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The diaphragmatic septum – a Caenogastropoda synapomorphy

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Abstract

The diaphragmatic septum is an important Caenogastropoda synapomorphy. It confines the blood inside the head-foot haemocoel and has physiological implications. It improves the pressure management inside the haemocoel. This has influenced further evolutionary pathways, three of them are explored in the paper: the gigantism, the proboscis, and the foot enlargement. All of them are more common or almost exclusive of the caenogastropods and appear to be related to the diaphragmatic septum.

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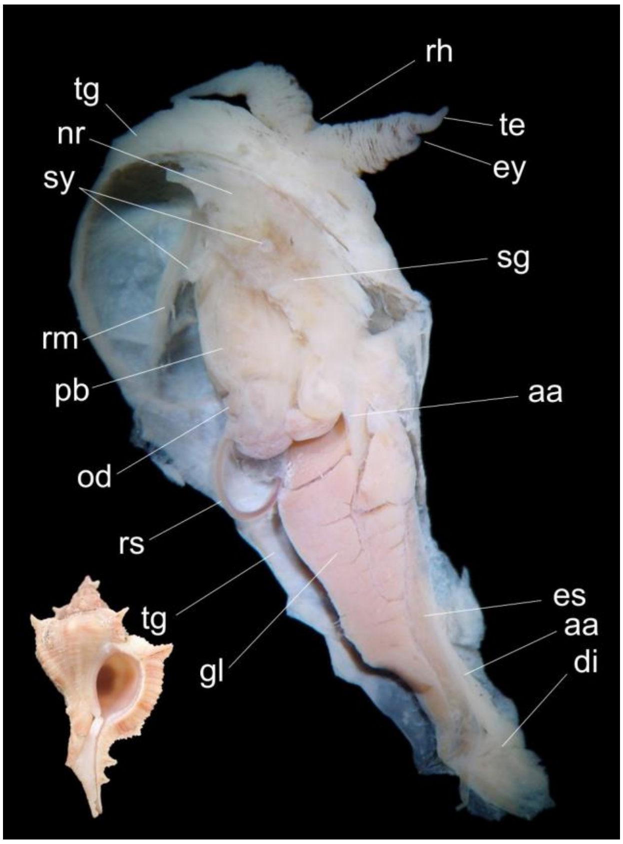
Keywords: morphology, anatomy, evolution, taxonomy, phylogeny.

Introduction

A phylogeny of the subclass Caenogastropoda was proposed by Simone (2011), it is based on 305 terminal taxa, from those, 32 were non-caenogastropod outgroups, the remaining are representatives of most caenogastropod branches. A total of 676 characters, divided into 2291 states, was surveyed, all mostly based on morphological features. In that paper, the taxon Caenogastropoda was supported by nothing less than 60 synapomorphies. An outstanding exclusive caenogastropod one is the diaphragmatic septum.

The diaphragmatic septum has never been reported before that paper, despite being an important morphological modification. Additionally, its consequences in the hydraulic skeleton of



1. *Siratus senegalensis* (Muricidae) (MZSP 33102), Shell (L 45 mm) and haemocoel (L ~30 mm), ventral view, foot and columellar muscle removed, inner structures as in situ. Lettering: aa, anterior aorta; di, diaphragmatic septum; es, esophagus; ey, eye; gl, gland of Leiblein; nr, nerve ring; od, odontophore; pb, proboscis; rh, rhynchostome; rm, proboscis retractor muscle; rs, radular sac; sg, salivary glands; sy, statocysts; te, tentacle; tg, integument

the head-foot raised several other evolutive significant novelties. The septum itself, and the consequent evolutions that have it as base, are explored in this issue.

The diaphragmatic septum (Fig. 1: di) is a conjunction of conjunctive tissue separating physically the head-foot's haemocoel (henceforward designated only as 'haemocoel') from the posterior regions, like the visceral mass and pallial cavity. It is designed "septum" because it blocks the physical communication of the liquid, i.e., the blood, inside the haemocoel (literally 'cavity of blood') with the remaining body's regions. As referred above, only caenogastropods have this feature, and, as far as known, no one of its internal branches lost it.

The block of the diaphragmatic septum only allows the passage of the esophagus, the anterior aorta, the afferent renal vessel, and some nerves. Nothing else can pass through it, neither the blood inside the haemocoel.

This special configuration causes the confinement of the haemocoel's liquid, increasing the internal pressure when the muscles surrounding the haemocoel contract. This does not happen in non-caenogastropods snails, as the internal liquid flows towards posterior, running to visceral mass.

