

## Atavisms and the Homology of Hyobranchial Elements in Lower Vertebrates

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**ABSTRACT** The homology of branchial arch segments in salamanders has been a matter of controversy since the last century. Many investigators term the most medial paired elements of salamander branchial arches "ceratobranchials" and the next distal paired elements "epibranchials." This suggests that the first two segmental elements of the salamander branchial arch are not homologous with elements occupying the same position in ray-finned fishes, *Latimeria*, "rhpidistians," and lungfishes, in which these bones are called hypobranchials and ceratobranchials, respectively. Three lines of evidence suggest that it is more parsimonious to interpret urodele branchial arch segments as being homologous with those of other vertebrate clades—1) comparative osteology, 2) comparative myology, and 3) the discovery of cartilaginous structures forming a third segmental unit that we interpret as atavistic epibranchials of the branchial arch in one population of the salamander *Notophthalmus viridescens*. These structures possess all the defining attributes of atavisms, and illustrate the special role that atavistic features play in resolving questions of homology recognition.

For more than a century, detailed descriptions of hyobranchial morphology in lower vertebrates have appeared in the scientific literature (Gegenbaur, 1865; Parker, 1877; Wiedersheim, 1877). As traditionally described, the hyobranchial apparatus of vertebrates contains postmandibular visceral arches consisting of the hyoid arch (visceral arch 2) and the branchial arches posterior to the hyoid arch, usually five in number in fishes. The hyoid and branchial visceral arches are involved, at least primitively, in cranial functions such as feeding and respiration.

The paired visceral arches are segmented and meet midventrally to articulate with one or more median elements. In the generalized vertebrate configuration, the branchial arch on each side of the head is composed of five basic elements, each of which originates developmentally as a cartilaginous structure that may ossify later (Nelson, '69; Jollie, '73, '86). The nomenclature of these five branchial arch elements has been widely accepted (see Nelson, '69 for a review), and is described (at least generally) in all textbooks of comparative anatomy (e.g., Jollie, '73; Romer and Parsons, '77; Walker, '87). The midline

structures of the hyobranchial apparatus are called basibranchials because they lie at the base of the branchial basket. The segmental component of each left and right branchial arch that articulates with the basibranchial is called the hypobranchial (Fig. 1). Distal to the hypobranchial is the ceratobranchial, which articulates distally with the segmental component called the epibranchial. Finally, the anterodorsally oriented elements of the branchial basket are called pharyngobranchials (Fig. 1). Anatomically, the hypobranchials and ceratobranchials are ventral elements of the branchial basket, whereas epibranchials and pharyngobranchials are dorsal elements.

This terminology for the branchial arch segments has been used widely by morphologists, except in the literature dealing with salamander morphology and evolution. Here, elements that would be called hypobranchials in fishes often are referred to as ceratobranchials and the next distal elements are called epibranchials (e.g., Alberch et al., '85; Dockx and DeVree, '86; Erdman and Cundall, '84; Krogh and Tanner, '72; Larsen and Guthrie, '75; Lombard and Wake, '76, '77; Özeti and Wake, '69; Regal, '66; Wake, '82).

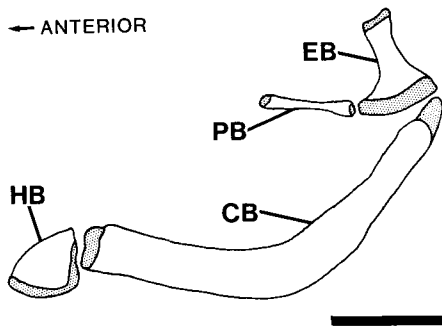


Fig. 1. Lateral view of the left first gill arch of *Polypertus senegalus*. The gill arch consists of a segmented series of endochondral ossifications in the following order (ventral to dorsal): Hypobranchial (HB), ceratobranchial (CB), epibranchial (EB), and pharyngobranchial (PB). Note the position of both the cartilaginous and bony portions of the epibranchial in relation to the tip of the ceratobranchial, and its similarity to the location of the additional segmental elements (which we term epibranchials) in Figure 3. Bony tissue is white, cartilage is stippled. Scale = 0.5 cm.

