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## Central control of air breathing in fishes

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### ABSTRACT

The diversity of sites and surfaces that are utilized for gas transfer from air to blood in fish is remarkable. While a few species do utilize their gills for gas exchange in air, this is a rare occurrence and most air-breathing fish utilize other surfaces including air-breathing organs and lungs. At present almost nothing is known about the central sites that initiate and regulate air breathing although hypotheses can be put forward based on our rudimentary understanding of the sites involved in water breathing in lampreys and teleost fishes, and those involved in air breathing in pre-metamorphic anuran amphibians. The pumps involved in producing both water and air breathing in fishes are highly conserved, a buccal pump, assisted by pharyngeal and/or parabranchial/opercular pumps, produce both forms of ventilation. What varies between species are the manner in which air breaths are produced (in two versus four phases), and the 'valving' involved in producing water flow over the gills versus air flow in and out of air-breathing organs. The latter suggests that a major step in the evolution of air breathing was the evolution of the mechanisms that control the flow of the respiratory medium. The neural matrix that underlies the co-ordination of the pump and the valving events remains enigmatic and in much need of further research.

### 1. Feedback control and the need to regulate gas exchange at multiple sites

The ability to air-breathe in fishes appears to have evolved independently many times (Graham, 1997) utilizing a remarkable array of sites and surfaces for aerial gas exchange. While a few species utilize their gills for gas exchange in air, this is a rare occurrence and most air-breathing fish utilize other vascularized surfaces. The transition to exclusive air breathing was a gradual one progressing from the intermittent use of accessory air breathing structures to the facultative and then obligate use of aerial gas exchange organs. This gave rise to bimodal breathing; the use of two different media for gas exchange (Graham, 1997; Johansen, 1970; Lefevre et al., 2013). In most bimodal breathers, the partitioning of gas exchange for O<sub>2</sub> and CO<sub>2</sub> is not equivalent at the two exchange sites; elimination of CO<sub>2</sub> exceeds the acquisition of O<sub>2</sub> at the aquatic exchange site whereas the opposite is true at the aerial exchange site. This would require monitoring and homeostatically regulating O<sub>2</sub> and CO<sub>2</sub>/pH levels by controlling gas exchange at both sites. At present almost nothing is known about how this is accomplished. There is a growing literature on the afferent inputs that differentially regulate water versus air breathing (discussed in the articles by Jonz et al., and Florindo et al. in this series) as well as of the mechanical events associated with each type of breath (Brainerd, 1994; Brainerd and Ferry-Graham, 2005; Liem, 1980, 1985; McMahon, 1969).

However, little is known of the central sites that integrate the sensory information and generate air-breathing although hypothesis can be put forward based on our understanding of the sites involved in central respiratory rhythm generation in lampreys, water breathing teleost fishes and water and air breathing anuran tadpoles.