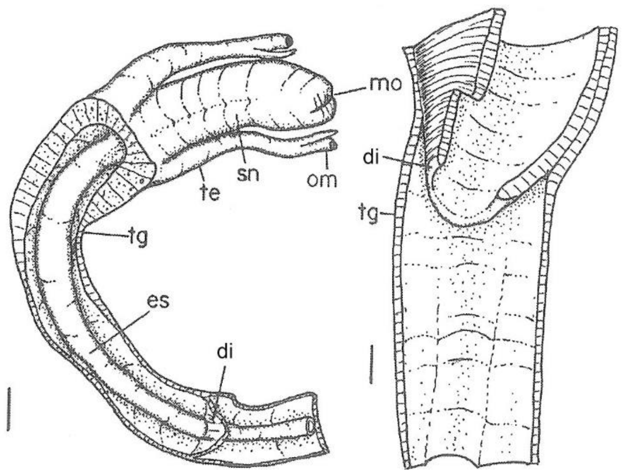
This caenogastropod apparently inconsequential somatic arrangement, if analyzed in detail, provides explanation for interesting character that are almost exclusive of caenogastropods, such as the proboscis, gigantism, etc. These subjects are explored in this issue.

Differently from the caenogastropods, the other gastropod taxa, such as the heterobranchs, the vetigastropods, the patellogastropods, the neritimorphs and the cocculiniforms, lacking the diaphragmatic septum, have not only the haemocoelic blood flowing posteriorly to visceral mass, but also have visceral structures invading the head-foot haemocoel. The four last groups, for example, usually have intestinal loops surrounding the esophagus; the former, the heterobranchs, have genital structures by side of the esophagus. These features are never found in caenogastropods.

Below some inferred consequent features connected to the previous appearance of the diaphragmatic septum are explained.

The giantism

A gigantic gastropod is a snail with a size over ~30 cm of shell. Despite the anatomical adaptations related to the gastropod giantism being subject of a future Malacopedia issue, an interesting feature can beforehand be inferred: the immense majority of them are caenogastropods. Famous giants, such as, e.g., *Eustrombus gigas, Eustrombus goliath, Adelomelon becki, Melo amphora, Syrinx aruanus, Triplofusus giganteus* and some giant fossil, such as *Campanile giganteum*, which reached almost one meter, are all caenogastropods.



2. *Eustrombus goliath*. Left: head and haemocoel, ventral view, foot and columellar muscle removed, scale- 10 mm; Right: same, detail of region of diaphragmatic septum, esophagus and other structures removed, septum sectioned longitudinally, scale= 2 mm. Extracted from Simone, 2005. Lettering: es, esophagus; di, diaphragmatic septum; mo, mouth; om, ommatophore; sd, salivary duct; sg, salivary glands; sl, sublingual organ; sn, snout; te, tentacle; tg, integument.

The possible explanation is that a haemocoel with a confined internal fluid triggers a more rigid and strong head-foot, able to sustain an enlarged body and shell. As the haemocoelic fluid cannot flow to visceral mass, blocked by the septum, it can reach larger a pressure degree. This higher pressure permits the functioning of a larger structure, sufficiently strong to sustain and to move the remaining increased structures.

The anatomical study of some giant snails has revealed a further reinforced diaphragmatic septum. That of the above mentioned *Eustrombus* species, for example, consists in some additional strong muscular layers (Fig. 2), which is not found in other smaller strombids. This is another indirect indicator that the septum plays a role in the size enlargement.

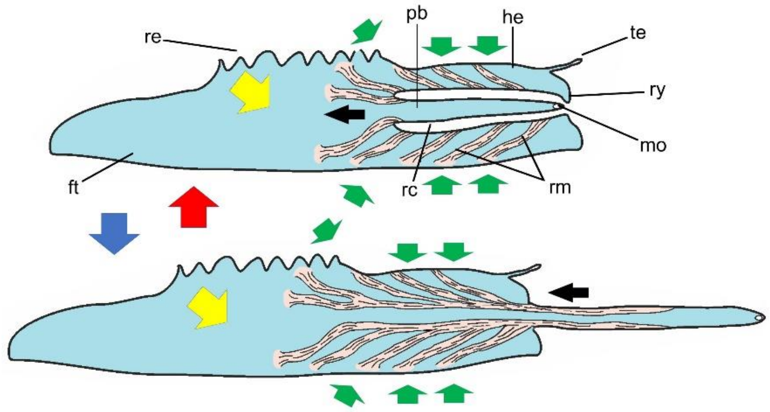
Outside of Caenogastropoda, giantism is rare. Only some aplysiids can be evoked, such as *Aplysia gigantea*, which can grow up to 60cm in length.

The proboscis

Most of the proboscis-bearing snails are caenogastropods. As already stated elsewhere (Simone, 2019, 2021), the proboscis appeared several times along the gastropod evolution, and most of these taxa are caenogastropod branches.

The confinement of the haemocoelic liquid caused by the diaphragmatic septum (Fig. 3: re), that is the base of any proboscis, improves a lot the proboscis functioning, as the liquid that inflates the proboscis does not compete with another flow going backwards. Thus, the diaphragmatic septum can be even interpreted as a pre-adaptation to a proboscis.

From the two types of proboscises (Simone, 2019), the pleurembolic one is an outstanding synapomorphy of the caenogastropod branch called, because of it, Rhynchogastropoda, as *rhynchos* is a Greek word meaning nose, snout, muzzle. In some branches of rhynchogastropods, the proboscis becomes enormous, even longer than the total animal's length. Some examples are tonnoideans of the families Ficidae, Tonnidae and Personiidae; most cancellarioideans; and some buccinoideans like colubrariids (Simone, 2011). Indeed, most of the caenogastropod branches after Hypsogastropoda have very large proboscises.



