit consideration.

At our present level of knowledge, the eight tongue modes summarize the greatest structural variation of any adaptive complex in plethodontid salamanders, and this diversity apparently determines variation in feeding function (Thexton et al., 1977). This morphological diversity is surprising when contrasted with the generally conservative nature of other structural systems in salamanders in general and plethodontids in particular (Wake et al., 1983a; Larson, 1984), but presents an opportunity for a reexamination of both the

TABLE 3. Autapomorphies for eight tongue-mode OTUs.

Mode	OTU	Autapomorphies
I	DES	3a', 20a, 21a, 24a'', 25a
II	PLE	15a
III	ENS	20b'
IV	EUR	None
V	HEM	20a''
VI	BOL	20b'''
VII	HYD	3b, 18b
VIII	BAT	20b, 25a

evolution of the plethodontid lineages and of the feeding system of the group.

In this paper, we are concerned both with evolutionary relationships among higher categories of plethodontids and the potential pathways along which the tongue has evolved. Our approach to these goals, in part, is explicitly cladistic. Cladistic methodologies generally have as a goal a statement of the historical relationships of organisms and are not usually concerned with what the final best statement may say about the evolution of the components of the organisms. The usual procedure in a cladistic study is to seek the phylogenetic statement that maximizes those character states that are uniquely derived and minimizes those that are convergent. The formation of such a phylogenetic statement is only a partial goal of this study. In the following, we proceed on the premise that any statement about evolutionary relationships within a group of organisms is also a statement about the evolution of any part, or complex of parts, of these organisms. We are combining aspects of the methodology of phylogenetic systematics with the explicit goal of generating a scenario for the evolution of a morphological complex. A similar approach was used by Lombard and Bolt

(1979) in a study of the evolution of the peripheral auditory system of early tetrapods.

DATA AND METHODS

Morphological data from the tongue and associated structures form 19 of the characters used in this study. These data come from the structural studies of Lombard and Wake (1976, 1977), Wake et al. (1983b), and Roth and Wake (1985a); these authors listed the organisms examined and techniques used, and also illustrated structural details. Data for 11 additional characters come from Wake (1966), Wake and Dresner (1967), Hinderstein (1971), Lombard (1977), and Leon and Kezer (1978).

For each of the 30 characters, primitive and derived states were identified on the basis of outgroup analysis, using the conditions found in other families (especially the Hynobiidae, Dicamptodontidae, and Ambystomatidae) as representing the ancestral condition. For each character we proposed a hypothesis of character-state revolution (see Appendix).

Our analysis uses generic assemblages in the eight feeding modes (Table 1) as primary operational taxonomic units (OTUs). The character states in the Appendix are combined with these eight OTUs to form a matrix in Table 2 that is the basis of our analyses.

RESULTS

Our data contain 13 derived states autapomorphic for one of the eight tongue-mode OTUs (Table 3). Except for EUR, each of the tongue-mode OTUs is defined by at least one autapomorphy. EUR has been defined by more subjective ecological and zoogeographic criteria by Wake (1966). No associations of genera other than that de-

TABLE 4. Autapomorphies uniting tongue-mode OTUs into four group OTUs.

Group OTU symbol	Autapomorphies	Included tongue-mode OTUs
D	3a', 20a, 21a, 24a'', 25a'	DES
P	3a'', 25a''	PLE + ENS
H	24a	HEM + EUR
B	1a, 3a, 4b, 5a, 9a, 11a, 19b, 22a, 30b	BOL + HYD + BAT

picted in Table 3 produce more strongly defined or equally (although differently) defined primary taxonomic units.

For preliminary analyses, the eight tongue-mode OTUs are condensed into four group OTUs. The autapomorphies that define the group OTUs are listed in Table 4. All of the four are defined by at least one autapomorphy. No alternative groupings of tongue-mode OTUs are more strongly or equally (although differently) defined by our data set.

For four taxa, assuming dichotomous branching and that no taxon may be ancestral to any other taxon, 15 cladograms are possible. The 15 possible cladograms for our four group OTUs are illustrated in Figure 1. Horizontally, there are five sets. Each of the upper four sets is constant with respect to the first group OTU derived. The bottom set is made of doublets. Vertically, there are three sets, each numbered. In each, the OTUs always have the same topological relationship and members of the set differ from one another only by location of the cladogram root.

Our 30 characters have a grand total of 49 derived states: 26 from the tongue; and 23 from other features. Of these 49 derived states, 25 either are autapomorphic for one of the eight tongue-mode OTUs or form an autapomorphy for one of the four group OTUs (Tables 3, 4). These derived states are cladogram-independent (i.e., uniquely derived for all 15 hypotheses in Fig. 1). Thirteen derived states are convergent and cladogram-independent (i.e., convergent in all 15 hypotheses). The distribution of these 38 cladogram-independent derived states is shown in Table 5. The remaining 11 derived states are cladogram-dependent (i.e., uniquely derived or convergent depending on the cladogram). These 11 derived states are those most useful for choosing a working phylogenetic hypothesis and will be considered in detail in the Discussion.

Seven of these 11 derived states are uniquely derived or convergent depending on the particular cladogram for four group OTUs. The taxa united by these seven derived character states are indicated

in Table 5. In Figure 1, the seven derived states are placed as black dots on each cladogram only when uniquely derived. Thus, derived state 19a (uniting P + H + B) is uniquely derived in each member of cladogram set V, but is convergently derived in all other sets, and so is indicated only in set V. Similarly, the suite of derived states (1a, 4a, 6a, 16a) uniting groups H + B, is convergently derived in all cladograms except for three members of root-family 3, and so is indicated only for these three. The fraction associated with each cladogram is the number of cladogram-dependent derived states that are uniquely derived (numerator) or convergently derived (denominator). A question mark on a branch indicates that no uniquely derived state defines the OTUs joined at the node (but the OTUs themselves are defined by autapomorphies, Table 3).

In only two cladograms, V2 and V3, are all branch nodes defined by uniquely derived characters. Cladogram V3 maximizes uniquely derived states and minimizes convergently derived states, and, in this sense, is the most strongly supported hypothesis; cladogram V2 is the next most strongly supported. All other cladograms have at least one undefined node.

Projectile tongues are indicated by a solid arrow in Figure 1. If the arrow is below a group OTU, all members have a projectile tongue; if above a group OTU, only some members have a projectile tongue. Free projectile tongues are indicated by an open triangle. Placement above a group OTU indicates that some members have free projectile tongues. Projectile tongues and free projectile tongues are derived at least twice in all cladograms: there is no hypothesis of historical relationship that indicates a unique and clinal evolution of attached projectile to free projectile tongues from protrusible tongues.

The attached projectile tongue of *Ensatina* (solid arrow over P in all cladograms in Fig. 1) is independently derived from those in other OTUs in all hypotheses, as are the free projectile tongues which arise independently within H and B. The major

