



## The development of lateral line placodes: Taking a broader view



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### ABSTRACT

The lateral line system of anamniote vertebrates enables the detection of local water movement and weak bioelectric fields. Ancestrally, it comprises neuromasts – small sense organs containing mechanosensory hair cells – distributed in characteristic lines over the head and trunk, flanked on the head by fields of electroreceptive ampullary organs, innervated by afferent neurons projecting respectively to the medial and dorsal octavolateral nuclei in the hindbrain. Given the independent loss of the electrosensory system in multiple lineages, the development and evolution of the mechanosensory and electrosensory components of the lateral line must be dissociable. Nevertheless, the entire system arises from a series of cranial lateral line placodes, which exhibit two modes of sensory organ formation: elongation to form sensory ridges that fragment (with neuromasts differentiating in the center of the ridge, and ampullary organs on the flanks), or migration as collectives of cells, depositing sense organs in their wake. Intensive study of the migrating posterior lateral line placode in zebrafish has yielded a wealth of information concerning the molecular control of migration and neuromast formation in this migrating placode, in this cypriniform teleost species. However, our mechanistic understanding of neuromast and ampullary organ formation by elongating lateral line placodes, and even of other zebrafish lateral line placodes, is sparse or non-existent. Here, we attempt to highlight the diversity of lateral line development and the limits of the current research focus on the zebrafish posterior lateral line placode. We hope this will stimulate a broader approach to this fascinating sensory system.

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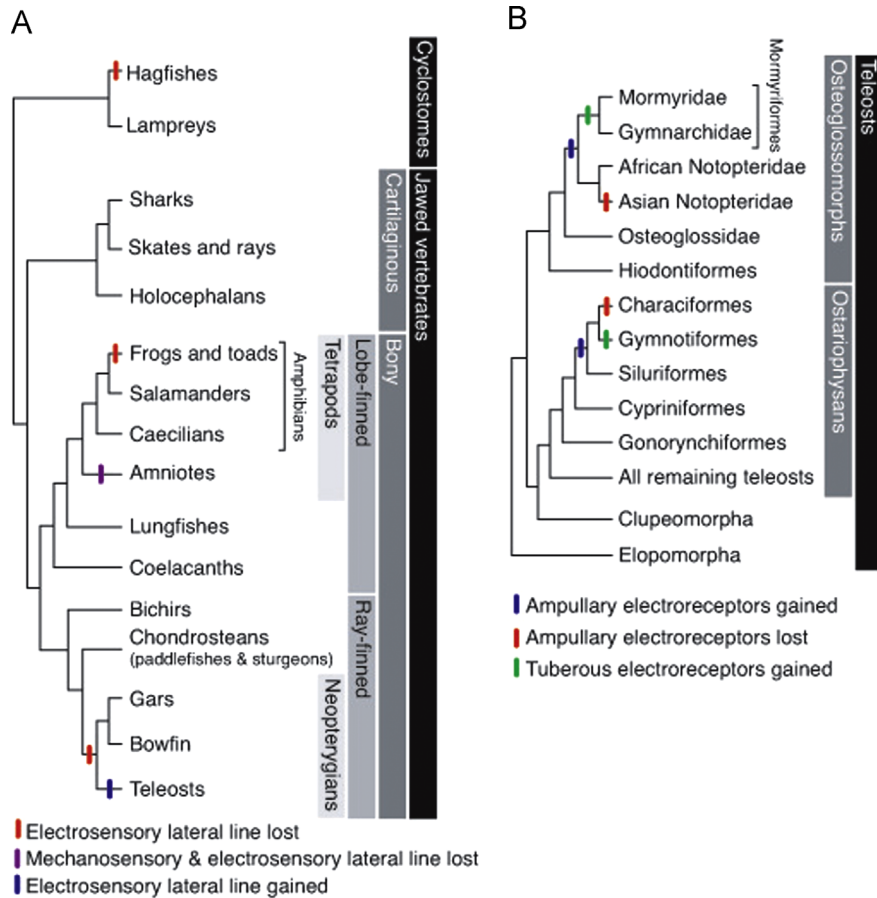
### Introduction

The development of the mechanosensory and electrosensory lateral line system of anamniote vertebrates is an excellent model system to study key developmental processes such as cell migration, cell fate specification and morphogenesis at the cellular and molecular level, and also evolutionary processes, since different components of this system – particularly the electrosensory component – have undergone numerous independent losses, modifications and gains in different lineages (Fig. 1A and B). The lateral line system (reviewed in Bullock, 1982; Blaxter, 1987; Coombs et al., 1989; Northcutt, 1997; Bullock et al., 2005; Coombs et al., 2014) primitively consists of lines of mechanoreceptive organs (neuromasts) in the skin (epidermis or dermis), flanked by fields of electroreceptive organs (ampullary organs), innervated respectively by afferent lateral line nerves projecting to the medial and dorsal octavolateral nuclei in the hindbrain. These organs sense local water motion and weak bioelectric fields (resulting from the leakage of ions across mucous membranes, including the mouth,

gills and cloaca; Wilkens and Hofmann, 2005; Bedore and Kajiura, 2013), and enable the animals to detect prey and/or predators, orient themselves and respond to their environment. The central components of the lateral line system may also have been fundamental to the evolution of the vertebrate cerebellum. The medial and dorsal octavolateral nuclei each have a cerebellum-like organization, and are located ventrolateral to the cerebellum in jawed vertebrates. They are also present in the jawless lampreys, which lack a true cerebellum (Ronan and Northcutt, 1990; Khonsari et al., 2009; Murakami and Watanabe, 2009). This has led to the proposal that the cerebellum evolved in the jawed vertebrate lineage via duplication of the dorsal (electrosensory) octavolateral nucleus, which itself evolved via duplication of the medial (mechanosensory) octavolateral nucleus (Montgomery and Bodznick, 2010; Montgomery et al., 2012).