Use of this nomenclature assumes that the hypobranchial of all other lower vertebrates either is lost or fused with the ceratobranchial, and that the epibranchials, which frequently are lost in vertebrates, are retained in salamanders. The first authors to use the terms ceratobranchials and epibranchials in salamanders (Huxley, 1874; Parker, 1877; Wiedersheim, 1877) stressed the importance of ascertaining the homology of structures among lower vertebrates, yet did not discuss their choice of the term ceratobranchial for the most medial branchial element of each arch in caudates, when it is termed the hypobranchial in all other lower vertebrates. Also, they did not offer any explanation of the fate of the hypobranchial.

Marche and Durand ('83) discussed the discordance of branchial arch terminology within salamanders and marshaled evidence to support their view that salamanders have true hypobranchials and ceratobranchials. Duellman and Trueb ('86) briefly reviewed this controversy, noting that although they adopted the term "ceratobranchial" in lieu of the often used "epibranchial" for caudates, there were no data in the literature that permitted a resolution of the homology of these gill arch segments.

The terminological confusion present in the literature reflects differing views on the homology of the segmental gill arch elements

in vertebrates. Here, we attempt to resolve the question of branchial-arch segmental homology in salamanders (Caudata) by presenting three lines of evidence. First, the morphology of hyobranchial skeletal elements in fishes and salamanders is compared. Second, muscles associated with these hyobranchial elements are compared and discussed in relation to the positional information that they provide on the homology of their insertions. Finally, we present new data on the occurrence of distal branchial arch elements in a population of newts. We interpret these elements as atavisms and as evidence that the true epibranchials have been lost in salamanders.

We contend that the most parsimonious interpretation of the comparative morphological data, together with the novel information on atavistic branchial arch segments, is that the most medial two paired structural elements of salamander branchial arches are hypobranchials and ceratobranchials.

#### MATERIALS AND METHODS

##### *Specimens*

Branchial morphology was examined in 65 branchiate adult *Notophthalmus viridescens*, collected from McGuire's Pond, 9.7 km south of Carbondale, Jackson Co., Illinois. All specimens were killed in chlorotone and fixed in 10% formalin. This population was used in two previous morphological analyses of metamorphosis in salamanders (Reilly, '86, '87). Sex, snout-vent length, and condition of external gills were recorded before the specimens were cleared and double-stained for bone and cartilage following the procedure of Dingerkus and Uhler ('77). Metamorphic condition of the skull and hyobranchial apparatus were examined and photographed using a Zeiss SV-8 binocular dissecting microscope. Voucher specimens are deposited in the Museum of Natural History, The University of Kansas (KU 203963-203987, KU 206794-206833).

##### *Comparative analyses*

Branchial arch morphology in several lower vertebrate clades was examined to provide a basis for positional analyses of segmental homology. Relevant clades for comparison were chosen on the basis of current phylogenetic hypotheses relating tetrapods, lungfishes, coelacanths, ray-finned fishes, and chondrichthyans (Lauder and Liem, '83; Maisey, '86).

