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## Air-breathing in fish: Air-breathing organs and control of respiration Nerves and neurotransmitters in the air-breathing organs and the skin

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### ABSTRACT

In fishes, exploitation of aerial gas exchange has evolved independently many times, involving a variety of air-breathing organs. Indeed, air-breathing occurs in at least 49 known families of fish (Graham, 1997). Many amphibious vertebrates, at some stage of their development are actually trimodal breathers that use various combinations of respiratory surfaces to breath both water (skin and/or gill) and air (skin and/or lung). The present review examines the evolutionary implications of air-breathing organs in fishes and the morphology of the peripheral receptors and the neurotransmitter content of the cells involved in the control of air-breathing. Control of breathing, whether gill ventilation or air-breathing, is influenced by feedback from peripheral and/or central nervous system receptors that respond to changes in PO<sub>2</sub>, PCO<sub>2</sub> and/or pH. Although the specific chemoreceptors mediating the respiratory reflexes have not been conclusively identified, studies in water-breathing teleosts have implicated the neuroepithelial cells (NECs) existing in gill tissues as the O<sub>2</sub> sensitive chemoreceptors that initiate the cardiorespiratory reflexes in aquatic vertebrates. Some of the air-breathing fishes, such as *Protopterus*, *Polypterus* and *Amia* have been shown to have NECs in the gills and/or lungs, although the role of these receptors and their innervation in the control of breathing is not known. NECs have been also reported in the specialized respiratory epithelia of accessory respiratory organs (ARO's) of some catfish species and in the gill and skin of the mudskipper *Periophthalmodon schlosseri*. Unlike teleosts matching an O<sub>2</sub>-oriented ventilation to ambient O<sub>2</sub> levels, lungfishes have central and peripheral H<sup>+</sup>/CO<sub>2</sub> receptors that control the acid-base status of the blood.

### 1. Introduction

Primitive fishes were the first vertebrates to exploit atmospheric respiratory gases, in addition to gases dissolved in their aquatic milieu, prior to the colonization of the terrestrial habitats by amphibians (see for review Hedrick and Katz, 2016). The ability to extract oxygen directly from the atmosphere enabled ancient fish to survive in hypoxic environments. Extant air-breathing fish are now the subjects of many studies coming from diverse laboratories since they are considered physiological models to study the evolutionary transition from gill to air-breathing ventilation. A consequence of this transition is the addition of accessory respiratory organs (ARO's) that necessitate changes in both the general circulatory system and the microcirculation of the respiratory epithelia, thus providing indication of the evolution associated with adaptation to the terrestrial habitats (Olsson et al., 1995).

The major shifts in the integration of organ systems have coincided with the evolutionary transitions from aquatic to aerial respiration and from aquatic to terrestrial life. In freshwater fish, respiration, ion and water regulation and acid-balance reside mainly within the gills. By contrast, in mammals, gas exchange and respiratory acid-base regulation are lung functions whereas ion and water regulation, nitrogen excretion, and metabolic acid-base regulation depend on the kidney. In larval amphibians, excretion, osmoregulation, and respiration are branchially mediated. However, the post-metamorphic amphibians show an intermediate position between fish and mammals in terms of kidney function, while auxiliary organs such as the skin and urinary bladder may be involved in respiratory and osmotic functions (Graham, 1997).

The ancient fish lineages are viewed as the archetypes for the physiological adaptations to amphibious life (Hedrick and Katz, 2016). Consequently, much research is now addressed on the basic metabolic

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and physiological modifications that have occurred during the transition to air-breathing. The main aspect of this transition is the reduction of the gill blood flow associated with air-breathing since it compromises basic gill functions such as CO<sub>2</sub> removal, osmotic regulation, acid-base balance and nitrogen excretion. Another important aspect is the control of air-breathing. Air-breathing fishes must be able to sense and to respond to changes in external and internal partial pressures of respiratory gases (O<sub>2</sub> and CO<sub>2</sub>) via chemoreceptors, as well as to sense changes in the volume of the air-breathing organ via mechanoreceptors (Hedrick and Katz, 2016). Some aspects related to nitrogen excretion in air-breathing fishes remain somewhat obscure since air-breathing interrupts or reduces branchial function. Data obtained in the amphibious fishes, the mudskippers, revealed that the gills, skin and urinary tracts were all involved in nitrogen excretion (Graham, 1997) and, that, during forced emersion, they switched from ammonotelism to urotelism.

