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Why are pulmonates the most successful land snails?

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Abstract

The intriguing question of why more than 80% of the land snails are pulmonates (Eupulmonata) has a possible explanation in the circumscription of the lung. The pulmonate lung, different from the lung of the other gastropod branches that also adapted to the terrestrial environment, is circumscribed. The single communication with the environment is a small orifice called pneumostome. The anterior lung closure is promoted by an anatomical fusion of the mantle edge with the nuchal region of the head. The pneumostome has muscular capacity of closure during the respiratory cycle. The circumscription itself, and the pneumostome closure, increase the internal pressure and, consequently, the O2 absorption, being an advantage in relation to non-pulmonate groups.

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Introduction

There are more than 24.000 known species of land snails worldwide (Rosenberg et al, 2022), from them, more than 80% are pulmonates or, more recently renamed, eupulmonates (discussed in a future Malacopedia issue) (Bouchet & Rocroi, 2005). Thus, the question arises: Why just they are so well-successful in relation to other gastropod branches that also conquered the land environment?

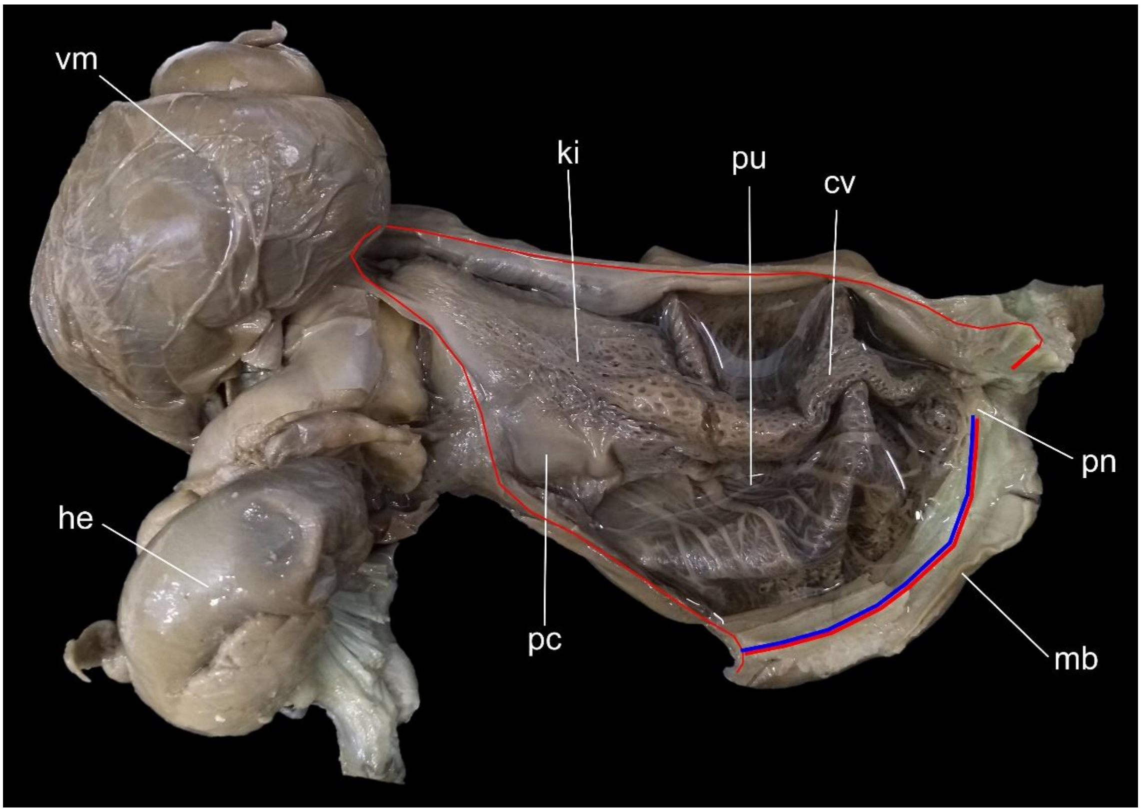
As well known, and this will be also subject of a future Malacopedia issue, several gastropod branches became air breathing organisms, getting rid from the aquatic environment (see below). Interestingly, no other mollusk classes achieved the land environment. The enigma of why the vast majority of them are pulmonates is intriguing, the answer is complex and, by the way, still not totally solved.

