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Lungs and gas bladders: Morphological insights

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ABSTRACT

This paper summarizes the main morphological tracts exhibited by lungs and gas bladders in fishes. The origin and organ location, the presence of a glottal region, the inner architecture, the characteristics of the exchange barrier and the presence of pulmonary arteries have been reviewed in the two types of air-breathing organs. With the exception of the dorsal (bladders) or ventral (lungs) origin from the posterior pharynx, none of the morphological traits analyzed can be considered specific for either lungs or gas bladders. This is exemplified by analysis of the morphology of the lung of the Dipnoi and Polypteriformes and of the bladder of the Lepisosteiformes. All of them are obligate air-breathers and show a lung-like (pulmonoid) air-breathing organ. However, while the lungfish lung and the bladder of the Lepisosteiformes occupy a dorsal position and are highly trabeculated, the polypterid lung occupies a ventral position and shows a smooth inner surface. Structural and ultrastructural differences are also highlighted. Noticeably, a large part of the inner surface area of the lung of the Australian lungfish is covered by a ciliated epithelium. A restricted respiratory surface area may help to explain the incapability of this species to aestivate. The respiratory bladder of basal teleosts displays a more complex morphology than that observed in more primitive species. The bladder of basal teleosts may appear divided into respiratory and non-respiratory portions, exhibit intricate shapes, invade adjacent structures and gain additional functions. The increase in morphological and functional complexity appears to prelude the loss of the respiratory functions.

1. Introduction

Air breathing in fishes is often taken as an evolutionary curiosity that comes as a surprise to many non-specialized researchers and amazes to the general public. However, the capacity of air-breathing constitutes a major milestone in vertebrate evolution: it enabled land colonization and the appearance of the tetrapods. Noticeably, fish air breathing cannot be considered a mere step in mammal evolution. Extant species have adopted air breathing to such an extent that many of them suffer or even die when forced to make extended submersions. Other species, such as lungfishes, become exclusive air breathers for long periods of time (e.g., [Graham, 1997](#); [Graham et al., 2011](#)).

The entire list of fishes known to (or suspected to) breath air has been provided in an early work ([Graham, 1997](#)). The original list appears to be incomplete but it includes up to 374 species of bony fish grouped into 49 families, with one or several members of each family showing this characteristic. Air-breathing species are distributed over a wide range of ecological niches, show variable dependence on aerial oxygen and may be able to travel over land in search of new habitats or food ([Liem, 1989](#); [Sayer and Davenport, 1991](#); [Graham, 1997](#)). This behavioral diversity is also reflected in the characteristics of the air

breathing organs (ABO). Primitive species rely on saccular organs such as lungs or respiratory gas bladders for air breathing. By contrast, modern teleosts have developed respiratory organs in the head (buccal, pharyngeal, opercular) and along the digestive tract (esophagus, stomach, intestine) ([Munshi, 1985](#); [Silva et al., 1997](#); [Satora and Winnicki, 2000](#); [Podkowa and Goniakowska-Witalinska, 2002](#)). The gills and gill derivatives, and the skin, also serve as ABOs in many species ([Munshi, 1985](#); [Graham, 1997](#); [Graham et al., 2011](#); [Maina, 2002a](#); [Hsia et al., 2013](#)). This work is focused on the structure of lungs and respiratory bladders. It aims to review basic morphological patterns and to highlight similarities and dissimilarities between lungs and gas bladders. The evolutionary aspects of these structures and the study of ABOs in more derived species are presented elsewhere in this issue. Neural and humoral control of ABO activity is also treated separately.

2. Lungs vs. respiratory gas bladders

Exposure to atmospheric air and development of an exchange barrier are basic requirements for air breathing. Adequate organ vascularization and adaptive modifications of the circulatory system are necessary to convey the extracted oxygen to the tissues and organs.

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Lungs and respiratory bladders, and, indeed, all other ABOs, fulfill these conditions.