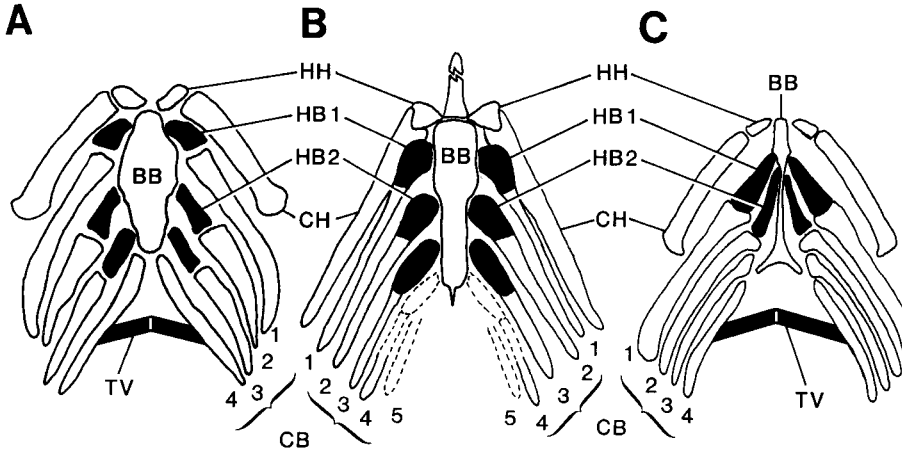


Fig. 2. Morphology of the hyobranchial apparatus in three lower vertebrates: A: *Polypterus senegalus*, a ray-finned fish (Actinopterygii); B: *Eusthenopteron fordii* (after Jarvik, '80), a "rhpidistian;" C: *Ambystoma tigrinum* (larval morphology). Abbreviations for this fig-

ure and Figure 3: BB, basibranchial; CB 1-5, Ceratobranchials 1 to 5; CH, ceratohyal; EB1, Epibranchial 1; HB 1-2, Hypobranchials 1 and 2 (solid black); HH, Hypohyal; TV, transversus ventralis muscle.

Information on hyobranchial osteology and myology in lower vertebrates is derived from both descriptive and comparative studies of fishes and amphibians in the literature (e.g., Allis, '17, '22; Drüner, '02, '04; Eaton, '36; Edgeworth, '35; Jarvik, '80; Jollie, '82; Lombard and Wake, '76; Ozeti and Wake, '69; Piatt, '39, '40; Rosen et al., '81; Wiedersheim, 1877; Wiley, '79a,b; Winterbottom, '74), as well as from our own previous studies of branchial arch morphology and function in lower vertebrates (Lauder, '80; '83; Lauder and Shaffer, '85; Reilly, '87; Reilly and Lauder, '88). Muscle terminology is adapted from Winterbottom ('74) for fishes and Edgeworth ('35) for salamanders.

Throughout the Results and Discussion sections, in order to avoid confusion, we will anticipate our final conclusions on the homology of the salamander branchial arch segments and refer to the most medial paired ventral segments as hypobranchials, and the next distal segments as ceratobranchials. We do this in order to have a name to place on the various segments of disputed homology as we present the evidence for our conclusions.

RESULTS

*Hyobranchial osteology*

The hyobranchial apparatus among lower vertebrates is very similar in gross morphol-

ogy (Figs. 1, 2). In chondrichthyans, the hyobranchial apparatus consists of median basibranchial elements which articulate with four or five hypobranchials, each of which in turn, articulates with the ceratobranchials, epibranchials, and pharyngobranchials in series. This arrangement forms a complete branchial basket posterior to the skull (Edgeworth, '35; Jollie, '73).

In primitive actinopterygians (e.g., *Polypterus*, Figs. 1, 2A), the same general pattern of elements is present (Allis, '22). The ventral gill arch elements consist of a large median basibranchial which articulates with short hypobranchials on each side. Elongate ceratobranchials articulate with the distal end of each hypobranchial (Fig. 2A: CB).

In rhipidistians, epibranchials and pharyngobranchials are found on the first two branchial arches and connect to the occipital bone (via infrapharyngobranchials). On the third arch only a small epibranchial remains; it joins to Ceratobranchial 2 by connective tissue (Jarvik, '80). The ventral gill arch elements consist of short hypobranchials articulating with the median basibranchial and elongate ceratobranchials (e.g., *Eusthenopteron*, Fig. 2B: HB, CB).

Salamanders have a median basibranchial, two pairs of hypobranchials, and from one to four ceratobranchials (e.g., *Ambystoma tigrinum* larva, Fig. 2C). The number of cera-

tobranchials depends on the metamorphic stage in transforming salamanders or the point at which metamorphosis is fixed in the various paedomorphic lineages. Occasionally, in some individuals, rudiments of Hypobranchial 3 (Drüner, '02, '04; Kallius, '01; Rosen et al., '81; Stadmüller, '24) and even Hypobranchial 4 (Drüner, '04) are found. On Arches 3 and 4, which usually lack hypobranchials, the proximally widened heads of the ceratobranchials articulate with the previous ceratobranchial. In salamanders, as in all other lower vertebrates, the ceratobranchials are the longest elements and they always project posterodorsally.