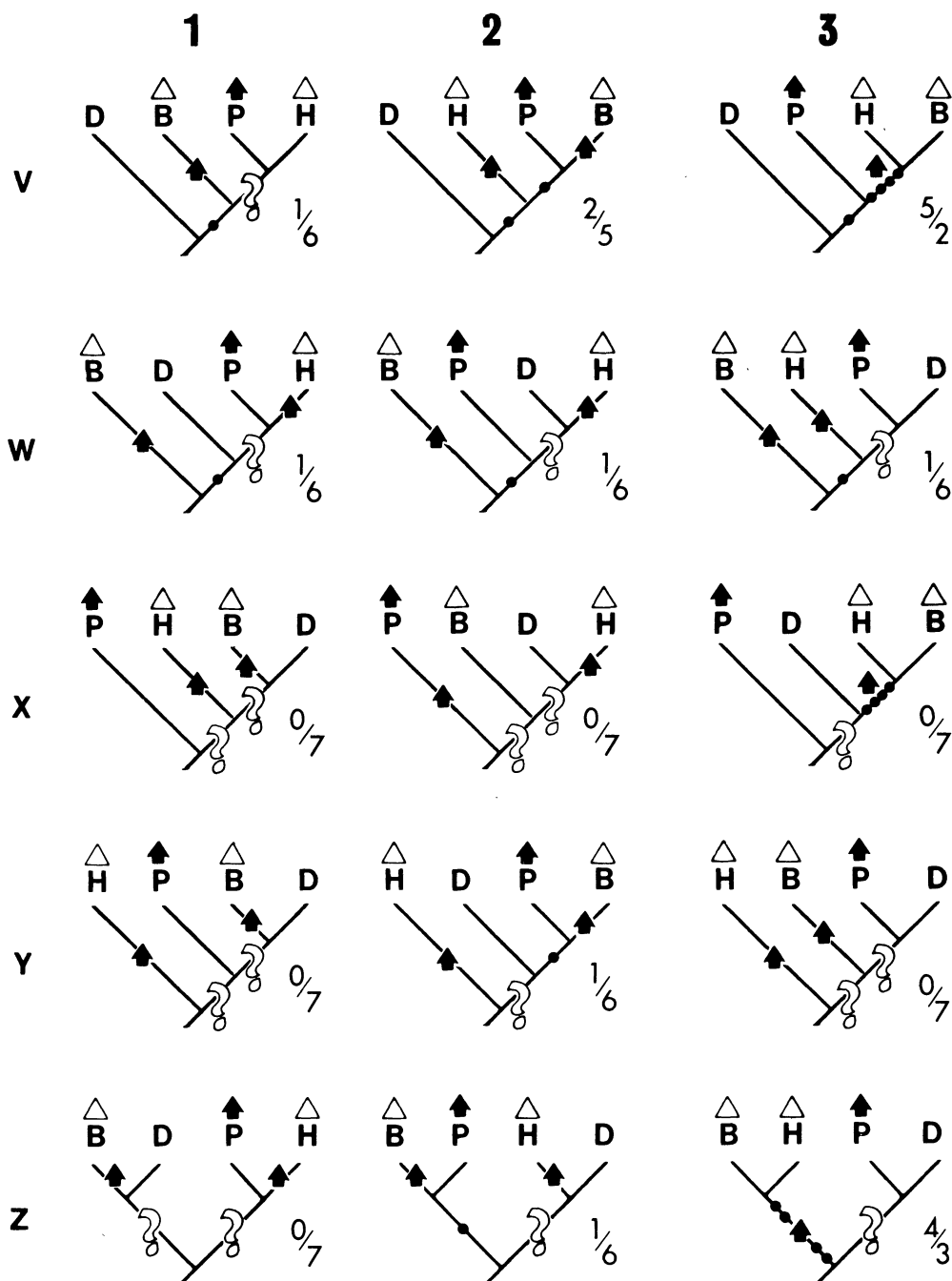


FIG. 1. The 15 cladograms possible for four group OTUs. Each horizontal row designated by a letter and each vertical column numbered. Solid dots indicate uniquely-derived characters attributable to all members of taxa beyond next node. Characters (black dots) uniting: B + P + H = 19a; P + B = 23a; H + B = 2a, 4a, 6a, 17a; D + P + H = 29a'. Definition of derived states in Appendix. Open triangles indicate free projectile tongues; solid arrows indicate attached projectile tongues. A question mark on a branch indicates that no uniquely derived state defines the OTUs joined at a node.

TABLE 5. Distribution of 49 derived character states into four classes..

Derived character state	OTUs	Cladogram independent		Cladogram dependent	
		Uniquely derived	Convergently derived	Within B only	Group OTUs
Tongue character states					
1a	B	(X) ^a			
2a	H B				X
3a	B (HYD implied) ^b	(X)			
3a'	D	(X)			
3a''	P	(X)			
3b	HYD	X			
4a	H (B implied)				X
4b	B	(X)			
5a	B	(X)			
6a	H B				X
7a	BOL HYD			X	
8a	BOL HYD			X	
9a	B	(X)			
10a	ENS HEM BAT		X		
10a'	EUR BOL HYD		X		
11a	B	(X)			
12a	ENS, some BOL		X		
13a	HYD, some BOL		X		
14a	P HEM HYD BAT		X		
15a	PLE	X			
16a	H B				X
17a	BOL HYD, some EUR		X		
18a	ENS (B implied)		X		
18b	HYD	X			
19a	P H (B implied)				X
19b	B	(X)			
Subtotal for 26 states		12	7	2	5
Nontongue character states					
20a	D	(X)			
20a'	PLE HYD		X		
20a''	HEM	X			
20b'	ENS	X			
20b''	BAT	X			
20b'''	BOL	X			
21a	D	(X)			
22a	B	(X)			
23a	P B				X
24a	H	(X)			
24a'	BOL BAT			X	
24a''	D	(X)			
25a	BAT	X			
25a'	D	(X)			
25a''	P	(X)			
26a	D, some EUR		X		
26a'	BOL, some BAT		X		
27a	BOL BAT			X	
28a	P B, some D		X		
29a	HYD, some BOL		X		
29a'	D P H				X
30a	ENS (B implied)		X		
30b	B	(X)			
Subtotal for 23 states		13	6	2	2
Total		25	13	4	7

^a Parenthetical Xs indicate cladogram-independent derived states that unite two or more of eight tongue-mode OTUs to form group OTUs. Nonparenthetical Xs in this column unique to tongue-mode OTU indicated.

^b "Implied" indicates that state does not occur in living members but must have occurred in ancestors if character transformation is correct.

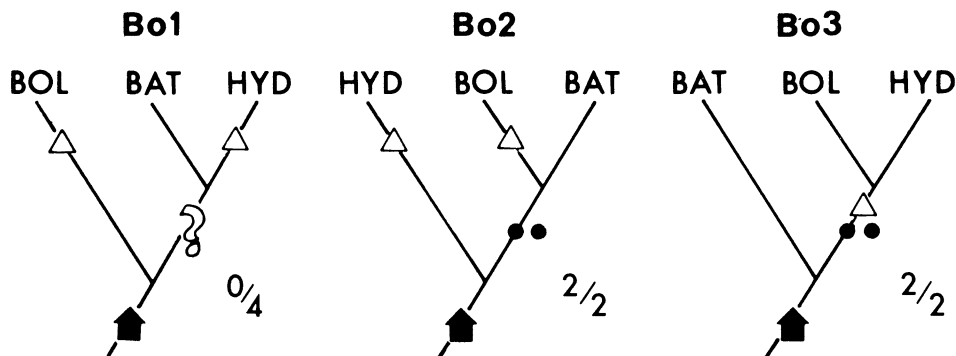


FIG. 2 Three possible cladograms for three OTUs of B. Derived, cladogram-dependent characters (black dots) uniting BOL + BAT = 24a, 27a; BOL + HYD = 7a, 8a. Definition of derived states in Appendix. Symbols as in Figure 1.

question emanating from Figure 1 is whether the attached projectile condition evolved once or twice in the ancestry of H and B. When H and B are sister taxa (Cladograms V3, X3, and Z3), the implication is that the attached projectile condition arose once in their common ancestor. When H and B are not sister taxa, the projectile condition must be hypothesized to have arisen twice.

Of the 11 cladogram-dependent derived states, four are uniquely derived or convergent depending on the arrangement of the tongue-mode OTUs in B. The taxa united by these four derived states are indicated in Table 5. In Figure 2, the four derived states are placed as black dots on each (when uniquely derived) of the possible cladograms for the three OTUs forming B. In each of two cladograms, the most derived pairing of taxa is defined by two uniquely derived states. The fraction after each cladogram summarizes the cladogram-dependent character states (numerator = uniquely derived; denominator = convergently derived). Cladograms Bo2 and Bo3 are equally well supported. While cladograms Bo1 and Bo2 depict free projectile tongues as having been derived twice, cladogram Bo3 depicts free projectile tongues as having arisen but once, in the ancestor of BOL + HYD.