Several morphologic features have been used to categorize ABOs and to distinguish lungs from respiratory bladders (Graham, 1997; Graham et al., 2011). For instance, lungs and respiratory bladders, as well as the non-respiratory bladders of chondrosteans, appear to originate from a respiratory, posterior pharynx (Perry et al., 2001; Hsia et al., 2013). However, lungs are paired organs that originate as ventral evaginations from the posterior pharynx. Consequently, only the Dipnoi (lungfishes) and the Polypteriformes possess true lungs. Although Australian lungfishes have a single lung, they show a paired lung anlage during the early developmental stages, the left lung being secondarily reduced (e.g., Lambertz and Perry, 2016). Noticeably, the coelacanth *Latimeria chalumnae* has a coelomic organ connected to the ventral pharynx. Although this organ is filled with fat, it is currently being considered a lung that shows two lobes of very different size (e.g., Hsia et al., 2013; Lambertz and Perry, 2016). Lung asymmetry is also observed in other species. In the Polypteriformes, the right lobe of the lung extends along the entire length of the coelomic cavity whereas the left lobe stops at the level of the stomach (Lechleuthner et al., 1989; Graham, 1997). It was early hypothesized that the expansion of the left side of the paired lung interfered with gut development (Marcus, 1929). However, there may be a tendency to reduce the lung surface area in basal vertebrates since the left lung of many lizards and snakes is also missing (e.g. Goniakowska-Witalinska, 1995). This simplification has alternatively been related to the adaptation of the lung to elongated body shapes, to the improvement of the hydrostatic functions and to the improvement of the ventilation by eliminating the surface tension problems associated with small organ size (e.g., Lechleuthner et al., 1989; Lambertz et al., 2015). On the other hand, gas bladders, whether they have a respiratory function or not, are unpaired organs that originate as dorsal evaginations of the posterior pharynx. It follows that the lungs occupy a ventral position in the coelomic cavity whereas the bladders are located dorsally. While the ventral origin from the pharynx and the paired structure appear to be exclusive of lungs, organ position may vary. For instance, the lung of lungfishes is placed dorsally, just under the vertebral column. In addition, the lung of the Polypteriformes undergoes a progressive displacement around the digestive tract in such a way that its caudal portion comes to occupy a dorsal position (Graham, 1997). Lung dorsal displacement has classically been related to an improvement of the hydrostatic functions (Goodrich, 1949).

The presence of a glottal region, giving direct access to the respiratory organ, is another feature typical of lungs. By contrast, gas bladders are connected to the pharynx through a pneumatic duct. However, there are many exceptions to this rule. The lung of lungfishes opens into the ventral pharynx through a small glottal orifice. However, there is a pneumatic duct interposed between the pharyngeal opening and the dorsally located lung (e.g., Graham, 1997). The pharyngeal opening of the Polypteriform lung is a mere slit-like orifice that shows thickened borders due to the presence of striated muscle (Icardo et al., 2017). The respiratory gas bladder of *Lepisosteus oculatus* also communicates to the pharynx by a slit-like opening. Noticeably, this orifice is delimited by two glottal ridges that contain large amounts of collagen and striated muscle (Icardo et al., 2015). In addition, a pneumatic duct is absent. A pneumatic duct is also absent in the osteoglossiformes *Arapaima* and *Heterotis*, the pharyngeal opening being reduced to a longitudinal slit with sphincter muscles (Greenwood and Liem, 1984). Thus, this situation appears to be very similar to that of the polypterid lung. A pneumatic duct, however, is present in other osteoglossiformes such as *Pantodon*, *Gymnarchus*, *Notopterus*, *Papyrocranus* and *Xenomystus*, as well as in other basal teleosts pertaining to the *Megalopidae*, *Phractolaemidae*, *Erythrinidae*, *Lebiasinidae*, *Pangasiidae*, *Gymnotidae* and *Umbridae* families, for which a respiratory bladder has been assessed (Graham, 1997; Graham et al., 2011 and references herein). Curiously, several of these ducts open into the caudal end of the esophagus (see Liem, 1989). Histological descriptions of the pneumatic duct are scarce.

The duct wall contains layers of smooth muscle in lungfishes (Hughes et al., 1976) and shows muscular walls and the presence of a sphincter in the basal *Gymnotus* (Liem et al., 1984).