Reduction of hyobranchial elements is seen in many lower vertebrate groups (Nelson, '69; Rosen et al., '81). The number and size of hyobranchial elements vary in actinopterygians, *Latimeria*, *Neoceratodus* (Dipnoi), and salamanders. In *Latimeria*, the pharyngobranchials are reduced or absent, and they are lost in lungfishes (Miles, '77). Both *Latimeria* and lungfishes have lost Hypobranchial 5, and Ceratobranchial 5 articulates with Ceratobranchial 4 (Forey, '81; Rosen et al., '81). In *Latimeria*, lungfishes, and salamanders, when hypobranchials are absent, the proximal head of the posterior ceratobranchial articulates directly with the head of the preceding ceratobranchial and not with the basibranchial. Many ray-finned fishes possess reduced pharyngobranchials and/or epibranchials, especially on the most posterior branchial arches (Nelson, '69). It is not surprising that these are the most commonly lost or reduced elements of the hyobranchial apparatus, as during ontogeny the hyobranchial apparatus of fishes typically develops from anteroventral to dorsoposterior.

*Comparative myology*

Ventral branchial muscles of gnathostomes are found in association with the hypobranchials and ceratobranchials but never attach to the third element distal from the basibranchial (epibranchials). Therefore, hyobranchial elements of the branchial arches that have ventral muscles attached to them must be either hypobranchials or ceratobranchials.

Several branchial muscles always are found connected to the same hyobranchial elements; the positions of three of these are indicated in Table 1. First, the transversi ventrales muscles of all lower vertebrates (Table 1; Fig. 2: TV) invariably originate on

TABLE 1. Muscles associated with hyobranchial elements in three lower vertebrate clades

Muscle <sup>1</sup>	Associated hyobranchial elements					
	Actinopterygii		Dipnoi		Amphibia	
	Origin	Insertion	Origin	Insertion	Origin	Insertion
Transversi ventrales	CB	Midline raphe CB1 <sup>2</sup>	CB	Midline raphe CB1	CB	Midline raphe CB1
Obliquus ventralis 1 <sup>3</sup> (subarcualis rectus 1)	HH/CH <sup>2</sup>	CB1 <sup>2</sup>	HH/CH	HH/CH	HH/CH	HH/CH
Pharyngocleithralis <sup>3</sup> (omoearcualis)	PG	CB5/CB4	PG	CB2-5	PG	CB4

<sup>1</sup>None of these ventral gill arch muscles ever attach to the third or fourth segmental units of the branchial arch (epibranchials or pharyngobranchials).

<sup>2</sup>Condition in primitive ray-finned fishes only.

<sup>3</sup>Note that the top term in this column is that used for fishes, while the bottom term of the pair is that traditionally used for salamanders.

ceratobranchials (identified as the elongate element of each branchial arch attaching medially to a smaller element that in turn articulates with the unpaired median element) and insert at the midline on a median raphe (Edgeworth, '35; Jollie, '82; Winterbottom, '74). Many ray-finned fishes possess several of these muscles which may extend between ceratobranchials of successive arches (Wiley, '79a; Winterbottom, '74). The most posterior transversus ventralis muscle invariably originates from the most posterior ceratobranchial.

Second, the obliquus ventralis one muscle (also called the subarcualis rectus one) of lower vertebrates originates from the hyoid arch (hypohyal, ceratohyal, or both) and extends posteriorly to insert on the first ceratobranchial.

Third, the pharyngocleithralis (Wiley, '79a; Winterbottom, '74) or omoarcualis (Edgeworth, '35) muscles always are associated with ceratobranchials. As indicated in Table 1, this muscle originates from the pectoral girdle and inserts on one or more of the posterior ceratobranchials (Wiley, '79a; pers. obs.).