Four possible cladograms are supported at all nodes: cladogram V2 (Fig. 1) with B arranged either as in cladogram Bo2 and

Bo3 (Fig. 2); and cladogram V3 with B arranged either as in cladogram Bo2 or Bo3. Two extreme possibilities for tongue evolution in the plethodontids are indicated by these cladograms, with intermediates also possible. The separate origins of attached projectile and free projectile tongues are at a minimum in cladogram V3 when B is arranged as in cladogram Bo3 (Fig. 2). In this combination, attached projectile tongues arise twice: once within P; and once in the ancestor of the derived pairing H + B. Free projectile tongues also arise twice: once within the H group; and once in the ancestor of BOL + HYD within the B group. The separate origins of attached projectile and free projectile tongues are at a maximum in cladogram V2 if the members of B group are arranged as in cladograms Bo2. In this combination, attached projectile tongues arise three times and free projectile tongues also arise three times.

If one accepts certain groups as monophyletic there is no alternative to substantial convergence. If P, H, and B each are monophyletic, attached projectile or free projectile tongues evolved independently in each. If *Ensatina* is a member of a monophyletic P, its specialized genioglossus must have evolved from a more primitive muscle configuration within that group (assuming no reversal of state). If *Hemidactylium* is a member of a monophyletic H, the genioglossus must have been lost within that group, assuming no reversal

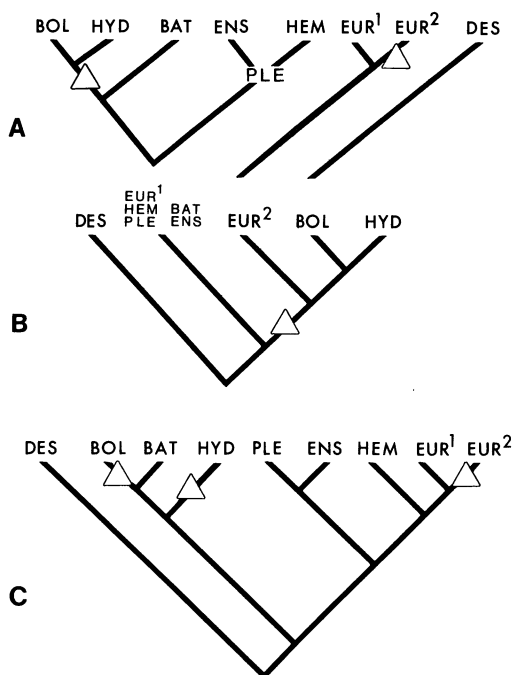


FIG. 3. Previously published hypotheses of plethodontid relationships and tongue evolution. OTU symbols identified in Table 1. Open triangles indicate origin of free tongues in each hypothesis, and all members of OTUs beyond an open triangle have free tongues. (A) Piatt, 1935. (B) von Wahlert, 1957; Regal, 1966; and grouping of EUR² + BOL + HYD, Tanner, 1952. (C) Wake, 1966.

of state. Similarly, if *Batrachoseps* is a member of a monophyletic B, the genioglossus must have been lost within that group. Since specialization of the genioglossus (either elongation or loss) is necessary for projectility (as the term is used in this paper), acceptance of these taxonomic units also requires acceptance that convergent tongue evolution has taken place.

DISCUSSION

In our view, a simple appeal to parsimony in order to select a working hypothesis of plethodontid relationships from those supported by derived states is unsatisfactory. Minimizing convergences as a selection technique indicates cladogram V3 (Fig. 1) as the strongest for the four group OTUs, while being equivocal with

respect to the relationships among the members of group B (Fig. 2). Detailed consideration of the 11 characters involved and some functional aspects of the feeding apparatus, however, leads us to prefer cladogram V2 for the four group OTUs and cladogram Bo2 for the members of B. Our rationale and the implications of our choice are outlined below.

Relationships among the four group OTUs.—Six pairings are possible for the four group OTUs. Three of these pairings have been proposed by previous workers. Piatt (1935) suggested a phylogeny in which B and P (plus HEM) are paired (Fig. 3A), and Tanner (1952) and von Wahlert (1957) proposed pairing H in part with B in part (Fig. 3B). Because the generic groupings used by these authors were slightly different than those used here, correspondence is not exact. Nevertheless, these pairings capture the major aspects of their phylogenetic hypotheses. Wake (1966) proposed pairing P and H (Fig. 3C). These three previously proposed pairings are found in different cladogram sets (Fig. 1): Wake's in Set 1; Piatt's in Set 2; and Tanner's and von Wahlert's in Set 3. Piatt paired P and B because both groups are terrestrial and have direct development. Tanner and von Wahlert paired H in part and B in part on the basis that the two groups (as they defined them) have free tongues. Wake paired P and H primarily by default, having first recognized D and B on morphological criteria. No features were used to unite P and H. Rather, H was envisioned as a continuously evolving, central group that gave rise sequentially to D, B, and P.

Our data support only two of the possible six pairings with derived character states: P + B with one derived state (23a—vomer with loss of bony shelf on preorbital process); and H + B with four derived states (2a, 4a, 6a, and 16a—expanded basibranchial, derived hyobranchial proportions, rectus cervicis profundus recurved at anterior end, discrete suprapericardularis muscle). The pairing H + B is the more strongly supported numerically. However, we prefer the pairing of P + B in framing our working hypothesis of re-

lationship, despite the fact that it is less well supported numerically by derived character states, based on further detailed consideration of the characters.

Since the two pairings supported by derived states both contain B, the two defining sets of derived states are in conflict. If the pairing is H + B, then state 23a must have been derived twice. If the pairing is P + B, then states 2a, 4a, 6a, and 16a must have been derived twice. We ask three questions concerning conflicting states: (1) Are the structural configurations present in the relevant taxa indeed identical? (2) Are the states indeed derived? (3) Do the states represent an elaboration of structure or a loss of structure?

Of the five derived states relevant at this point, two (2a, 4a), or even three (16a), have a good chance of not being identical. While the basibranchial of the members of both B and H is expanded to form flanges (2a), the flanges have different configurations. In B, the expansion extends for much of the length of the basibranchial, including the region of the ceratobranchial I articulation. In addition, the shelves formed by the flanges are relatively narrow (Lombard and Wake, 1976:fig. 11). In H, the flanges are restricted to that part of the basibranchial anterior to the articulation of ceratobranchial I and are comparatively broad (Lombard and Wake, 1976:fig. 10). The basibranchial flanges in the two groups are not identical in detail, and the flanged or flattened and expanded condition may have evolved independently in the two groups (i.e., two derived states may be present, not one). In state 4a, the hyobranchial skeleton is characterized by a relative increase in the length of the epibranchial coupled with a decrease in the relative length of the second ceratobranchial, in relation to the primitive condition. State 4a is characteristic of and restricted to H. In state 4b, the epibranchial is relatively even longer and the second ceratobranchial relatively even shorter. State 4b is characteristic of and restricted to B. In the character-state phylogeny used in this work, 4a (the condition in H) is intermediate between the primitive con-

dition and that found in 4b of B. Thus, by implication the ancestor of group B at some time possessed state 4a (i.e., 4a cannot be definitely assigned to any known extant member of B). Although a continuum of hyobranchial proportions exists (Lombard and Wake, 1977:fig. 5) and a clinal hypothesis of the evolution of proportion is reasonable a priori, it is also quite possible that the ancestral state of B is not represented by the state characteristic of H; again, two derived states may exist, not one. In state 16a the suprapeduncularis is enlarged and more sharply delimited than in state 16. Because of the limits of our materials, we cannot be certain that this condition is identical in H and B, although it appears to be. The point of this analysis is to make clear that function of the entire organ as it evolves toward the projectile condition may well entail a series of necessary morphological changes that superficially give the impression of homology; subtle differences, on the other hand, suggest that these states were independently derived.

