Dipnoi group - extreme adaptation to drought and muddy water

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Abstract. Subclass Dipnoi includes 6 extant species in three genera, in Australia, Africa and South America. These species are especially interesting because of their characteristic anatomy and morphology, large body size, disjunct distribution along the tropical regions, and peculiar living habits. Many various fish species have independently developed the ability to use the atmospheric oxygen through a variety of specific adaptations. The most common adaptations involve the physostomous gas bladder, which is most developed in the Dipnoi group. The lung in Dipnoi does not have a muscular diaphragm to facilitate the circulation of air. There is sacculation inside the lung which increase the surface of contact for diffusion. Recent studies show that Dipnoi fish are evolutionarily related to *Latimeria* spp., a living fossil group called coelacanths , which they resemble from many points of view.
Key Words: neoformation, lungs, air breathing, respiratory system.

Subclass Dipnoi (Phylum Chordata), known also as the lungfish group, consists of a number of six species of extant air-breathing fish and several extinct relatives belonging to the Class Sarcopterygii and characterized by the fact they hold either one or two lungs. The group is taxonomically split in three genera, more exactly: the Australian lungfish (genus *Neoceratodus*), the African lungfish (genus *Protopterus*), and the South American lungfish (genus *Lepidosiren*) (Longrich 2017).

We have three families within this subclass: Neoceratodontidae (with one species, *Neoceratodus forsteri* (Krefft, 1870)), Lepidosirenidae (with one representative, *Lepidosiren paradoxa* Fitzinger, 1837), and Protopteridae (with four species, *Protopterus annectens* (Owen, 1839), *Protopterus aethiopicus* Heckel, 1851, *Protopterus amphibius* (Peters, 1844) and *Protopterus dolloi* Boulenger, 1900).

The Dipnoi branch first appeared in the Early Devonian Epoch (419.2 million to 393.3 million years ago), and the extant species (Figure 1) occur in rivers and lakes from South America, Africa, and Australia (Frederickson & Cifelli 2017; Bhat & Ray 2018; Harrell & Ehret 2019). These fish are especially interesting because of their characteristic anatomy and morphology, large body size, disjunct distribution along the tropical regions, and peculiar living habits (Romano et al 2019; web.utk.edu).

Environment played a special role in the evolution of this animal group. The low oxygen level of some muddy aquatic habitats has created conditions for high selection pressure for air breathing in fish species (Agnolín et al 2017). In all cases of air breathing we know, the solution found by nature is bringing oxygen rich air in contact with a highly vascularized organ (transformed organ, or organ of neoformation) having a large surface of contact so that diffusion can occur (Bud et al 2004; Petrescu & Mag 2006; Petrescu-Mag & Rasiga 2009; Fernandes 2016; web.utk.edu).

Many various fish species have independently developed the ability to use the atmospheric oxygen through a variety of specific adaptations, such as: modified skin (in eels, *Anguilla anguilla* (Linnaeus, 1758), or weatherfish, *Misgurnus fossilis* (Linnaeus,

1758) (see details in Ishimatsu 2017)), the gills (in the case of knifefish, e.g. *Brachyhypopomus occidentalis* (Regan, 1914)), head cavities called pseudolungs (in the case of labyrinthine fishes, for instance gourami fish species, e.g. *Trichopodus trichopterus* (Pallas, 1770), or the Siamese fighting fish, *Betta splendens* Regan, 1910 (see details in Pop & Mag-Mureșan 2004a,b)), the intestine (e.g. guntea loach, *Lepidocephalichthys guntea* (Hamilton, 1822), see research in Roy et al (2018) and gas bladder (in bichirs, *Polypterus bichir* Lacepède, 1803) (Icardo et al 2017). The most common adaptations involve the physostomous gas bladder. The most developed gas bladder-lung is found in the Dipnoi group.