A comparison of branchial myology across lower vertebrates (Table 1) reveals that no ventral branchial muscle ever attaches to an epibranchial (identified as the third paired element from the ventral midline).

#### *Segmental variation within branchial arches*

The morphology of the branchial arches of most individual *Notophthalmus viridescens* examined is similar to the modal condition described in the literature for salamanders; each of the first two arches contains two paired elements (e.g., Fig. 2C). However, 17 instances of cartilaginous or ossified elements located distal to the ceratobranchials were observed in nine of the series of 65 neotenic newts examined (Table 2; Fig. 3). In each case, a clearly separate cartilaginous (and sometimes ossified) element is connected to the distal end of a ceratobranchial. Fourteen cases can be interpreted as first epibranchials, because the novel element is located distal to Ceratobranchial 1. The subarcualis rectus one muscle does not attach to the novel epibranchial element, and retains its normal morphology in wrapping around the posterior end of the ceratobranchial. These individuals thus have a first branchial arch with three paired segments. One specimen (Table 1: KU 206814) has a

TABLE 2. Atavistic epibranchials (EB) found in adult *Notophthalmus viridescens* from southern Illinois, on the left (L), right (R), or on both (L + R) sides

Specimen	EB 1	EB 3	EB 4
KU 206808	R	—	—
KU 203972 <sup>1</sup>	L* + R	—	—
KU 206814 <sup>1</sup>	L + R	—	—
KU 203966	L + R	—	—
KU 206814	L + R	—	—
KU 206801 <sup>1</sup>	L + R	—	—
KU 206826	L + R	—	—
KU 203965	R*	L	—
KU 206812	—	—	L + R

\*Ossified

<sup>1</sup>Photograph in Figure 3

small cartilaginous rod extending from the end of each Ceratobranchial 1 (Fig. 3A). Closer examination of the articulation of this terminal element clearly shows that it is an independent structure (Fig. 3B). A second specimen (KU 203972) has a large bony Epibranchial 1 on the left side (Fig. 3C) and a small, round, cartilaginous Epibranchial 1 on the right (similar to that shown in Figure 3D). An additional five specimens (Table 2) have small, round epibranchial cartilages on Ceratobranchial 1 (as in Fig. 3D). Another specimen (KU 203965) has a small bony epibranchial 1 on the right side. It also has retained bony Ceratobranchials 2 and 3 with a cartilaginous Epibranchial 3 on the left side. The last specimen (KU 206812) has cartilaginous remnants of all four ceratobranchials, and has epibranchial cartilages on the fourth pair of ceratobranchials.

#### DISCUSSION

The view that the two segmental elements of the salamander branchial arch are ceratobranchials and epibranchials implies that hypobranchial elements have been lost. The alternate view is that the salamander elements are homologous to those of other vertebrates, and represent hypobranchials and ceratobranchials. Which of these two interpretations is most parsimonious in light of the three classes of evidence presented above?

We suggest that there are three reasons for interpreting salamander arch segments as hypobranchials and ceratobranchials: 1) The first segment of the urodele branchial arch articulates with the midline basibranchials (about which there is no debate) as in other vertebrates. 2) The early ontogenetic stages of *Notophthalmus viridescens* or *Ambystoma talpoideum* examined for this paper show no