Finally, one of the conflicting characters (23a) supporting the pairing P + B is derived through loss. Based on Hecht and Edwards' (1977) reasoning, this character has a higher chance of representing a homoplasious condition than of representing a unique event, and its value as a systematic character is diminished.

Thus, of the five conflicting characters important in choosing a group OTU pairing, only one or possibly two appear to be robust after the considerations above: 6a, a recurved rectus cervicis profundus; and possibly 16a, a discrete suprapeduncularis. State 6a, at least, may be considered correctly identified in all relevant taxa, and both states are derived through structural elaboration. Even if the potential problems in the other three character states here are substantiated, 6a plus 16a would still support the pairing H + B. Although the considerations above do not change the most strongly supported pairing, they weaken the case.

In members of H, all of which have projectile tongues, the force for projection is

passed from the epibranchial to the basi-branchial through the first ceratobranchial (Lombard and Wake, 1977). As the tongue is projected, the hyobranchial skeleton is folded such that the first ceratobranchial is coplanar with the epibranchial in the projected state (Lombard and Wake, 1977:fig. 16). In contrast, in members of B, all of which also have projectile tongues, the force for projection is passed from the epibranchial to the basibranchial through the second ceratobranchial. As the tongue is projected, the hyobranchial skeleton is folded such that the second ceratobranchial is coplanar with the epibranchial in the folded state (Lombard and Wake, 1977:fig. 16). As a part of this unique pattern, the first ceratobranchial—the force-transmitting element in members of H—is greatly reduced in cross section to a thin flexible rod. Thus, though both groups have projectile tongues, the mechanics and folding of the hyobranchial skeleton are different and that of H is similar to the primitive condition. A pairing of H + B implies that the H projection and folding pattern is ancestral to that of B. This would mean that, during the evolution of B, one projection and folding pattern was lost and another rather different one put in its place. We consider this a very unlikely scenario. Any pairing except H + B, however, implies separate origins for the mechanism and folding patterns in the projectile tongues of H and B. This is consistent with the differences in the tongue mechanics in the two groups and may be consistent with the life-history patterns in the two taxa as well (Wake, 1982; Roth and Wake, 1985b). Members of H retain the primitive condition of having aquatic larvae. All members of B, in contrast, have direct development. The unique force transmission mechanism and folding pattern in B may have arisen as a novelty “permitted” by the lack of constraints imposed on the skeleton by the requirements of aquatic feeding and respiration. In contrast, the retention of aquatic larvae in H may constrain the skeleton to the primitive pattern, ultimately restricting the degree to which projectile tongues can evolve (Wake, 1982; Roth and Wake, 1985b).

Because of these considerations of tongue functional morphology and because some characters that might pair H and B may be misidentified, we prefer the pairing P + B as a working hypothesis. In this hypothesis, P and B are sister groups united by possession of a unique character state, 23a, a vomer lacking an anterior shelf, a character admittedly weakened by the fact that it has evolved through loss. In addition, the hypothesis proposes that a suite of four tongue characters (2a, 4a, 6a, 16a) is necessary for highly derived projectile tongues and that the suite evolved independently from the primitive condition. Both P and B also have direct development (28a), a condition shared with a species of *Desmognathus* (all other members of which have aquatic larvae) and *Phaeognathus*, both in D. An implication of the preferred working hypothesis is that direct development is present in P and B as a result of the evolution of this condition in their common ancestor (i.e., direct development is a synapomorphy). The sharing of this derived condition was the major reason why Piatt (1935) first proposed pairing P with B, but his hypothesis was muddled by the inclusion of *Hemidactylium*, which has aquatic larvae, within group P. He thought that *Hemidactylium* had secondarily adapted an aquatic mode of development.

Accepting the pairing of P + B constrains consideration of possible plethodontid phylogenies to those of Set 2 in Figure 2. The pairing P + B occurs in cladograms V2, Y2, and Z2, any of which could represent Piatt's (1935) hypothesis (Fig. 3A). Only in cladogram V2, however, are all branch points defined by a derived state. In cladogram V2 the pairing H + P + B is defined by derived state 19a—three larval or embryological epibranchials. This character long has been used to separate these three OTUs from D, which retains four larval epibranchials (the primitive condition for salamanders, Wake, 1966); no modern hypothesis of plethodontid phylogeny has proposed any assemblage of three groups other than H + P + B.

State 19a is in conflict with state 29a', a periotic canal with a ventral loop after the

canal leaves the periotic cistern, as a definer of D + P + H. This assemblage has never been proposed. For two reasons, we prefer to resolve the conflict in favor of character 19a. First, we employ parsimony: If state 29a' is preferred as uniquely derived, no further derived pairing is supported by a derived character (P + H, D + H, P + D; cladogram set W; Fig. 1). If, however, state 19a is preferred as uniquely derived, then in two cladograms (V2 and V3; Fig. 1) there are derived pairings that can be supported (P + B, H + B). Second, character 29 is not well understood and the primitive condition for plethodontids cannot be determined with confidence (Lombard, 1977). State 19a does have potential faults, however, not the least of which is that the condition is hypothetical as an ancestral state for the B group, all members of which have but one embryonic epibranchial.

Relationships within the B group.—The pairing of HYD and BOL (cladogram Bo3; Fig. 2) has been that most commonly proposed (Piatt, 1935; Tanner, 1952; von Wahler, 1957; Regal, 1966). Wake (1966) recommended pairing BOL and BAT (as in cladogram Bo2; Fig. 2). The pairing of BAT and HYD has never been suggested. The basis of the most common proposal has been the possession of a free tongue, and this has been given heavy weight by previous authors. In contrast, Wake (1966) proposed pairing BOL with BAT, because each possesses 13 pairs of chromosomes and has a lateral spur on the parietal—both derived conditions for plethodontids.

These pairings, supported by two derived states in Figure 2, are in conflict. BOL is paired with HYD by 7a (loss of the lateral slip of the rectus cervicis superficialis) and 8a (loss of the omohyoideus muscle). BOL is paired with BAT by states 24a' (a parietal with a lateral spur) and 27a (13 pairs of chromosomes). States 7a and 8a are weakened as uniquely derived features because they are achieved by loss of ancestral structures. Furthermore, states 7a and 8a together represent loss of a muscle complex. The omohyoideus is joined at one end to the middle of the lateral slip of the

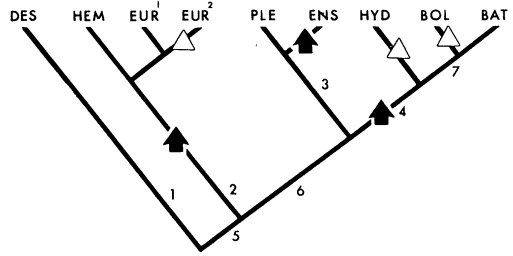


FIG. 4. Preferred working hypothesis of plethodontid relationships. Autapomorphies for OTUs listed in Table 2. Solid arrows indicate origins of attached projectile tongues. Open triangles indicate origins of free projectile tongues. (1) 3a', radii rod-like and articulated to basibranchial; 20a, tail base with two caudosacral vertebrae; 21a, specialized jaws; 24a'', parietal with groove; 25a', enlarged maxillary facial lobe. (2) 24a, parietal with ventrolateral aspect. (3) 3a', radii expanded and fused to basibranchial; 25a'', maxillary facial lobe posterior. (4) 1a, absence of urohyal; 3a, radii tapered rods and articulated to basibranchial; 4b, proportions of hyobranchial skeleton altered; 5a, ceratobranchial II transmits force; 9a, muscular cylinder; 11a, circumglossus absent; 19b, one embryonic epibranchial; 22a, one class of motor column cells; 26a', unique premaxillary; 30b, isometric otic semicircular duct growth. (5) 19a, three larval or embryonic epibranchials. (6) 23a, vomer without anterior shelf; 28a, direct development. (7) 24a', parietal with lateral spur; 27a, 13 pairs of chromosomes.

rectus cervicis superficialis in plethodontids (Lombard and Wake, 1977:fig. 8). State 7a could not occur without 8a also occurring, although 8a could occur without the occurrence of 7a. In summary, the pairing BOL + BAT is slightly more strongly supported when the nature of the conflicting characters is considered. Acceptance of the pairing BOL + BAT requires that the omohyoideus and the lateral slip of the rectus cervicis superficialis were lost twice in the B group. In turn, acceptance implies that 13 pairs of chromosomes and a lateral spur on the parietal were derived once in the common ancestor of BOL + BAT.