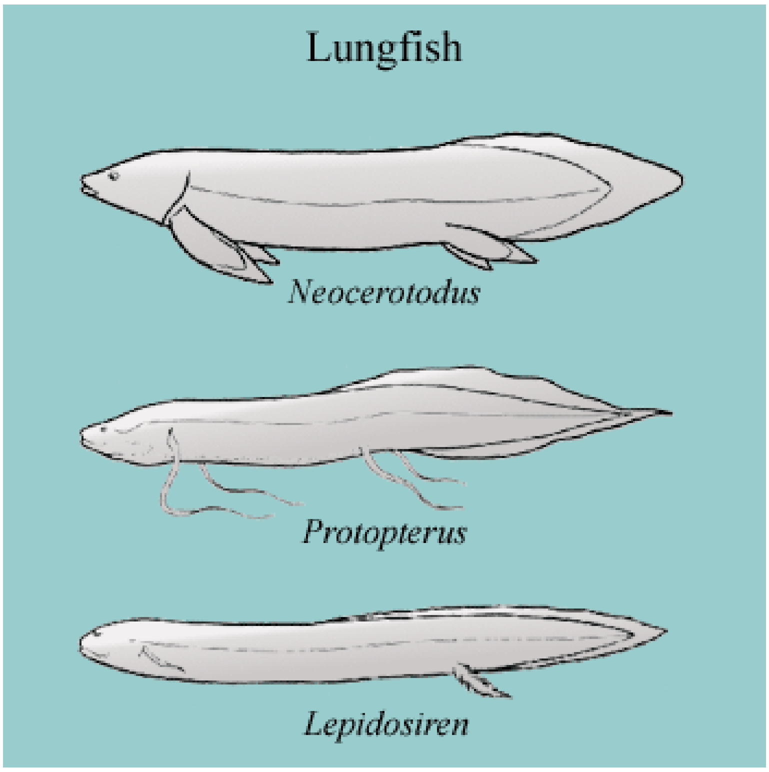

Figure 1. The three extant genera of the group Dipnoi.
Source: http://web.utk.edu/~rstrange/wfs550/html-con-pages/p-lungfish.html.

Gas bladders have been adapted for oxygen uptake in fish like bichirs, longnose gar (Lepisosteus osseus (Linnaeus, 1758)) and bowfin (*Amia calva* Linnaeus, 1766) (gars and bowfins are holostean species), primitive bonytongues (e.g. African bonytongue, Heterotis niloticus (Cuvier, 1829)) (osteoglossoid species, Paugy (1990)), and mudminnows (*Umbra* spp.) (web.utk.edu).

The lung in Dipnoi does not have a muscular diaphragm to facilitate the circulation of air. There is sacculation inside the lung which increase the surface of contact for diffusion. However, this sacculation does not reach the level of development of mammalian alveoli, which is the most specialized structure for respiration in terrestrial environment (web.utk.edu).

The South American and African Dipnoi species have developed the ability of air breathing as a way of surviving seasonal dry spells and are able to remain alive, hidden in the mud, large part of the year. During this estival season, they inhale air through vents into their cocoons (Figure 2). In the rainy season when they become free living again, they continue to rely on lungs rather than gills as a primary means of respiration (web.utk.edu).

Recent studies show that Dipnoi fish are evolutionarily related to *Latimeria* spp., a living fossil group called coelacanths (Petrescu-Mag et al 2007) (Figure 3), which they resemble from many points of view (Lambertz 2017; Biscotti et al 2018).