The two major clades of Osteichthyes, the Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes), diverged sometimes in the late Silurian (438 to 408 million years ago). It is generally accepted that air-breathing evolved in the two major lineages prior to the fish-tetrapod transition in the Devonian (approximately, 385 to 360 million years ago) (Graham, 1997; Clack, 2012; Hedrick and Katz, 2016). Among the extant actinopterygians, the most primitive forms include bichirs (*Polypterus*), gars (*Lepisosteus*) and the bowfin (*Amia*). Among the sarcopterygians, the only remaining extant air-breathing group corresponds to the Dipnoi (lungfishes: *Protopterus*, *Lepidosiren* and *Neoceratodus*). Our primary focus in this chapter will be the presumptive peripheral respiratory chemoreceptors of air-breathing fishes that were initially located in the gills of the teleosts (Zaccone et al., 2006; Jonz and Nurse, 2009; Jonz and Zaccone, 2009; Jonz et al., 2016). Morphological and physiological studies of the peripheral O<sub>2</sub> sensing cells have been performed in a few number of air-breathing fishes, being compared to those of water-breathing fishes and mammals to study the evolution of O<sub>2</sub> chemoreception. This chapter also focuses on the characteristics of the air-breathing that occurred in a group of teleosts that were secondarily adapted to aerial respiration. These include the air-breathing organs (ABO's) and the aerial respiratory surfaces of the higher euteleosts (ABO's derived from the gills and the modified branchial chambers) that are present in the members of the Clariidae and Heteropneustidae families, grouped into the superfamily Clarioidea (Sullivan et al., 2006). The gills and the skin of the amphibious fishes are also considered to be functional for aerial respiration. In mudskippers, the sensory system required to switch the site of gas exchange in emersed air-breathing species and in those having terrestrial habits, is not well characterized. Extrabranchial sites of respiration in the mudskippers include the cutaneous surfaces, where rapid circulatory adjustments increase blood flow and facilitate O<sub>2</sub> transfer (see for review Wright and Turko, 2016). According to Wright and Turko (2016), the cutaneous surfaces of amphibious fishes such as the rivulines and the mudskippers are primed for aerial respiration, and several plastic traits associated with locomotion, gas exchange, nitrogen excretion, ionoregulation and osmoregulation must be taken into account when explaining ABO specialization. The skin surfaces are also the histological site for the occurrence of putative oxygen receptor cells (the neuroepithelial cells, NECs) that show peculiar neurotransmitter profiles (Zaccone et al., 2017). Unlike in teleosts, where the control of breathing is influenced by feedback from peripheral and/or central nervous system by O<sub>2</sub> sensing cells, the function of the NECs in the skin of amphibious fishes remains obscure.

NECs are present in the gill filaments of fish, appear strategically located at the interface between the respiratory water and the arterial blood flow, and exhibit morphofunctional characteristics that are typical of the O<sub>2</sub> chemoreceptors present in the lung of the air-breathing vertebrates (reviewed by Bailly, 2009; Jonz and Nurse, 2009). Several responses to hypoxia such as hyperventilation, variation in gill vascular resistance arise, as stated above, from O<sub>2</sub> peripheral chemoreceptors