Preferred hypothesis of plethodontid relationships.—Combining our conclusions from the previous two sections, we select as our choice of a working hypothesis of plethodontid relationships the cladogram depicted in Figure 4. The arrangement of OTUs is compatible with the current taxonomy of the family if one does not demand that taxonomic ranks be strictly parallel to the cladogram. For example, H +

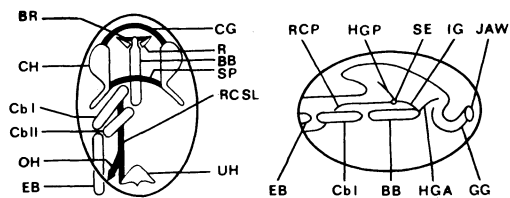


FIG. 5. Primitive configuration of tongue for plethodontid salamanders. Abbreviations: BB, basi-branchial I; BR, basiradialis muscle; Cb I, ceratobranchial I; Cb II, ceratobranchial II; CG, circumglossus; CH, ceratohyal; EB, epibranchial; OH, omohyoideus; R, radii; RCSL, lateral slip of rectus cervicis superficialis; GG, genioglossus; HGA, anterior hyoglossus; HGP, posterior hyoglossus; IG, intraglossus; RCP, rectus cervicis profundus; SE, Sehnenplatte.

P + B is equivalent to the present subfamily Plethodontinae, and D is the subfamily Desmognathinae. However, the three OTUs in the Plethodontinae are presently given equal rank as tribes. An alternative would be to recognize three subfamilies—Desmognathinae for D, Hemidactyliinae for H, and Plethodontinae for P + B—and to recognize two tribes in the latter group. We prefer not to make any taxonomic changes at this time, because we do not believe that the arrangement in Figure 4 is overwhelmingly supported and prefer

to await the results of ongoing research involving as yet incompletely analyzed morphological characters (e.g., vertebrae and vertebral development).

In comparison with the proposal of Wake (1966), the arrangement in Figure 4 appears to have more support, but discovery of a single derived state supporting a group P + H could shift attention once again to Wake's earlier hypothesis.

Evolution of the tongue.—Although the following scenario relates to the preferred working hypothesis of plethodontid relationships, it could apply to any of the 12 possible cladograms that indicate a convergent evolution of tongue projectility. Thus, although future data may indicate preference for an alternative phylogeny of plethodontids, the following general scenario will remain viable so long as B + H are not united.

Figure 5 illustrates, in schematic form, the primitive condition of the tongue for plethodontid salamanders. The distributions of derived features of the feeding apparatus on the working hypothesis are diagrammed in Figure 6. All feeding modes are depicted, and EUR has been subdivided into EUR¹ (attached tongue

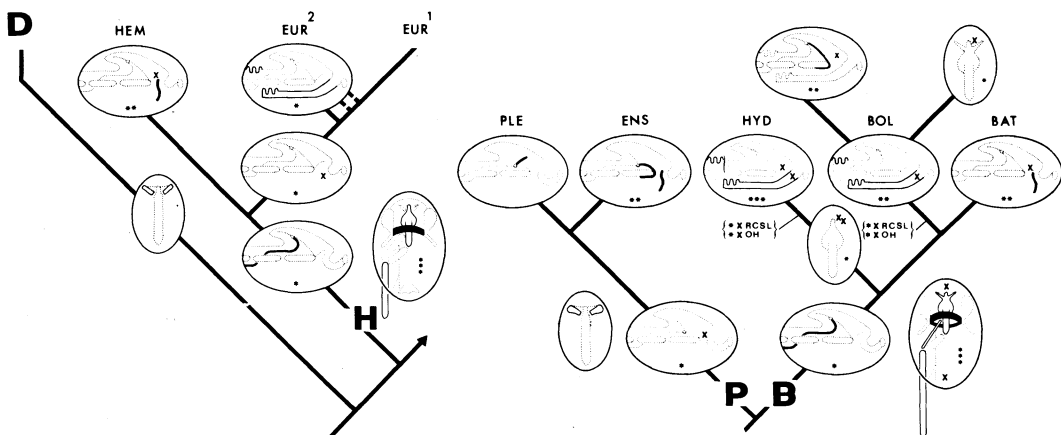


FIG. 6. Schematic representation of feeding-system evolution under working hypothesis of plethodontid relationships. Cladogram equivalent to that in Figure 4, and shows changes from primitive configuration of tongue of plethodontid salamanders (Fig. 5). Portion of cladogram shown on right connects to that on left at arrow. Insets on cladogram locate origin of derived states. In each, only portions of apparatus that change are emphasized; unchanged parts formed by dotted lines to permit orientation. Loss indicated by an X at appropriate location. Asterisk (*) indicates a convergence. Horizontal ellipses enclose schematic midsagittal sections. Vertical ellipses enclose dorsal views.

forms; Table 1) and EUR² (free tongue forms).

Primitively, the hyobranchial skeleton and its associated musculature form the essential machinery of lung ventilation in amphibians. In plethodontids, which are lungless, these structures have been freed from the role of a buccal respiratory pump. Buccal pumping is used in aspirating the olfactory mucosa in plethodontids, but this is a weak and intermittent activity, relying mainly on the intermandibular muscles. The loss of lungs in the ancestor of plethodontids was a key event in tongue evolution. The hyobranchial structures became available for subsequent modification to become the machinery of tongue protrusion and ultimately projectility; relative to primitive members of other families, even the least specialized plethodontids employ extensive tongue movements during feeding (see also Wake, 1982; Roth and Wake, 1985b). The origin of a suprapeduncularis, hyoglossus anterior, intraglossus plus *Sehnenplatte*, and glossal ligament (not shown here, but illustrated in Lombard and Wake, 1977:fig. 22) in the ancestral plethodontids constitutes an evolutionary novelty basic to tongue protrusion and pad flipping. Subsequent evolution of attached projectile and, ultimately, free projectile tongues proceeded from this base. The probable roles of these structures in tongue movement are discussed in Lombard and Wake (1977) and, together, these tongue movements constitute a suite of synapomorphies for the Plethodontidae, none of which occur in any other salamanders. In all other features, the hyobranchial apparatus of the ancestral plethodontid was general and unspecialized.

Group D retains the primitive plethodontid tongue apparatus (attached protrusible), but has a specialized feeding system in that the jaws and associated musculature are in a highly derived condition for salamanders in general and plethodontids in particular (Wake, 1966; Hinderstein, 1971; Dalrymple et al., 1985). The tongue of desmognathines is modified little from the primitive plethodontid condition, dif-

fering only in that the radii are untapered cylinders.

