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## The evolution of the amphibian lateral line system and its bearing on amphibian phylogeny

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### Abstract

In modern amphibians that are aquatic the lateral line system is organized, by order, as follows: caecilians have electroreceptive ampullary organs and single rows of mechanoreceptive neuromast organs; generalized anurans have single rows of neuromasts that divide in a transverse plane to form secondary neuromasts or stitches, they do not have ampullary organs; generalized urodeles have ampullary organs, transverse stitches, and double or triple rows of neuromasts. Fossil evidence indicates that early amphibians had both ampullary organs and single rows of neuromasts embedded in bone. With time, receptors became epidermal in all three orders. Modern caecilians have retained the primitive receptor arrangement. I propose that the common ancestor of anurans and urodeles had transverse stitches, and that this character allies these two groups. Subsequent to the anuran-urodele split, anurans lost their ampullary organs, perhaps concomitant with developing specializations for herbivory. Urodeles developed orthogonal neuromast couplets and triplets. In modern anurans and urodeles, transverse stitches are correlated with pond dwelling, while ampullary organs are correlated with carnivory, suggesting that the anuran-urodele ancestor(s) was a (were) pond-dwelling carnivore(s).

**Key words:** Lateral line system – Amphibian phylogeny – Neuromast organs – Ampullary organs

The origin of modern amphibians and the relationships of the three extant orders to each other remains unclear (e. g., FROST 1985; HALL and HANKEN 1985). For example EATON (1959), ESTES (1965) and GARDINER (1983) propose an amphibian origin from labyrinthodonts, SZARSKI (1962), PARSONS and WILLIAMS (1963) and ROMER (1971) suggest a lepospondyl origin, while SCHMALHAUSEN (1968) and CARROLL and HOLMES (1980) favor a lepospondyl origin for urodeles (Caudata) and caecilians (Gymnophiona) but a labyrinthodont anuran (Anura) origin.

The lateral line system is present in all aquatic amphibians and has not been given much weight in these phylogenetic assessments. In part this is because up to now there has not been a clear picture of the organization of the lateral line systems of living amphibians to compare with those of fossils. However, data have now been collected on the mode of sensitivity, arrangement, and organization of lateral line organs in caecilians (TAYLOR 1950; HETHERINGTON and WAKE 1979; FRITZSCH and WAKE 1985; WAHNSCHAFFE et al. 1985), urodeles (FRITZSCH 1981; MUNZ et al. 1982, 1984; LANNOO 1987 a), and anurans (SHELTON 1970, 1971; FRITZSCH et al. 1984; LANNOO 1987 b). These data allow a comparison not only among extant orders but also between current and fossil amphibians. In many amphibian fossils, lateral line canals and grooves are well preserved and provide much anatomical and systematic information (SCHMALHAUSEN 1968; ROMER 1971; MOY-THOMAS and MILES 1971; THOMSON 1977; NORTHCUTT and GANS 1983). Here I examine what is known about the lateral line systems of early and modern amphibians to gain further insights into the phylogenetic relationships of the recent orders.

The following observations have been made:

1. Like their rhipidistian ancestors (e. g., see JARVIK 1980; MALLATT 1986; STENSIÖ 1947), the earliest recognizable amphibian fossils are characterized by having on their

heads supraorbital, infraorbital, and mandibular neuromast canals embedded in bone (MOODIE 1908; SZARSKI 1962; SCHMALHAUSEN 1968; Fig. 1A). Electroreceptive ampullary organs were probably also present, associated with these neuromast canals (MOY-THOMAS and MILES 1971; THOMSON 1977; BULLOCK and SZABO 1986; FINGER et al. 1986).

2. Later amphibian fossils had neuromasts in open bony grooves. These grooves become wider and shallower in progressively later forms (SCHMALHAUSEN 1968). This peripheral migration of neuromasts is correlated with dermal bone loss in early amphibians and appears to have occurred simultaneously in several lineages (SCHMALHAUSEN 1968).

3. In modern caecilian larvae the lateral line organization resembles the pattern in early amphibians with one important exception – in caecilians receptor organs are located in the epidermis rather than embedded in bony canals (Fig. 1B). Like early amphibians, caecilians have supraorbital, infraorbital, and mandibular neuromasts that are organized into single rows and lines (TAYLOR 1970) plus ampullary organs (HETHERINGTON and WAKE 1979; FRITZSCH and WAKE 1985; WAHNSCHAFFE et al. 1985).