3. Schematic representation of a generic head-foot of a proboscis-bearing gastropod in sagittal section (modified from Simone, 2019). **above**, proboscis fully retracted; **below**, proboscis fully extended. **Blue arrow**: protraction; **red arrow**: retraction; forces to proboscis protraction: **green arrows**: forces of head-foot muscular walls, **yellow arrow**: cardiac pressure; **black arrow**: forces for proboscis retraction produced by proboscis retractor muscles. Lettering: **ft**, foot; **he**, head; **mo**, mouth; **pb**, proboscis; **rc**, rhynchodeal cavity; **re**, remaining animal portions (pallial cavity and visceral mass); **rm**, proboscis retractor muscles; **ry**, rhynchostome; **te**, cephalic tentacle. **Light blue color**: blood inside haemocoel. **Beige**: muscles.

For more details of the proboscis functioning, check Simone (2019), from which Fig. 3 was extracted. This Fig.3 represents a sagittal section in a proboscis-bearing generic gastropod. If the blood inside haemocoel (barely represented by light blue) cannot flow backwards (Fig. 3: re), because of the diaphragmatic septum, thus the liquid pressure inside haemocoel is higher with the contraction of the head-foot musculature (green arrows). In this case the proboscis can be exteriorized more easily. The proboscis retraction back inside haemocoel (black arrow) is only promoted by muscular contraction, mainly of the proboscis retractor muscles (Fig. 3: rm).

Few non-caenogastropod branches possess proboscises. It is virtually absent in archaeogastropod grade, and is only found in a few branches of the basal heterobranchs, such as, e.g., amathinids and pyramidellids.

Foot enlargement

Details of the foot evolution, functioning and phylogenetic implications of its modifications are a matter of a future Malacopedia issue. Related to the foot enlargement and its possible relation with the diaphragmatic septum, some initial information is possible to be explored herein.

The gastropod foot is an important locomotory structure, and it is obviously adapted to the substratum that the animal lives in. Snails that live in hard substrata, like rocks and coral, usually have small-sized feet. On the other hand, those aquatic forms that live in unconsolidated substrate, like sand and mud, usually possess large feet. It is intuitive to deduce that large feet are more effective to anchor the animal in an unconsolidated substrate, and it is further useful to move the animal through it, amplifying the friction area, and pushing the substrate away like a plow (Fig. 4).

The gastropod foot enlargement depends on a more efficient hydraulic skeleton, that helps in molding the foot form joined to muscular contraction. As reported in some points above, the diaphragmatic septum improves the management of the internal pressure inside the head-foot, as it confines the blood in a single hermetic compartment – the haemocoel.

Despite several exceptions exist, most of the non-caenogastropod aquatic snails live on hard substrates. Caenogastropods, on the other hand, are abundant in unconsolidated substrata. Particularly, the majority of the, e.g., ampullarioideans, viviparoideans, cerithioideans, stromboideans, naticoideans, tonnoideans and neogastropods (Simone, 2011), live in those.

4. *Polinices lacteus* (Naticidae from Brazil). **left**, fully retracted specimen inside its shell; **righ**, crawling specimen with foot mostly expanded (shell L~20 mm).

Another interesting phenomenon is that the shelled gastropods that have large feet are able to retract it completely inside their shell (Fig. 4). If compared, the extended foot is larger than the shell volume itself. Thus, how is it possible to retract it completely?

Despite no functional experiment has been done by me, the anatomical investigation has shown that gastropods that possess large foot also have a large afferent renal vessel. This vessel is one of the few structures that cross the diaphragmatic septum. The observation of the foot retraction also reveals that the larger is the foot, the longer and more complicated its retraction is. Thus, before reading books on molluscan physiology, it is already possible to deduce that the blood inside haemocoel must be conducted to the kidney through the afferent renal vessel for an effective foot retraction in aquatic forms. In an emergency, the foot must be retracted the quicker possible. If the blood inside it was connected directly to the environment, the foot retraction would be quicker, but the animal would lose precious electrolytes, nutrients, etc. The haemocoelic blood passing through the renal tissue before externalizing gives a chance for the animal saving them. Gastropods with large foot also have large and complex renal tissue.

Thus, this complex process looks much more efficient in an animal that has the haemocoelic liquid confined by the diaphragmatic septum.

Final comments

The diaphragmatic septum, firstly noticed by Simone (2011), beyond to be an interesting Caenogastropoda synapomorphy, has interesting physiological and evolutive implications. Of course, several ones could be evoked, only the more important were explored herein. As long as I checked, no physiological investigation has been produced so far to prove experimentally the conclusions explored in this paper. However, they are easily deduced analyzing the morphological arrangement and the phylogenetic position of the main gastropod branches. Additional experiments are, thus, suggested to be performed by specialists.

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Notice

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