located in the gills. These O<sub>2</sub> sensors correspond to the NECs that have been localized in the gill filaments of a wide variety of fishes, including teleosts (Zaccone et al., 1997; Jonz and Nurse, 2003; Jonz and Zaccone, 2009; Porteus et al., 2015) and non-teleost (Zaccone et al., 1997; Jonz et al., 2016) species. Fish gill NECs share several morphological features with other peripheral O<sub>2</sub> chemoreceptors such as the carotid body cells of mammals and the NEC-like cells found in the lung of lungfishes and bichirs (Zaccone et al., 2007, 2012). Although the specific O<sub>2</sub>-sensitive chemoreceptors and gill arch mechanoreceptors that mediate the gill ventilatory and air-breathing responses to hypoxia have not been conclusively identified (Hedrick and Katz, 2016), the NECs of teleost gills are being considered to be the O<sub>2</sub> sensitive chemoreceptors (Jonz and Nurse, 2009; Porteus et al., 2013).

We devote the bulk of this chapter to review the neurochemical profiles of the NECs located in the gills and air-breathing organs of a selected group of primitive fishes and advanced teleosts that have developed air-breathing structures, probably as a plastic response to environmental modifications.

## 2. Phylogenetic origin of air-breathing

As emphasized by Gilmour and Milsom (2009), the respiratory passages of all the vertebrates have arisen from digestive passages and, that, with regard to CO<sub>2</sub>, and/or pH, the taste, smell and cardiorespiratory chemoreception are arbitrary distinctions. It seems probable that airway chemoreceptors aroused from digestive (olfactory, gustatory) chemoreceptors including, possibly, a diffuse system of chemoreceptors that are found in the skin, gills and oropharyngeal surfaces of primary aquatic vertebrates. These chemoreceptors constitute the so-called solitary chemosensory cell (SCCs) system (Sbarbati et al., 2009). All the chordates including vertebrates have a pharyngeal branchial basket that is regarded to have respiratory function. This occurs in jawed fish (Hsia et al., 2013). In particular, a pharyngeal slit is a peculiar characteristic of vertebrates during their development (Cameron et al., 2000). In primitive chordates, the first pharyngeal slits evolved into jaws required for feeding. Subsequently, pharyngeal slits and buccal pumps, that primarily evolved for feeding, gave rise to gills for breathing, with water flow being driven by a buccal pump involving muscles primarily innervated by the trigeminal and facial nerves (Gilmour and Milsom, 2009). A recent study by Icardo et al. (2017) has shown that the lungs in two polypterid fish, the bichir, *Polypterus senegalus*, and the reedfish, *Erpetoichthys calabaricus*, originate from the ventral side of pharynx at about the level of oesophageic aperture. It demonstrates that the structures that function both as air-breathing and buoyancy organs aroused from the alimentary tract. The term 'lung' is not consistently used to describe the air-breathing organs found in all the primitive fishes (Hedrick and Katz, 2016). Graham (1997) uses the term 'gas bladder' and suggests there are fundamental differences in embryonic origin, location of the glottis and differences in pulmonary circulation. The lungfishes (*Neoceratodus*, *Lepidosiren*, *Protopterus*) and the polypterids (*Polypterus* and *Erpetoichthys*) all possess lungs that arise from a ventral glottis, a muscle-ridged slit. Respiratory gas bladders are present both in *Amia* (Halecomorpha) and the gars (*Lepisosteus* and *Atractosteus*, *Ginglyostoma*).

Air breathing first evolved in fishes and, over the 400 million year history of this group, this capacity has persisted in certain lineages and has been reacquired by others. Graham (1997) suggests that the air-breathing is one of several adaptive responses utilized by fishes dwelling in habitats where O<sub>2</sub> supplies may be severely depleted. Rather than having tendencies toward invading the land, most of these fishes remain tied to an exclusively aquatic existence. Various theories have been advanced concerning how the transition from bimodal to unimodal respiration could have affected the evolution of tetrapod gas exchange, to eliminate gill function. The ecological radiation has occurred in groups such as anabantoids, clariids, and callichthyids in which bimodal breathing has been integrated with their natural history.

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