Another distinct characteristic of the lung is the presence of a complex, compartmentalized architecture: the inner lung wall is subdivided by numerous septa into respiratory spaces termed air cells (Maina, 2002a,b), alveoli (Graham, 1997) or ediculae (Perry, 1998). This increases the respiratory surface and facilitates gas exchange. As stated above, true lungs are only present in Dipnoi and in the Polypteriformes. However, while the lungfish lung shows numerous septa and inner divisions, the inner surface of the polypterid lung is essentially smooth (see below). By contrast, the respiratory bladder of holosteans is highly trabeculated (see below). Nonetheless, small differences in complexity have been reported between bowfins and gars (e.g., Graham, 1997).

The morphology of the respiratory bladder in basal teleosts is very variable. Among the Osteoglossiformes, *Arapaima* and *Heterotis* have large gas bladders with intricate inner structures and large respiratory areas (da Cruz-Hofling et al., 1981; Liem, 1989; Graham, 1997) that resemble the gas bladder of the bowfin *Amia calva* (Liem, 1989). Thus, they resemble trabeculated lungs. On the contrary, the siluriform *Pangasius* and the esociform *Umbrina* exhibit bladders with little trabeculation. The situation of the gas bladder in other basal teleosts is more complex since the wall of the bladder may extend into other areas to gain functional capabilities. For instance, it may extend into the vertebrae to maximize buoyancy (*Pantodon*), or project toward the ear to improve hearing (*Notopterus*). This is often accompanied by bladder division into respiratory and non-respiratory chambers. Additionally, in the elopiform *Megalops*, the respiratory surface is reduced to four longitudinal bands in a pattern that has been interpreted as being an intermediate evolutionary stage between the lung-like (pulmonoid) bladder and the swim bladder of teleosts. A detailed account of all these different morphologies has been provided in early works (Liem, 1988, 1989; Graham, 1997; Graham et al., 2011, and references herein).

The extent of the respiratory surface is important for oxygen uptake as the air moves across the ABO. However, the characteristics of the exchange barrier are even more important. The exchange barrier is formed by the respiratory epithelium, the subjacent capillary endothelium and the interposed extracellular space. This structural arrangement appears to be universal since it has been demonstrated in both aquatic and terrestrial vertebrates, and in non-vertebrates as well (e.g., Bloom and Fawcett, 1994; Goniakowska-Witalinska, 1995; Maina, 2002a, b; Orgeig et al., 2007; Hsia et al., 2013). Of note, only a few invertebrates have closed circulatory systems to distribute the respiratory gases in an efficient manner (e.g., Hsia et al., 2013). In fishes, the characteristics of each of the three components of the exchange barrier may vary widely (e.g., Maina, 2002b). For instance, the respiratory cells may show a very attenuated cytoplasm, or the cytoplasm may be thick and contain numerous pinocytotic vesicles. A single pneumocyte type occurs in lungfishes (Hughes and Weibel, 1978; Maina, 2002a) but two types of pneumocyte are present in the polypterid lung (Lechleuthner et al., 1989; Icardo et al., 2017). The respiratory bladder of gars (Icardo et al., 2015), and that of the siluriform *Pangasius* (Podkowa and Goniakowska-Witalinska, 1998), exhibits a single type of pneumocyte. This also occurs in the stomach (Satora and Winnicki, 2000) and intestine (Podkowa and Goniakowska-Witalinska, 2002) of other siluriformes. However, catfishes constitute a very diverse group and two pneumocyte types have been described in the respiratory stomach of another species pertaining to the *Loricariidae* family (da Cruz et al., 2009). Between the respiratory epithelium and the capillary endothelium, the interstitial space may be very thin, being formed by fusion of the epithelial and endothelial basement membranes, or it may be much thicker containing, in addition to the basement membrane material, collagen, other extracellular fibrils and cytoplasmic extensions of interstitial cells (Maina and Maloij, 1985; da Cruz et al., 2009; Fernandes et al., 2012; Icardo et al., 2015, 2017).

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