4. In generalized modern urodele and anuran larvae, primary neuromasts, laid down embryonically, divide to form secondary neuromasts (i. e., LANNOO 1985; WINKLBAUER and HAUSEN 1983). Secondary neuromasts together are termed a stitch (HARRIS and MILNE 1966; LANNOO 1985). Typically the long axis of each stitch is perpendicular to the long axes of its component neuromasts (LANNOO 1987 a, b). These transverse stitches are unique to anurans and urodeles; they have not been reported in caecilians and fishes. In amphibians transverse stitch formation could have only occurred after neuromasts became freed from the physical constraints of bony canals (SCHMALHAUSEN 1968; also see below).

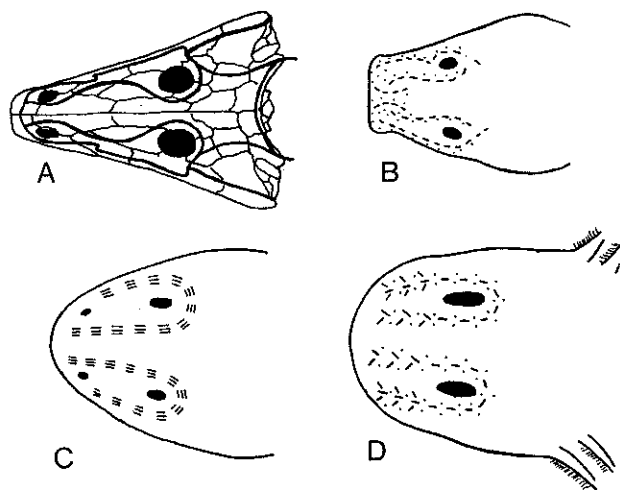


Fig. 1. Schematic diagrams of lateral line organization in amphibians in dorsal view. A: Lateral line canal pattern in the Stegocephalian *Benthosuchus* (after SCHMALHAUSEN 1968, Fig. 48c, p. 80). Note the supra- and infraorbital canals medially and laterally, respectively. Although not noted in this diagram, ampullary organs were thought to be present in these animals. B: Lateral line pattern in the caecilian *Ichthyophis* (after HETHERINGTON and WAKE 1979). In this drawing and the following two, neuromasts are linear and ampullary organs are small circles. Neuromast maximum sensitivity is parallel to its long axis. C: Neuromasts and transverse stitch formation in generalized anurans. Note that the long axis of transverse stitches is perpendicular to the long axes of its component neuromasts. D: The complex pattern of neuromast organization typical of urodeles. Note that both neuromasts and ampullary organs are present and that on the snout neuromasts are arranged into orthogonally oriented couplets or triplets. Although generalized urodeles have transverse stitches like those illustrated for anurans, they have not been included in this drawing for clarity.

5. Modern anuran larvae, which are typically herbivorous (WASSERSUG 1975), no longer form ampullary organs (FRITZSCH et al. 1984; LANNOO 1987b; Fig. 1C).

6. Like caecilians, modern urodele larvae have retained ampullary organs (FRITZSCH 1981). Unlike caecilians however, urodeles are characterized by having neuromasts arranged into orthogonal arrays of couplets and triplets on their nasal and maxillary snouts (LANNOO 1985; 1987a; Fig. 1D).

7. Modern stream-dwelling urodeles and anurans, which are considered derived, do not form stitches. In urodeles this stitch loss occurs at the familial level (LANNOO 1987a), in anurans it occurs at the genus (LANNOO 1987b) or species (LANNOO et al. 1987) level.

8. Additional derived neuromast characteristics of amphibians include parallel stitch formation in proteid urodeles (LANNOO 1987a) and the formation of stitch »plaques« (see MURRAY 1955) in midwater suspension feeding anurans such as *Xenopus*, *Rhynophrynus*, and *Phrynomerus* (LANNOO 1987b).

From these observations on the lateral line system it appears that modern caecilians have carried the trend begun in earlier amphibians of peripheral organ migration to its conclusion with little modification: they have epidermally located neuromast and ampullary organs arranged into single rows. Because several lineages of early amphibians show a trend towards bone loss (SCHMALHAUSEN 1968) the lateral line system does not give many clues to the origin of this order.

Compared to caecilians and early amphibians, modern salamanders and frogs have highly modified lateral line systems. The key factor in these modifications was probably the early peripheral migration of receptors from bony canals to the epidermis. Bony canals appear to constrain modifications in neuromast topography; within species, canal neuromast numbers on the heads of teleosts tend to be invariant (WEBB 1985; COOMBS et al. 1986 and references therein), whereas numbers of apparently homologous epidermal neuromasts in amphibians can differ by up to 30% bilaterally (LANNOO 1985, 1987a, b).