The tongue of group H has undergone substantial derivation. The basibranchial is expanded and flattened; the proportions of the hyobranchial skeleton are altered; the rectus cervicis profundus is folded back on itself; the suprapeduncularis is enlarged and well defined. The flanges on the basibranchial support the recurved rectus cervicis profundus muscles. The flanges are broad and do not extend posteriorly past the articulation of ceratobranchial I. The hyobranchial proportions are altered in that the second ceratobranchial is somewhat shortened and the epibranchial is lengthened. This latter is essential for increased distance of tongue projection. The enlargement of the suprapeduncularis forms a dorsal muscular sheath over the tongue stalk that controls projection. These derivations of the primitive condition are present in all members of this group and constitute the essential functional elements of the projectility of their tongues. During projection, ceratobranchial II transmits force from the epibranchial to the basibranchial as in the primitive condition. In *Hemidactylium*, the modifications described are supplemented by derivation of the tongue-tip musculature. The anterior hyoglossus is lost. The origin of the genioglossus has shifted from the region of the mandibular symphysis laterally to the ramus of the mandible, thus elongating the muscle and enhancing the potential for projection of the tongue. In the remaining genera of the Hemidactyliini, the genioglossus is vestigial or (usually) lost altogether. Following loss of the genioglossus, free projectile tongues arise in EUR² through restriction of the connective tissue and buccal mucosa, which together with the genioglossus primitively bind the anterior part of the tongue to the floor of the mouth. Free projectile tongues may have arisen more than once in the Hemidactyliini through loss of the connective tissue attachment and the ventral in-pocketing of the buccal mucosa to form a folded sheath. *Hemidactylium* clearly has an attached tongue and *Eurycea*, *Gyrino-*

philus, and *Pseudotriton* have entirely free tongues. However, *Stereochilus* and *Typhlotriton* retain mucosal and connective tissue attachment, and *Typhlotriton* even has a few vestigial fibers of the genioglossus. In *Typhlotriton*, a cave-adapted group closely related to *Eurycea* (Wake, 1966), the attached tongue could be a paedomorphic reversal, since the genus is paedomorphic in other respects. It also is possible that *Typhlotriton* represents a stage in the evolution of free projectile tongues.

In the B group, a second major derivation of the tongue apparatus has evolved. The basibranchial is flanged; the proportions of the hyobranchial skeleton are altered; the rectus cervicis profundus again folds back on itself and the suprapeduncularis again becomes enlarged to form a dorsal sheath over the tongue stalk. In addition: the urohyal is lost; ceratobranchial function is altered (ceratobranchial I becomes very slender and ceratobranchial II is the force transmitting element such that the tongue skeleton folds in a unique manner during projection); the musculature ventral to the tongue stalk is modified such that together with the suprapeduncularis a complete sheath is formed about the tongue stalk; the radii fuse to the basibranchial; the circumglossus is lost. The first four modifications are convergent on the modifications basic to the projectile tongue of hemidactylines. The 10 derived states common to all bolitoglossines characterize a highly derived and unique projectile apparatus and form the foundation for the attached projectile and free projectile tongues in the group. In *Batrachoseps*, loss of the anterior hyoglossus and modification of the origin of the genioglossus recall roughly similar changes in *Hemidactylium*. The genioglossus of *Batrachoseps* is far more elaborately specialized than that of *Hemidactylium*. The genioglossus of *Batrachoseps* passes posteriorly from the tongue along the mandible to a point near the angular-quadrangle joint (Piatt, 1935; Lombard and Wake, 1977:fig. 7). If one ignores the absence of the hyoglossus anterior, *Batrachoseps* possesses the most primitive pro-

jectile tongue of living bolitoglossines. Free tongues have arisen independently in *Hydromantes* and in the ancestor of the supergenus *Bolitoglossa*. In both events, the lateral slip of the rectus cervicis superficialis, the omohyoideus, and the genioglossus were lost. In addition, the connective tissue and buccal mucosa were modified to free the tongue from anterior and ventral attachment. The tongue of *Hydromantes* differs from that found in members of the supergenus *Bolitoglossa*; in addition to the above modifications, the anterior hyoglossus is lost (for the second time in the cladogram) and the radii and basiradialis muscle are lost. In addition, the basibranchial is unique in that it is elongated and has a flexible region (Lombard and Wake, 1977). Within the supergenus *Bolitoglossa*, the anterior hyoglossus is lost, the intraglossus is further derived in *Chiropterotriton priscus*, and the basiradialis is lost in all genera save *Thorius*.

In the ancestor of the P group, the anterior hyoglossus is lost for the fourth time, and the radii become spatulate. In *Ensatina*, a projectile tongue arises for the third time on the cladogram. The projectile tongue of *Ensatina* is based on a tongue apparatus that is primitive for plethodontids in most respects. The elaborate modifications found in the ancestor of hemidactylines or bolitoglossines are not present. In *Ensatina*, the anterior hyoglossus is modified (as in *Chiropterotriton*), and the origin of the genioglossus is shifted backwards from the region of the mandibular symphysis (as in *Hemidactylium* and *Batrachoseps*).

In summary, our scenario involves the independent evolution of projectile tongues three times from the primitive attached protrusible state, but each time with a different set of derivations (see Fig. 7). The least modified of the genera with projectile tongues from the primitive condition is *Ensatina* (ENS). An intermediate suite of derivations occurs in the ancestor of the Hemidactyliini, and these (or, as we propose, ones similar to them) plus additional derivations form the basis for the projectile tongue of the Bolitoglossini. The more

highly modified, attached projectile tongues each give rise to free projectile tongues—the hemidactyline form once and the bolitoglossine form twice. Finally, each of the projectile forms has a member with an attached tongue but with a modified genioglossus muscle (i.e., *Ensatina*, *Hemidactylium*, and *Batrachoseps*). In this scenario, the evolutionary pathway to the free projectile condition includes a phase in which the genioglossus muscle has undergone moderate to extreme elongation before being lost (i.e., the attached projectile tongue is a precondition to the free projectile tongue). Under this hypothesis, which is the most parsimonious one in relation to the preferred phylogeny and tongue-evolution scenario, the tongues of *Hemidactylium* and *Batrachoseps* represent retention (probably with extensive subsequent derivation in *Batrachoseps*) of the attached-projectile-tongue condition in their representative tribes. Otherwise, one would be forced to hypothesize that the projectile conditions of these two taxa were derived from ancestral, attached tongue conditions independently from those of the other members of their tribes.

The entire exercise reported in this paper has been devoted to a parsimonious analysis of a nonparsimonious system. We cannot escape the apparent fact that tongue evolution has occurred convergently in the plethodontid salamanders. Perhaps the tongue freedom achieved by elongation of the genioglossus muscles is a precursor to loss of those muscles and subsequent complete freedom, as Piatt (1935) argued. However, in view of the extensive convergence in this system, we raise a final alternative. Elongation of the genioglossus in *Batrachoseps* may have led to more elongation and, finally, to a condition in which the freedom achieved approximates that of the free projectile groups, while nonetheless being technically attached. It seems unlikely that such "superspecialization" would be a precursor to loss. Rather, it may be an example of a stopping-point in evolution, in which at the beginning of specialization there is substantial opportunity for change. However, as in the

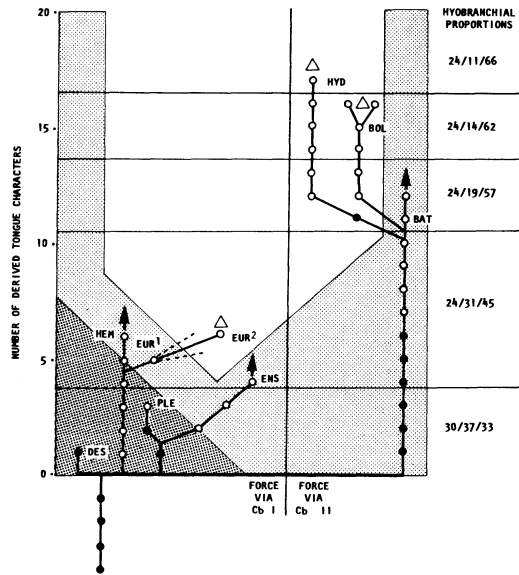


FIG. 7. Ground-plan diagram illustrating tongue and lineage evolution in family Plethodontidae. Three general zones of tongue use shown: attached protrusible tongue (ancestral condition, heavy stipple); attached projectile tongue (light stipple); and free projectile tongue (clear). Cladogram placed over this tongue-function zone diagram. Open triangle indicates free projectile tongue; closed arrow indicates attached projectile tongue. Vertical distance on diagram equates with number of derived tongue features possessed by OTU. Vertical placement of OTU also equates with relative ability at tongue projection. Open circles represent convergently-derived tongue features; closed circles are uniquely-derived tongue features. Below zero level, the following four tongue features primitive for plethodontids, but derived with respect to all other salamanders, are indicated: discrete anterior hyoglossus; intraglossus muscle plus *Sehnenplatte*; suprapeduncularis muscle; and glossal ligament. Hyobranchial proportions are (in order): percent basibranchial; percent ceratobranchial II; percent epibranchial.