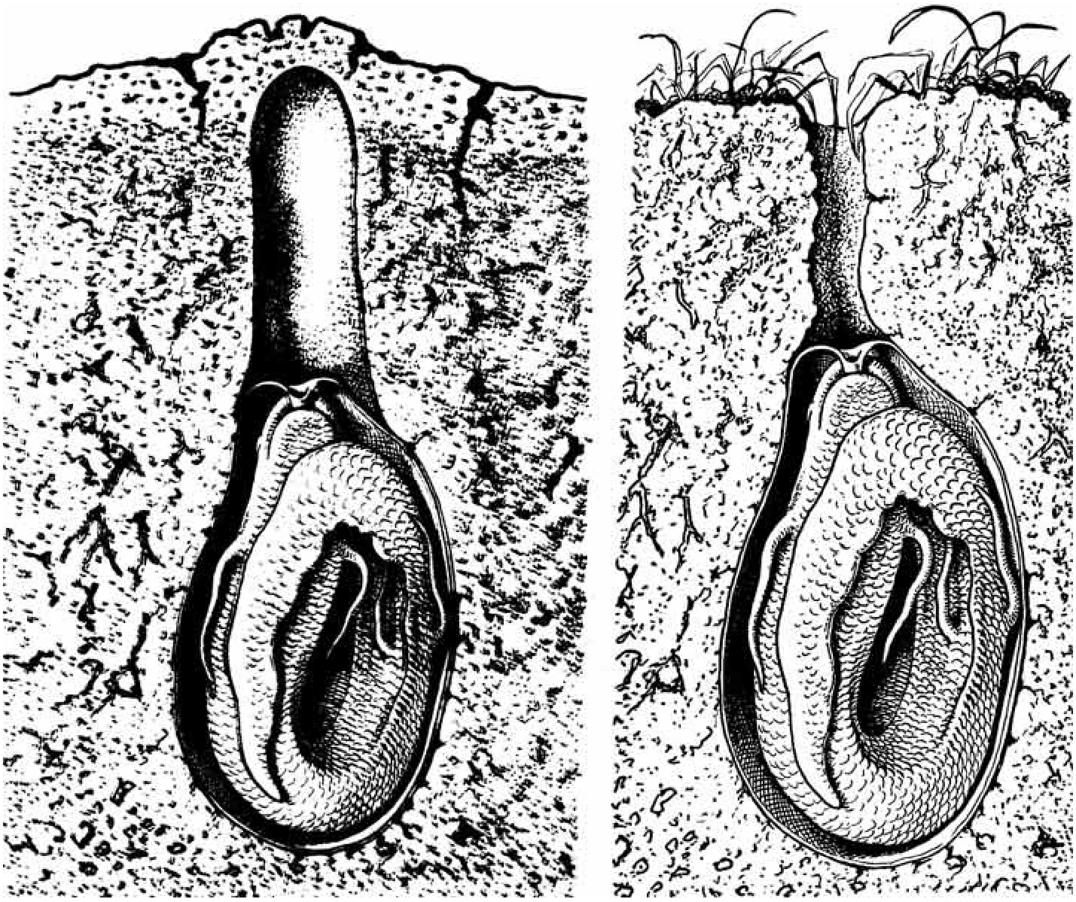

Figure 2. Lungfish in cocoons, during the estivation. Source: https://toinhoffilho.blogspot.com/2013/09/ciencias-vale-pena-saber-truques-para.html.

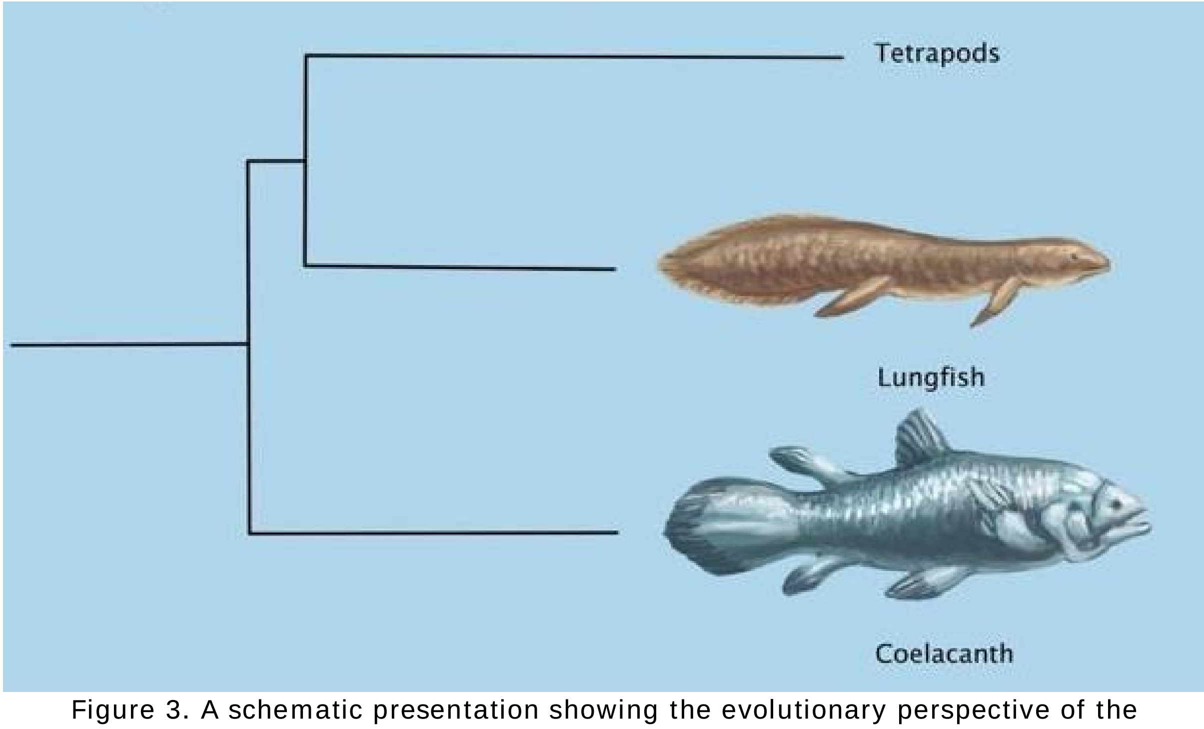

Figure 3. A schematic presentation showing the evolutionary perspective of the coelacant's relationship with Dipnoi fish. Source: https://www.newegg.com/artwork-reproduction-frameless-prints/p/2NM-0084-2D579.

Conclusions. Nature has endowed animals with the ability to generate and modify tissues and organs, developing various respiratory systems within the Pisces group. Of these, the oddity among vertebrates is represented by the Dipnoi group. The lung in Dipnoi does not have a muscular diaphragm to facilitate the circulation of air. There is sacculation inside the lung which increase the surface of contact for diffusion. The South American and African Dipnoi species have developed the ability of air breathing as a way of surviving seasonal dry spells and are able to remain alive, hidden in the mud, large part of the year. During the estival period, they inhale air through vents into their cocoons. In the rainy season when they become free living again, they continue to rely on lungs rather than gills as a primary means of respiration.

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Received: 02 September 2019. Accepted: 20 November 2019. Published online: 30 December 2019.
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How to cite this article:
Oroian I. G., Balint C., Oroian C. F., Gavriloaie C., 2019 Dipnoi group - extreme adaptation to drought and muddy water. ELBA Bioflux 11(1):27-31.