In addition to the mechanical constraints that bony canals may exert on neuromast parameters there may also be developmental constraints. Neuromasts may induce dermal bone formation in fishes (although this fact is debated, see discussion in HALL and HANKEN 1985). If however this is true, epidermal neuromasts would be freed from this induction process and could therefore be modified in response to environmental pressures independent of developmental constraints.

The two major modifications of the neuromast system in modern amphibians are transverse stitch formation, characteristic of both generalized salamanders and frogs, and rostral couplets and triplets of orthogonal neuromasts, characteristic of all salamanders (LANNOO 1987a, b). Both of these modifications must have occurred after neuromasts became epidermal. Bony canals could probably not easily accommodate the expanding width of transverse stitches, which continue to add secondary neuromasts with larval growth. In fact, secondary neuromast proliferation has not been described in the fossils of early amphibians and is not known to occur in fish bony canals (e. g., COOMBS et al. 1986), although it may occur in superficial neuromasts. When stitches form in epidermal grooves in modern amphibians (i. e., *Necturus* and *Proteus*; MALBRANC 1876; LANNOO 1987a), the plane of neuromast division is shifted 90°, making the stitch long axis *parallel* to the long axis of the groove.

This reorientation of the plane of secondary neuromast division is a fundamentally different modification than variation in neuromast numbers per stitch, or even the presence of stitches. Stitch reorientation in proteids is a new invention, probably the result of a gene mutation that shifted the plane of secondary neuromast division. On the other hand, variation in the number of secondary neuromasts, including an absence of secondary neuromasts, is probably the result of heterochronic events, with the rate of secondary neuromast formation either accelerated or decelerated relative to larval growth (LANNOO 1987a).

As is the case with stitch formation, the orthogonal neuromast couplets and triplets characteristic of salamanders could not have arisen in bony canals. In bony fish canals and in the semicircular canals of the vertebrate vestibular system, neuromasts (or hair cell epithelia) are always oriented with their long axis (i. e., their axis of maximum sensitivity) parallel to the canal (e. g., COOMBS et al. 1986). This orientation makes hair cells sensitive to fluid motion along the canal. If neuromast orientation is shifted relative to the canal axis, neuromast sensitivity decreases as a cosine function of its angle (FLOCK 1965; 1971). If the urodele neuromast pattern had developed in bone the original straight supra- and infraorbital canals would have had to split into short sections that each contained a single neuromast, then these canal segments with their neuromasts would have had to become perpendicularly oriented. Subsequently, the canal bones would have had to be reduced to allow neuromasts to become epidermal. So far, there is no evidence of this complex process from the fossil record, or from ontogenetic studies (e. g., STONE 1933; HANKEN and HALL 1985).

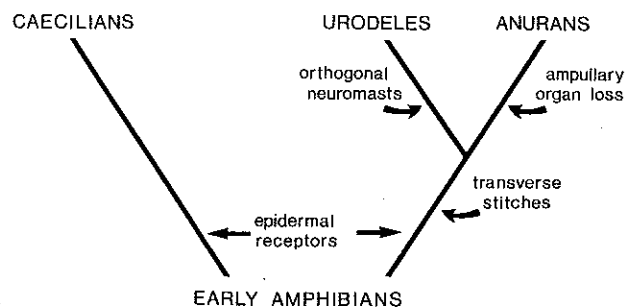


Fig. 2. Phylogeny of amphibians based solely on lateral line parameters. In this scenario early amphibians are characterized by having neuromasts in single rows that do not form stitches, and ampullary organs. In both caecilian and anuran-urodele lines receptors became epidermal. The anuran-urodele common ancestor developed transverse stitches. After the anuran-urodele split anurans lost ampullary organs while urodeles developed orthogonal neuromasts

The most parsimonious explanation for the neuromast pattern in modern amphibians is that the common ancestor of both urodeles and anurans had epidermal neuromasts and transverse stitches that have persisted to this day in the generalized forms of both groups (Fig. 2). Transverse stitches therefore ally urodeles and anurans. The relationship of caecilians to this clade is not clear but the common ancestor of all modern amphibians must have occurred before transverse stitches were invented. According to this scenario, urodeles and anurans must have split late in the Paleozoic or very early in the Mesozoic; the discovery of *Protobatrachus* in the early Mesozoic indicates anurans originated before this time. This evolutionary scenario is not consistent with those proposed for example by SCHMALHAUSEN (1968) or CARROLL and HOLMES (1980), which ally caecilians with urodeles based on other characters.