Certainly, the steps in direction of the understanding of the pulmonate prevalence must pass through comparative anatomy and physiology, among them and representatives of the other air-breathing gastropod branches.

Adaptations to the terrestrial environment depend on modifications of several structures that, as reported above, will be explained in a future Malacopedia issue. But, in short, the snail must modify its integument to avoid loss of water, increase the kidney to save water and electrolytes, reinforce the cardio-vascular system to support shell weight and visceral mass in a hydrostatic skeleton, modify the spawn to support the air exposure, change the respiratory structure from a gill to a lung, etc. All of them have clear anatomical implications easily verifiable.

The main anatomical difference between pulmonates and remaining air-breathing snails

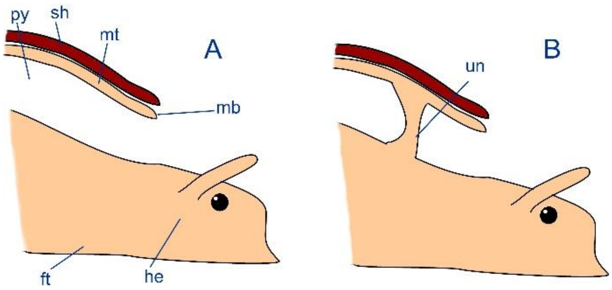
All land snails look relatively similar in the studied representatives of all air-breathing gastropod branches. The single exception is that pulmonates have their lung circumscribed (Fig. 1), separated from the environment in a proper chamber, while the lung of the other air-breathing gastropods is widely anteriorly opened.



1. *Megalobulimus oblongus* MZSP 136679. Dissected specimen (W ~120 mm), pallial cavity removed from head-foot and deflected to right, showing circumscription of pallial cavity. Red line showing sections in mantle, blue line section in nuchal region of head's nuchal region. Lettering: cv, pulmonary vein; he, head-foot; ki, kidney; mb, mantle border; pc, pericardium; pn, pneumostome; pu, lung, vm, visceral mass.

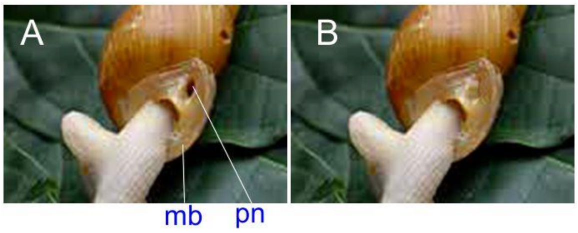
The photo above (Fig. 1) is of an ordinary pulmonate. The specimen was extracted from its shell and the pallial cavity was entirely removed from its anatomical position – dorsal to head-foot – and deflected to right. The red lines show where the mantle needed to be sectioned. The pallial cavity is an almost entirely closed sac, only opened in a small aperture called pneumostome (pn).

This kind of dissection shows the integrate pallial roof as a whole, and can be done in any shelled gastropod cutting the mantle along its left and right margins, edging the floor of the pallial cavity; an additional posterior cut is necessary to separate it from the visceral mass. In all shelled gastropods, the pallial roof separation ends this way (Fig. 2A). In pulmonates, in particular, another cut is necessary – along the nuchal region – separating the mantle edge (mb) from pallial-nuchal floor (Fig 1: blue line; Fig. 2B: un).