case of the projection system in H based on a strong first ceratobranchial, a stopping point is reached eventually, beyond which no additional specialization is possible (Roth and Wake, 1985b). Evolution of projectile tongues has involved the entrance of different lineage components into similar evolutionary channels, constrained by the different histories of the lineages. We believe it possible that there have been as many as six separate episodes

in the evolution of tongue projection in plethodontid salamanders, most with unique features and some (e.g., *Batrachoseps*) possibly at evolutionary stopping-points.

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APPENDIX

Data Analyzed

The tongue data published by Lombard and Wake (1976, 1977) are a major source for this paper. These data have been organized and coded for analysis as most of characters 1 to 19 below. In addition, information on other aspects of plethodontid biology have been added, primarily characters 20 to 30. A source reference is indicated for each character. For each character it is assumed that the ancestral state is still represented among the plethodontid genera. This state has been detected mainly by outgroup comparisons with other families of salamanders. Sometimes it was not possible to use this criterion. In such cases we specify the criterion used in recognizing the primitive state. Ancestral states are indicated by the pure integers and derived states are designated by integers plus letters. A proposed character-state phylogeny is indicated—in brackets or in Figure 8—for each character. The distribution of states for each character is shown in Table 2.

1. *Urohyal* (Lombard and Wake, 1976:fig. 2).—Urohyals are present in most salamanders, and their presence in plethodontids is assumed to be the ancestral condition. State 1a is loss of the element. [1 → 1a]

2. *Basibranchial* (Lombard and Wake, 1976:fig. 6).—The basibranchial has a wide variety of shapes in salamanders (Özeti and Wake, 1969; Krogh and Tanner, 1972), but a cylindrical one is frequently encountered. Further, there are reasons for believing that expanded forms in different families have specialized functions. Accordingly, we assume that the cylindrical state is ancestral and expanded basibranchials are derived (2a) within the family. [2 → 2a]

3. *Radii* (Lombard and Wake, 1977:fig. 6).—Radii are anterior hyobranchial elements associated with the basibranchial. The radii are discrete, rounded elements, tapered toward their tips, and distinctly separated from and articulated with the basibranchials in ambystomatids (Krogh and Tanner, 1972) and salamandrids (Özeti and Wake, 1969); we consider such a condition to be ancestral in plethodontids. Radii that are closely attached to and essentially continuous with the basibranchial are considered to be one derived state (3a), and these may be much reduced in length; the extreme derivation in this direction is loss (3b). The radii are rodlike structures of near constant diameter which retain their individuality in another derived state (3a'). The independent radii are broadened and flattened, and may be expanded for part of their length in another independently de-

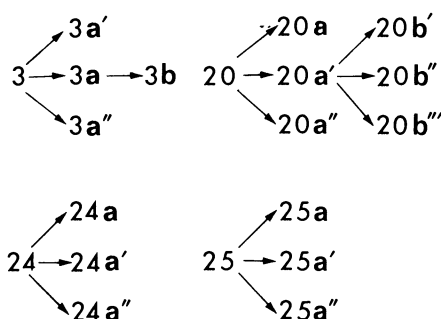


FIG. 8. Proposed character-state phylogenies for characters 3, 20, 24, 25.

derived state (3a''). See Figure 8 for the character-state tree.

4. *Hyobranchial proportions* (Lombard and Wake, 1977:figs. 5, 6).—We assume that an articulated hyobranchial apparatus in which the basibranchial, first ceratobranchial, and epibranchial are of approximately equal length is ancestral for the plethodontids. This is the general situation in most ambystomatids (Krogh and Tanner, 1972) and many salamandrids (Özeti and Wake, 1969), and the exceptions seem to be special cases. A derived state is increase in the relative length of the epibranchial (4a), and a more derived state is even greater increase in the relative length of the epibranchial, coupled with decrease in the relative length of the ceratobranchials (4b). An alternative interpretation would have 4a and 4b independently derived from 4, and we discuss this possibility in the text. [4 → 4a → 4b]

5. *Ceratobranchial function* (Lombard and Wake, 1977:fig. 15).—The first ceratobranchial is the primary force transmission element and is the larger of the two ceratobranchials in generalized salamanders (Wake, 1966; Özeti and Wake, 1969; Krogh and Tanner, 1972). We consider this to be the ancestral state. The situation in which the second ceratobranchial is the main force transmitter and is larger in minimal diameter than the first is a derived state (5a). [5 → 5a]

6. *Rectus cervicis profundus* (Lombard and Wake, 1977:figs. 9, 10).—The rectus cervicis profundus muscle is linearly arranged in generalized ambystomatids (Krogh and Tanner, 1972) and salamandrids (Özeti and Wake, 1969), and this is accepted as the ancestral state. The muscle is folded dorsally near its anterior end in the derived state (6a). [6 → 6a]

7. *Rectus cervicis superficialis* (Lombard and Wake, 1977:figs. 9, 10).—The rectus cervicis superficialis has a lateral slip in many plethodontids that corresponds with the main muscle in the generalized arrangement in salamandrids and ambystomatids. This is considered to be the ancestral state. Loss of the slip is derived (7a). [7 → 7a]

8. *Omohyoideus* (Lombard and Wake, 1977:figs. 9, 10).—An omohyoideus muscle is present in most salamanders, and its presence is considered to be the ancestral state (see Özeti and Wake, 1969; Krogh and

TABLE 6. Modifications found in derived states of tail-breakage character.

State	Cutaneous wound healing ^a	Caudosacral vertebrae number	Caudal vertebrae	Tail breakage localized ^b
20	—	3	Normal	—
20a	—	2	Normal	—
20a'	+	3	Normal	—
20b'	+	3	First specialized	+
20b''	+	2 or 3	Normal	—
20b'''	+	2	First specialized	+
20a'	+	3	First and second specialized	+

^a + = healing occurs; — = healing does not occur.

^b + = localized; — = not localized.

Tanner, 1972). Simple loss is considered to be a derived state (8a). We reject Tanner's (1952) interpretation that this muscle shows several stages of reduction in the Plethodontidae. [8 → 8a]

9. *Muscular cylinder*.—Lombard and Wake (1977:fig. 19) described a complex aiming cylinder in certain plethodontids. This is a unique feature, and it is considered to be derived when present (9a). [9 → 9a]

10. *Genioglossus* (Lombard and Wake, 1977:fig. 10).—The genioglossus arises primitively from the region of the mandibular symphysis. The shifts of the origin of the muscle posteriorly along the mandible are considered to be one derived state (10a), and the loss of the muscle is a separate derivation (10a'), in a different direction. An alternative interpretation is that this is a linear morphocline, with 10a giving rise to 10a'. [10a → 10 → 10a']

11. *Circumglossus* (Lombard and Wake, 1977:fig. 2).—A circumglossus muscle was first formally described in salamanders by Lombard and Wake (1977). However, it is present in more generalized salamanders and was figured by Magimel-Pelonner (1924). Its presence is considered to be the ancestral state, and it is lost in the sole derived state (11a). [11 → 11a]