After urodeles and anurans split, anurans lost their ampullary organ subsystem and urodeles developed orthogonal neuromasts (Fig. 2). The loss of ampullary organs in anurans is correlated with the development of herbivorous food habits and the »tadpole« morphology, with its numerous adaptations to herbivory (WASSERSUG 1975). As an aside, early teleost fishes also lost their ampullary system (BULLOCK et al. 1982) but the ecological correlations associated with this loss are not so clear cut.

Among amphibians, orthogonal neuromast couplets along the snout are unique to urodeles. Orthogonal neuromasts may be present in the superficial neuromast system of teleosts but this morphology does not predominate in fishes the way it does in salamanders. It is impossible to say at this point whether the urodele neuromast pattern developed

in response to a specific need (perhaps zooplanktivory?; LANNOO 1986) or whether it was adaptive because it increased the precision of the system.

Alternate phylogenetic views are possible but less likely. For example, because both caecilians and urodeles have neuromasts and ampullary organs they might be considered more closely related to each other than to anurans, which have lost ampullary organs. This explanation however requires that the common ancestor of all modern amphibians invented transverse stitches and that caecilians subsequently lost them, or that transverse stitches were invented separately by both urodeles and anurans. According to the weighting criteria of HECHT and EDWARDS (1977) character loss is more likely than character invention, therefore this alternative, which involves more inventions than my original scenario, is not the most parsimonious explanation. However, comparing the supraorbital (medial) lines in Figures 1b with 1d it is relatively easy to derive the urodele pattern from the caecilian pattern by shifting the two lines and reorienting their neuromasts. Unfortunately, no developmental studies exist that describe how these supraorbital lines form. It is also not clear from this scenario how multiple lines would form in the maxillary row.

Caecilians could be allied with anurans on the basis that both groups have single neuromast rows. This trait is, however, the generalized condition in all early aquatic vertebrates (SCHMALHAUSEN 1968; ROMER 1971). This scenario would also require the separate invention of transverse stitches by both anurans and urodeles, or the invention of transverse stitches in the common amphibian ancestor and their subsequent loss in caecilians.

In modern amphibians, ampullary organs are associated with carnivorous food habits; both caecilians and urodeles have ampullary organs. There are a few carnivorous anuran tadpoles (e. g., *Hymenochirus boettgeri* and *Scaphiopus* sp.), but these forms do not have ampullary organs and are presumably secondarily derived carnivores (LANNOO 1987b). If ampullary organs were to be found in amphibian fossils it would suggest that these forms were carnivorous in water. In modern urodeles and anurans transverse stitch formation is also correlated with pond habitats (LANNOO 1987a, b). It is possible, therefore, that the early amphibians that developed transverse stitches were also pond dwelling.

In any definitive assesment of amphibian phylogeny, all available evidence will have to be weighed, and the lateral line system will be one of many factors considered. However, the lateral line system provides a morphological perspective on amphibian diversity that has not been considered before; one that may prove important in future phylogenetic judgements.

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#### Zusammenfassung

##### *Die Evolution des Seitenliniensystems der Amphibien und seine Bedeutung für die Stammesgeschichte der Amphibien*

Bei rezenten wasserlebenden Amphibien ist das Seitenlinienorgan in folgender Weise aufgebaut: Caecilia haben elektrorezeptive ampulläre Organe und mechanorezeptive Neuromasten in einzelnen Reihen. Bei primitiven Anuren sind die Neuromasten in einzelnen Reihen angelegt; sie teilen sich quer und bilden sekundäre Neuromasten oder »Stiche«. Primitive Urodelen haben ampulläre Organe, querliegende Stiche und Neuromasten in doppelten oder dreifachen Reihen. Fossilfunde zeigen, daß bei frühen Amphibien sowohl die ampullären Organe als auch die Neuromasten in Knochen eingebettet waren. Allmählich wurden die Rezeptoren in den drei Ordnungen epidermal, rezente Caecilia behielten die primitive Anordnung der Rezeptoren. Daraus schließe ich, daß der ge-

meinsame Vorfahre der Anuren und Urodelen querliegende Stiche hatte und daß diese Charakteristik die beiden Gruppen verbindet. Im Laufe der Stammesgeschichte haben die Anuren die ampullären Organe verloren, vielleicht als Begleiterscheinung zur pflanzenfressenden Spezialisierung der Anurenlarven. Bei Urodelen entwickelten sich doppelte und dreifache orthogonale Neuromasten. Bei rezenten Anuren und Urodelen werden querliegende Stiche vorwiegend bei Teichbewohnern gefunden, während ampulläre Organe bei Fleischfressern auftreten. Daraus läßt sich schließen, daß die Vorfahren der Anuren und Urodelen fleischfressende Teichbewohner waren.

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