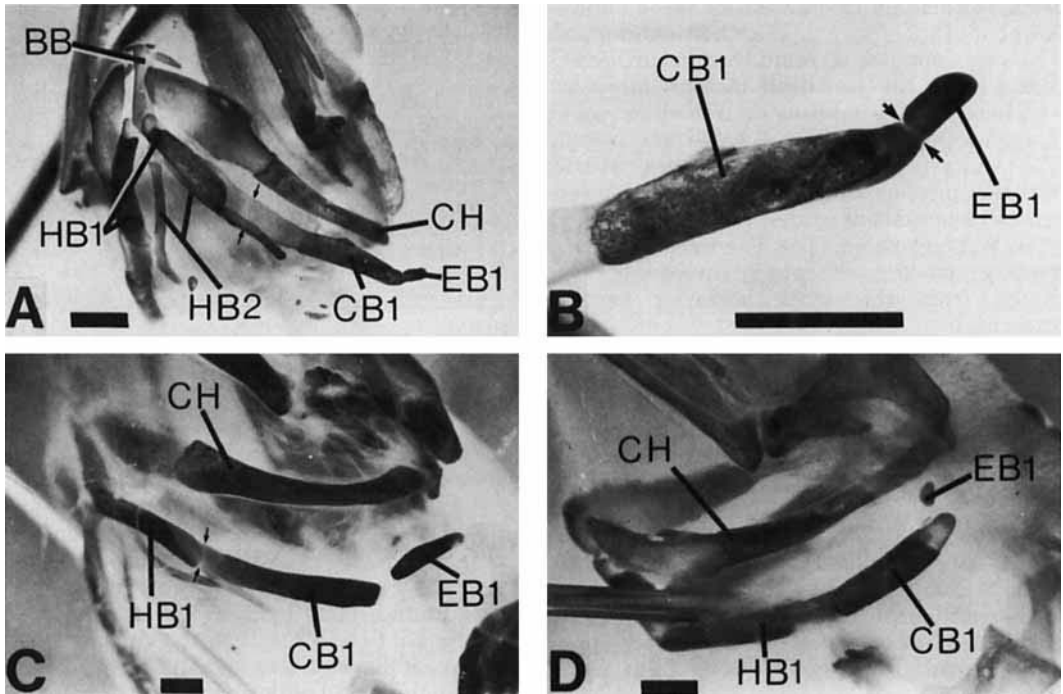


Fig. 3. Photographs of the hyobranchial apparatus of adult *Notophthalmus viridescens* to show representatives of the structures interpreted here as atavistic epibranchials. A: ventrolateral view of the entire hyobranchial apparatus (in KU 206814) illustrating the first gill arch on the left side which consists of a hypobranchial, articulating proximally with the basibranchial, a ceratobranchial, and a small cartilaginous epibranchial (EB1). Note that the second branchial arch lies behind the junction between Hypobranchial 1 (HB1) and

Ceratobranchial 1 (CB1). B: enlargement of the distal end of gill arch one from panel A to show the junction between the ceratobranchial and the atavistic epibranchial. C: Ventrolateral view of the left hyoid and first branchial arch (in KU 203972). The atavistic epibranchial in this specimen is ossified completely. D: Specimen KU 206801 showing the small cartilaginous Epibranchial 1. Arrows indicate the junction between adjacent gill arch elements; for abbreviations see caption to Figure 2. Scale = 1 mm.

small elements adjacent to the basibranchial that might have been lost during ontogeny. 3) The relative size of the ceratobranchial (the longest ventral element) and its shape and position (Figs. 1, 2) is consistent with that of other lower vertebrates.

Interpretation of the second segment as an epibranchial requires the following assumptions about transformations of branchial arch characters: 1) loss of the hypobranchials; 2) alteration of the shape of the ceratobranchials to look like the hypobranchials of other vertebrates; and 3) alteration of the shape of the epibranchial to look like the ceratobranchials of other vertebrates. Alternatively, the view that first element is the fusion of the hypobranchial and ceratobranchial assumes:

1) that there has been fusion during ontogeny (which has never been observed); 2) alteration of the shape of the fused element to look like hypobranchials of other vertebrates; and 3) alteration of the shape of the epibranchial to look like the ceratobranchials of other vertebrates. The view that salamanders have hypobranchials and ceratobranchials involves no character-state transitions. The comparative myological evidence also is interpreted most parsimoniously as an indication that salamanders have hypobranchials and ceratobranchials. In order to interpret the second arch segment of salamanders as an epibranchial one must accept the following assumptions about character transitions in branchial myology. Each of the

three ventral branchial muscles, that attach to the ceratobranchials in all other vertebrates (Table 1), must shift their insertions from the ceratobranchial to an epibranchial, as the ceratobranchial moves ventrally to occupy the place of the lost (or fused) hypobranchial. If one accepts the view that salamanders have hypobranchials and ceratobranchials, then no character transitions in branchial myology are required; thus, salamanders are hypothesized to retain the primitive condition.