12. *Intraglossus* (Lombard and Wake, 1977:fig. 2).—The intraglossus muscle has been found only in plethodontids, and its probable homologue is a part of the hyoglossus. In most plethodontids, this muscle arises from the *Sehnenplatte* and attaches to the anterior end of the basibranchial, the lingual cartilage, or equivalent. In some genera, however, the muscle attaches instead to the anterior end of the glossal ligament, ventral to the basibranchial (12a). Because of its limited and dispersed distribution, we consider 12a to be derived. [12 → 12a]

13. *Basiradialis* (Lombard and Wake, 1977:fig. 2).—The basiradialis or an equivalent muscle is present in most generalized terrestrial salamanders (Drüner, 1901, 1904; Özeti and Wake, 1969; Krogh and Tanner, 1972), and we consider its presence to be the ancestral state in plethodontids. It is lost in the sole derived state (13a). [13 → 13a]

14. *Hyoglossus anterior* (Lombard and Wake, 1977:figs. 20, 21).—Generalized salamanders have a relatively large hyoglossus, with a portion comprised of anteriorly directed fibers (Drüner, 1901, 1904; Özeti and Wake, 1969); in plethodontids, this forms a nearly distinct muscle. We consider representation of all

parts of the anterior portion of the hyoglossus to be the primitive state and, in the only derived state, this anterior section is lost (14a). [14 → 14a]

15. *Hyoglossus posterior* (Lombard and Wake, 1977:figs. 20, 21).—The posterior fibers of the hyoglossus are oriented posteriorly in generalized salamanders (Drüner, 1901, 1904; Özeti and Wake, 1969; Krogh and Tanner, 1972), and we consider this condition to be the ancestral state in plethodontids. The sole derived state is one in which these fibers are oriented anteriorly (15a). [15 → 15a]

16. *Suprapeduncularis* (Lombard and Wake, 1977:figs. 18, 19).—The suprapeduncularis is a muscle unique to plethodontids (Piatt, 1935), and we consider weak development to be primitive (18). Presence of a discrete muscle is the sole derived state (16a). [16 → 16a]

17. *Tongue attachment* (Lombard and Wake, 1977:figs. 20, 21).—In some plethodontid salamanders, the tongue pad is free of cutaneous attachments to the floor of the mouth. This boletoid or adetoglossal state (Uzzell, 1961) is considered to be derived (17a). [17 → 17a]

18. *Peripheral innervation of the tongue* (Wake et al., 1983b).—Ramus hypoglossus, the motor innervation of the tongue tip, bifurcates distally, with a branch to the tongue tip and a branch to the musculature of the gular region. The bifurcation is primitively far forward, near the tip of the basibranchial (18). In derived states the bifurcation is posterior, between the attachment of the first ceratobranchial to the basibranchial and to the epibranchial (18a). An even more derived state has the supply to the tongue from the posterior bifurcation joining with the ramus lingualis branch of cranial nerve IX to form a common twisted trunk (18b). [18 → 18a → 18b]

19. *Epibranchial number* (Wake, 1966).—In the larval state, generalized salamanders have four to five epibranchials, and such a pattern is considered to be ancestral. Desmognathines have four, and this state is judged to be ancestral for plethodontids. The presence of three in larvae or embryos is considered to be derived (19a), and presence of but one in embryos is a further derivation (19b). [19 → 19a → 19b]

20. *Tail breakage* (Wake and Dresner, 1967).—In primitive salamanders, the base of the tail has no cutaneous wound-healing specializations, there are three caudosacral vertebrae, the caudal vertebrae at the base of the tail are unspecialized, and there is no

localized tail breakage. This condition is considered primitive for plethodontids (20). We recognize six derived states in plethodontids, each a unique combination of modifications of these features as listed in Table 6.

There are two trifurcations in this character as we have coded it (Fig. 8). The b-series of states is most easily derived from state 20a', because all three b-states must have been derived from a form with cutaneous wound-healing, and that eliminates state 20a. State 20a'' is an unlikely ancestral condition because of the uniquely derived localized tail-breakage pattern involving two special vertebrae. That leaves state 20a', which is a possible ancestor for all of the three b-states; thus, on grounds of parsimony, it is the suggested ancestral state for them.

21. *Jaws* (Wake, 1966; Hinderstein, 1971; Dalrymple et al., 1985).—Jaws of some plethodontids are uniquely structured in having a continuous ligament extending from the jaw to the atlas vertebra. There is a series of associated features, and this is considered to be a derived state (21a). [21 → 21a]

22. *Brain stem motor column* (Roth and Wake, 1985a).—In generalized vertebrates and in urodeles examined from families other than the plethodontids, there are two distinct classes of cells in the motor column of the neck and trunk; such a state is considered to be primitive. In the derived state, there is only one class of motor column cells (22a). [22 → 22a]

23. *Vomer* (Wake, 1966).—Vomers are relatively large in generalized salamanders and, in plethodontids, two stages are encountered. The most generalized is one in which the tooth row lies anterior to a bony shelf of the preorbital process. A derived state is loss of this shelf (23a). [23 → 23a]

24. *Parietal* (Wake, 1966).—Parietal bones are relatively simple, scalelike structures in generalized salamanders, as well as in some plethodontids, and we consider this primitive. Three additional states, all derived in a separate direction, are encountered in the family. One derived state has a distinct ventrolateral shelf present on the bone (24a). A different derived state is the presence of a distinct lateral spur (24a'). The third is the presence of a deep, saddlelike groove extending across the posterolateral portion of the bone to accommodate the ligament that extends from the lower jaw to the atlas (24a''). See Figure 8 for the character-state tree.

25. *Maxilla* (Wake, 1966).—The facial lobe of the maxillary bone of generalized salamanders lies in a position near the anterior end of the maxilla, with a

distinct section of the pars dentalis extending anterior to it (25). In plethodontids three divergent derived states of the maxilla are also found. The facial lobe may lie at the very anterior end of the bone (25a). It may be so greatly enlarged as to extend into the area vacated by the prefrontal bones (25a'). Finally, the facial process may be located in a relatively posterior position, near the center of the pars dentalis (25a''). See Figure 8 for the character-state tree.

26. *Premaxilla* (Wake, 1966).—The premaxillary bone or bones surround and embrace an intermaxillary gland that lies directly behind the pars dentalis in generalized salamanders. This condition is found in many plethodontids, but two derived states are also seen. In one, the premaxillary bones are fused and the intermaxillary gland is entirely surrounded and, occasionally, completely roofed by the expanded bony growth (26a). In the other, the bones are relatively slender, and the gland is moved to a posterior position relative to the pars dentalis (26a'). In the latter state the frontal processes of an often single premaxillary may fuse in front of the intermaxillary fontanelle, and then diverge when the margins of the fontanelle are reached. [26a ← 26 → 26a']

27. *Chromosome number* (Leon and Kezer, 1978).—Most plethodontids have 14 pairs of chromosomes, a number also found in amphiumids and ambystomatids, both possibly related groups. A derived state (27a) is the reduction to 13 pairs of chromosomes in some plethodontids. [27 → 27a]

28. *Development* (Wake, 1966).—Salamanders primitively have a larval stage. In plethodontids there are many species that lack larvae and have direct development (28a). [28 → 28a]

29. *Amphibian periotic canal* (Lombard, 1977:fig. 62).—The amphibian periotic canal is straight in most salamanders, and this is considered to be the ancestral plethodontid state. Two derived states are known for plethodontids. One derived state is for the canal to have a dorsal loop just after it leaves the periotic cistern (29a). An independent derivation is a canal with a ventral loop just after it leaves the periotic cistern (29a'). [29a ← 29 → 29a']

30. *Otic semicircular ducts* (Lombard, 1977).—The bore radius of the otic semicircular ducts shows strong negative allometry relative to body weight in most salamanders; this is considered to be the ancestral state. A derived state shows only slight negative allometry (30a), and a more derived state is one in which growth of the ducts is nearly isometric (30b). [30 → 30a → 30b]