2. Schematic representation of anterior region of a general shelled gastropod. Right view, superior region in sagittal section, inferior region (head-foot) integrate; **A**, non-pulmonate; **B**, pulmonate (eupulmonate), showing anatomical connection between nuchal surface and mantle edge (un) (not for proportions). Lettering: ft, foot sole; he, head; mb, mantle border; mt mantle; py, pallial cavity; sh, shell; un, anatomical connection between nuchal surface and mantle edge.

In the pulmonate evolution, the mantle dorsal region of the mantle edge, which is free in most shelled gastropods, being the pallial cavity's entrance, became anatomically attached to the pallial cavity floor, i.e., to head-foot nuchal region (Fig. 2B: un). It divides the former pallial cavity into two chambers: a larger, posterior one – the lung, and an anterior one, which can be called nuchal chamber (Fig. 2B: left and right from "un" respectively). The only lung connection with the environment, from which the air flows, as well as dejects and excrements, is a small orifice called pneumostome (pn).

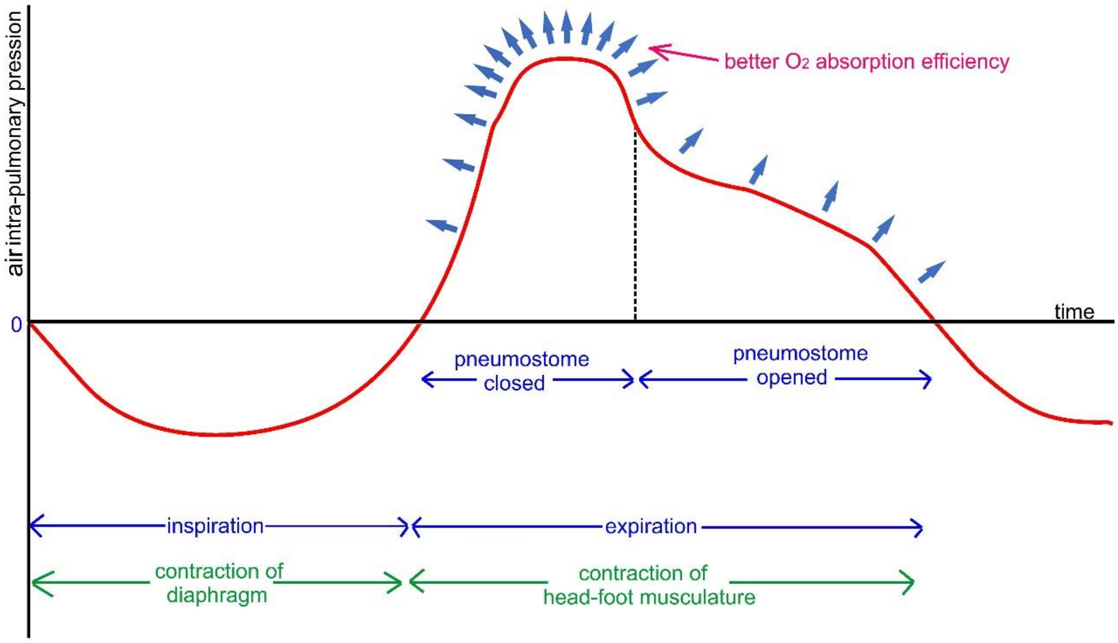


3. *Neobeliscus calcareus* MZSP. Living specimen, detail of shell aperture with specimen protruded outside and mantle edge inflated with pneumostome opened (**A**) in inspiration or expiration, and closed (**B**), in moments preceding expiration (shell width ~30 mm). Lettering: mb, mantle border; pn, pneumostome.

The pneumostome (Fig. 3: pn) has capacity of opening (Fig. 3A) and closing (Fig. 3B), by its surrounding musculature. The animals can do inspiration and expiration movements mostly promoted by the diaphragm and other body muscles, like columellar and foot ones. The diaphragm is a strong muscular layer that covers the dorsal wall of the head. It is substantially thick in the anterior, nuchal region, becoming gradually thinner posteriorly. It is composed mainly of a flat net of transverse and oblique fibers. As it is domed inside the lung, its contraction plans it, and promotes the air entrance, i.e., the inspiration. The expiration apparently is achieved by somatic muscles, like contractions of the columellar and head-foot muscles. In this alternating inspiration-expiration process, why does the pneumostome close between each respiratory cycle? Answer below.