The lateral line system and its morphology was observed by biologists several hundred years ago. As reported by Parker (1904) and Johnson (1917), Steno and Lorenzini in the seventeenth century described what are now known to be the pores of the electroreceptive ampullary organs of elasmobranchs (sharks and rays). Lateral line organs were originally thought to be mucus-secreting glands: a sensory function was not proposed until 1850, by Leydig (1850), and developmental studies were not performed

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**Fig. 1.** Phylogenies for (A) extant vertebrates and (B) teleost fishes (neopterygian and teleost phylogenies after [Near et al., 2012](#)). The mechanosensory lateral line system is found in all groups of extant vertebrates except the amniotes (mammals, birds and non-avian reptiles). The electrosensory lateral line system was independently lost (red bar) along several lineages, including the cyclostome lineage leading to hagfishes, the ray-finned bony fish lineage leading to neopterygian fishes (gars, bowfin and teleosts) and, within the lobe-finned bony fish clade, the lineages leading to anuran amphibians (frogs, toads) and to amniotes (the entire lateral line system was lost in amniotes, including the mechanosensory component). Lateral line electroreceptors (with a different electrophysiology to non-teleost electroreceptors) later evolved independently (blue bar) within the teleost fishes. (B) Within teleost fishes, the phylogenetic distribution of electroreception suggests the convergent evolution of ampullary electroreceptors once in the osteoglossomorphs (blue bar), along the lineage leading to notopterids (featherbacks or knifefishes) and mormyriiforms (elephantnose fish plus the aba [African knifefish], *Gymnarchus niloticus*), followed by loss in the Asian notopterid lineage (red bar); and once in the ostariophysans (blue bar), along the lineage leading to characiforms (tetras), gymnotiforms (American knifefishes) and siluriforms (catfishes) ([Near et al., 2012](#)), followed by loss in characiforms (red bar). Electric organs and the tuberous electroreceptors that detect electric organ discharges (green bar) subsequently evolved independently along the lineages leading to the osteoglossomorph mormyriiforms and the ostariophysan gymnotiforms. (Figure modified from [Baker et al., 2013](#) with permission from the Journal of Experimental Biology).

for almost another 40 years. In his 1878 monograph on the development of elasmobranch fishes, [Balfour \(1878\)](#) described how the lateral line grows posteriorly. Similarly, [Beard \(1884\)](#) observed that the posterior lateral line in a teleost fish, the brown trout (*Salmo trutta*) (*Salmo fario*), does not increase in length by recruitment of ectodermal cells but that the lateral line itself “grows back longitudinally along the whole length of the body. This cord of cells gives origin to the sense organs of the lateral line” (quoted in [Wright, 1951](#)). [Platt \(1896\)](#) studied a urodele amphibian, the aquatic salamander (mudpuppy) *Necturus*, and stated that the growth of the lateral line is chiefly through division and migration and that the growing lateral line ‘plows’ through the skin, “leaving a row of sense-organs in the wake” ([Fig. 2A](#); [Platt, 1896](#)). In the twentieth century, the first experimental approaches to lateral line development were taken by [Harrison and Stone](#), whose elegant transplantation, ablation and dye labeling experiments in anuran and urodele amphibians proved that the posterior lateral line primordium migrates and gives rise to sense organs on the trunk ([Fig. 2B–D](#)), and that lateral line sense organs on the head, together with lateral line neurons, are derived from placodes ([Harrison, 1904](#); [Stone, 1922, 1928b, 1928c, 1929, 1933, 1937](#)) (reviewed in [Wright, 1951](#); [Northcutt et al., 1994](#);

[Schlosser, 2002a](#)). Ablation, grafting and vital dye labeling studies in a urodele amphibian (the axolotl *Ambystoma mexicanum*), a chondrosteian ray-finned fish (the Mississippi paddlefish *Polyodon spathula*) and a cartilaginous fish (the little skate *Leucoraja erinacea*) have also confirmed experimentally that ampullary organs as well as neuromasts originate from lateral line placodes, at least in non-teleost jawed vertebrates ([Northcutt et al., 1995](#); [Modrell et al., 2011a](#); [Gillis et al., 2012](#)).

Although a neural crest contribution to cranial and trunk lateral line neuromasts was reported after Dil-labeling experiments in two teleosts (the zebrafish *Danio rerio* and the Siamese fighting fish *Betta splendens*) and a frog, *Xenopus laevis* ([Collazo et al., 1994](#)), it is very difficult to ensure specific injection of cranial neural crest versus immediately adjacent cranial placodes in these embryos, and neural crest-derived cells seen in trunk neuromasts could be the neural crest-derived glia (Schwann cells) that are intimately associated with the afferent lateral line axons that track the migrating posterior lateral line primordium and innervate neuromast hair cells ([Metcalf, 1985](#); [Gilmour et al., 2002](#)). Furthermore, despite intensive study of trunk neuromast formation from the zebrafish posterior lateral line placode by numerous different groups in recent years, using a variety of transgenic lines, no

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