The occurrence of terminal segmental structures illustrated herein (Fig. 3) also supports the view that salamanders possess hypobranchial and ceratobranchial elements, because the novel segments resemble epibranchials of other vertebrates both in shape and position. An alternative view is that the true hypobranchials of caudates have been lost (or fused with the ceratobranchial), and that the novel structures found in *Notophthalmus viridescens* are pharyngobranchials. This interpretation predicts that early in development a small remnant of an element just lateral to the midline basibranchials occasionally should be found, and that rare atavistic segments intercalated between the midline and the bone we are terming the hypobranchial should be discovered. To our knowledge, no such anomalies have ever been reported. In contrast, several authors have reported atavistic *posterior* hypobranchials in just the position we would expect if the first paired segments are in fact true hypobranchials. Drüner ('04) noted the presence of atavistic Hypobranchials 3 and 4 in *Cryptobranchus*, and atavistic third hypobranchials have been found in *Salamandra maculosa* (Drüner, '02; Kallius, '01; Stadmüller, '24; Francis, '34) and *Salamandra atra* (Tarapini, '09).

Lost characters typical of remote ancestors and not seen in the parents or recent ancestors of the organisms displaying them are referred to as atavisms. Particularly well-known examples of atavisms are the cases of naturally occurring supranumerary digits in horses (Ewart, 1894) and the induced production of teeth in chicks (Kollar and Fisher, '80). Four essential attributes that define atavistic characters are 1) "persistence into adult life," 2) "absence in the parents or recent ancestors," 3) "presence in one or only a few individuals within a population," and 4) "close resemblance to . . . the same charac-

ter possessed by all members of an ancestral population" (Hall, '84: p. 89). We interpret the extra branchial arch elements observed here in *Notophthalmus viridescens* as atavistic epibranchials. These structures have all the essential features of an atavism.

Atavisms need not arise as the result of gene mutations (Hall '84). Epigenetic events such as timing of development, tissue interactions and/or growth and morphogenesis can activate previously quiescent portions of the genome. This population of *Notophthalmus viridescens* found to contain the atavistic epibranchials is known to contain branchiate (gilled) adults (Brandon and Bremer, '66). Detailed studies of the cranial and hyobranchial ontogeny of members of this population have shown that neoteny is limited to the variable retention of larval ceratobranchials and external gills (Reilly, '86, '87). The atavistic epibranchials in this population clearly resemble epibranchials found in other lower vertebrates, and their presence in a few individuals shows that the genetic potential to produce this character has persisted and is once again being expressed. Whatever causes delay in the completion of metamorphosis (many adults delay the complete resorption of larval ceratobranchials and external gills, see Reilly, '87) in this population of newts also occasionally may remove the repressive mechanism that is blocking the formation of epibranchials.

The special significance of atavistic characters in the context of this investigation is that they provide evidence of homology. The reappearance of an ancestral character in descendent taxa tests hypotheses of homology in these descendent taxa. In this case, the reappearance of an atavistic structure that closely resembles an epibranchial in shape and position indicates that any elements previously considered to be epibranchials must be homologous to another structure. Since two distinct morphological structures in salamanders cannot both be epibranchials, one must be homologous to another branchial arch segment.

The comparative morphological and developmental evidence presented here show that the elongate branchial arch element in the salamander hyobranchium is a ceratobranchial. In all respects it is comparable to ceratobranchials in ray-finned fishes, lungfishes, *Latimeria*, and *Eusthenopteron* in both relative topographic position and in the muscles

originating from and inserting on it. Consequently, the basic segmental arrangement of parts in the visceral arches has been conserved across the transition from aquatic to terrestrial life in vertebrate evolution.

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