Physiological advantage of the circumscription of the lung

Incarcerated in a sealed sac, as in the case of the pulmonates, the gas exchange looks much more efficient than in an opened chamber as in the case of other non-pulmonate land snails. This is because the pressure inside this sac can be better controlled. During the inspiration, the pressure is negative, promoting the entrance of air. This low pressure facilitates the CO_2 extraction from the blood to the lung. The contrary happens during the expiration phase, in which the pressure inside the lung is high, promoting the exteriorization of the air – the expiration. A higher pressure inside the lung facilitates the absorption of the O_2 from the air inside the lung to the blood, where the gas is carried by the hemocyanin or, in some rare cases, hemoglobin (e.g., planorbids). The pressure inside the lung becomes particularly higher if the pneumostome is closed (Fig. 4).



4. Graphic empirical representation of internal air pressure of lung during a respiratory cycle in a generic pulmonate gastropod. The text brings more detailed explanation, but the closure of the pneumostome promotes an extra increase in internal air pressure, increasing the efficiency of O_2 absorption through the lung epithelium.

The graphic of Fig. 4 is empirical, theoretical, based on observations and interpretations of several living animals. No precise physiological experiments were so far performed. It is possible to interpret in it the negative pressure during the inspiration and the positive one during the expiration. The expiration, however, has two phases, an initial phase with the pneumostome closed, in such the head-foot contraction, associated to the final diaphragm contraction, causes a high augment of the air inner pressure; and a second phase that the pneumostome opens, the pressure suddenly decreases, but still remains positive, in order to enable the final expiration. The concentration of blue arrows in the Fig. 4 is a symbol of the increase of absorption of O2 in the pneumostome closure phase.

The pneumostome closure in the respiratory cycle in pulmonate land snails, which is observed, but theoretically is not necessary, certainly has the physiological function of further increasing the pressure inside the lung. This facilitates the O2 absorption through the lung epithelium, to be captured by the blood pigments. This has a parallel in vertebrates, especially in well-known human physiology. The long non-respiratory tubes like trachea, pharynx, larynx, are barriers that the thorax musculature must overcome during expiration. This causes increase of the lung pressure, and improvement of the O2 absorption. This is particularly clear during heavy physical exercises, in which the person instinctively forces the air through a more closed mouth in the expiration. The single reason for that is further increasing the lung internal pressure. As pulmonates do not have so long tubes to overcome, the evolutionary solution was to close the pneumostome.

The other non-pulmonate land snails, which, as referred above, will be covered in another Malacopedia issue, the above-mentioned mechanism is not clear. This is because the mantle edge has not the anatomical connection with the nuchal surface of the head like that of the pulmonates (Figs. 1, 2B). This does not mean that they cannot develop similar ways to improve the O2 absorption, possibly by momentarily occluding the pallial cavity entrance by a conjunct muscular contraction of the head and of the mantle edge. Exclusive land snail branches are found in neritimorphs (Helicinidae and allies) (e.g., Simone, 2018) and in caenogastropods (Cyclophoroidea and some Rissooidea-Littorinoidea branches, e.g., Annullariidae, Pomatiidae) (e.g., Simone, 2004, 2006). Some land groups, like Siphonariidae and Systellommatophora, have their taxonomic and phylogenetic relationship still fluid (Simone & Seabra, 2017), and any inference is still premature.

Anyway, as the anatomical comparison with the shelled land snails of the pulmonates and non-pulmonates shows as main difference the above-mentioned lung feature, with a clear advantage to the pulmonates, it is a quite possible that this can be an explanation for the pulmonate predominance in that habitat.

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