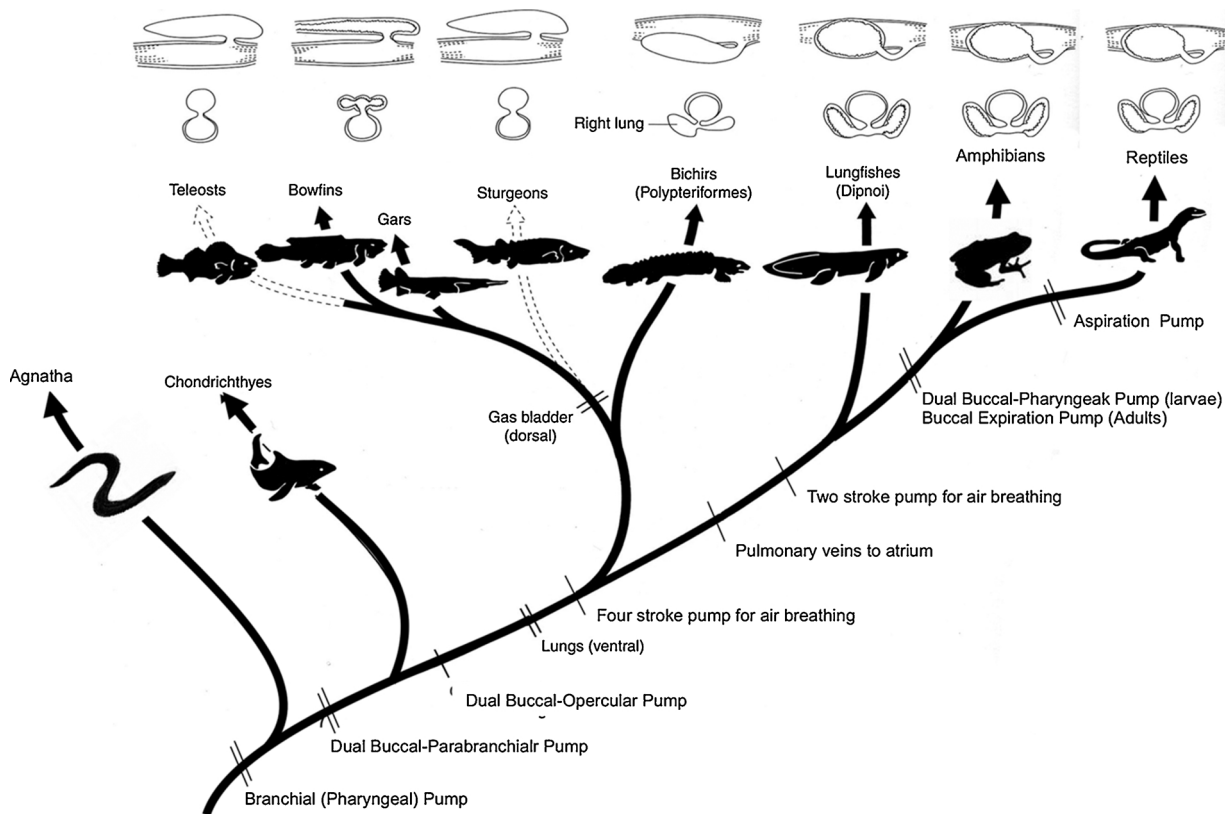
### 2. Sites of aerial gas exchange

Graham (1997) put forward a simplified classification scheme for structures utilized by fish for aerial gas exchange. This scheme divides structures into three groups, 1) those associated with the skin, 2) structures associated with organs in the head region or along the digestive tract, and 3) lungs and respiratory gas bladders (air breathing organs or ABOs). Gas bladders appear to have evolved early; after the origin of the cartilaginous fish but before the evolution of the bony fishes (Actinopterygii) and lung fishes (Sarcopterygii) (Brainerd and Ferry-Graham, 2005) (Fig. 1). It is still not clear whether the original function was for gas exchange or for buoyancy control but these functions are not mutually exclusive and either one could easily have given rise to the other (Graham, 1997; Liem, 1988). While several different sets of criteria have been used to classify ABOs as lungs or gas bladders, the scheme put forward by Graham (1997) is the most thorough and explicit. By this scheme, gas bladders have an embryonic origin from the side or dorsal aspect of the alimentary canal, are not paired, do not

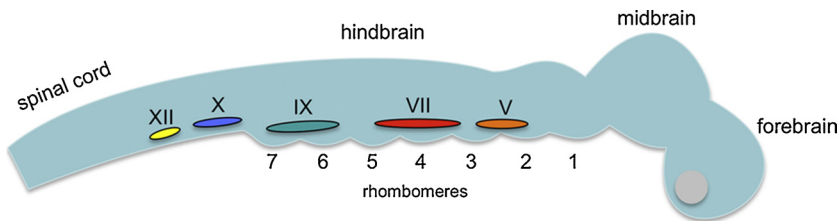
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**Fig. 1.** Evolution of lungs and gas bladders. The schematics above the dendrogram are sagittal and cross sectional views of the air breathing organs and their connections to the digestive tract. Dashed arrows indicate lineages where the respiratory function of the gas bladder has been lost. Diagram modified from [Kardong \(2006\)](#). Details taken from [Brainerd and Ferry-Graham, 2005](#).



**Fig. 2.** Schematic sagittal section through the developing vertebrate brain showing the location of the motoneuron pools of cranial nerves associated with respiratory movements in fish (indicated by Roman numerals) within the developing rhombomeres (indicated by Arabic numbers). Adapted from [Butler and Hodós, 1996](#).

always have a glottis and in most cases receive blood in parallel with the systemic circulation and lack a specialized pulmonary circulation. Lungs, on the other hand, have an embryonic origin from the ventral wall of the alimentary canal, are paired, possess a valvular glottis in the floor of the alimentary canal and have a proper pulmonary circulation in which efferent vessels return blood directly to the heart (not the vena cava). By this scheme, lungs are possessed only by the lungfishes (*Neoceratodus*, *Lepidosiren* and *Protopterus*) and the polypterids (*Polypterus* and *Erpetoichthys*) (see review by [Icardo in this series](#)) (Fig. 1).

Of note for our discussion, virtually all respiratory exchange surfaces in fish from gills to respiratory gas bladders and lungs are ventilated by modifications of the same basic mechanism. The primary differences that are seen are in the coordination of the various ‘valves’ that determine the flow of the respiratory medium be it water or air. The section that follows will use an evolutionary context to shed light on the possible basis of the central neural control of the muscles and valves that lead to an air breath versus a water breath in fishes using air breathing organs and lungs.

### 3. Central respiratory rhythm generation

#### 3.1. Developmental basis of central respiratory rhythm generators (CRG)

During development, in the rostral part of the neural tube, which will eventually become the brain, a series of rostro-caudal bulges, called neuromeres, develop. Each neuromere expresses a unique set of regulatory genes and has an independent developmental fate ([Wilkinson and Krumlauf, 1990](#)). In the hindbrain, the neuromeres are called rhombomeres of which there are at least seven, the exact number depending on species ([Butler and Hodós, 1996](#)). Differentiation and spatial distribution of both branchio-motor neurons as well as rhythm generating nuclei conform to this rhombomeric pattern initially (Figs. 2 and 3).

By the end of the segmentation period in birds and mammals the fifth (V, trigeminal), seventh (VII, facial), and ninth (IX, glossopharyngeal) cranial nerves begin to exhibit respiratory activity simultaneously ([Fortin et al., 1994](#)). At this stage, the neuronal network is already organized with distinct reticular and motor neurons that are intersegmentally coordinated through multisynaptic reticular processes ([Champagnat and Fortin, 1997](#); [Fortin et al., 1995](#)) (Fig. 3). Hence, the trigeminal, facial and glossopharyngeal motor nerves fire in synchrony.

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