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The mollusk shell coiling

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Abstract

The shell coiling is a phenomenon related to elongated shells, to make them easier to carry. It is notorious in Cyrtosoma. In gastropods 3 types of coiling were detected: 1) with visceral mass dorsal to columellar muscles, exclusive, in living snails, of Vetigastropoda; 2) with visceral mass between both columellar muscles, typical of the Neritimorpha; and 3) visceral mass at right from a single columellar muscle, found in all Apogastropoda (Caenogastropoda and Heterobranchia). In cephalopods, the shell is mostly found in fossil groups, and was originally straight, evolving both, to dorsal and ventral coiling, usually planispiral. Some rare shell coiling is also found in Bivalvia, in some fossil ostraoideans and rudists, and weakly coiled umbos of some living forms.

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Introduction

Shell spiraling or coiling is an important evolutionary phenomenon that happens in Mollusca evolution. It is almost exclusive to the Cyrtosoma (cephalopods and gastropods), although some rare bivalves can also have a somewhat spiralized shell as seen below.

The coiling is developed to facilitate the transport of an elongated shell. The animal may have some difficulty in carrying a long straight shell, which is much easier carried if coiled. An interesting analogous experience happened in wind musical instruments, such as cornet and tuba (Fig. 1). Although they may be some meters long, they are manufactured in a coiled architecture to facilitate carrying them. Interestingly, coiling an elongate structure like those tubular musical instruments, does not necessarily decrease its internal volume. Thus, coiling the structure practically does not decrease its internal

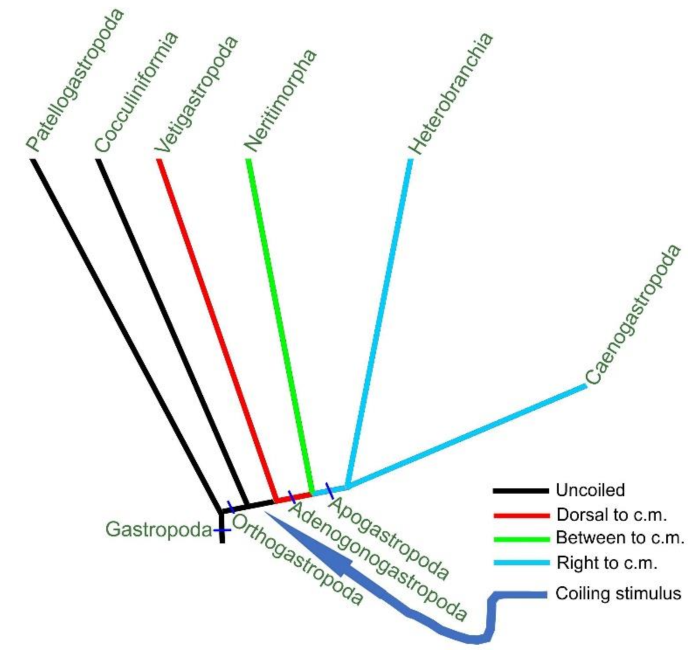
1. Wind musical instruments. Built in a coiled shape for easy carrying (extracted from internet) space. This is an important data to explain the reasons why the animals that possess elongated shells tend to coil them.

Analyzing the molluscan phylogeny presently known (e.g., Simone, 2011), and the occurrence of taxa having coiled shells, it is possible to realize that this feature happened several times along the phylum's evolution. In Monoplacophora, an almost certainly paraphyletic taxon, some coiled fossil forms exist, such as Helcionelloid (e.g., *Pseudoyangtzespira*), and Pelagielloidea (e.g., *Pelagiella, Aldanella*), and others (Parkhaev, 2008). As these early (mostly Cambrian-Ordovician) fossils have complicated taxonomical history, associated with the transition monoplacophoran-gastropod border, these taxa are not approached here.

More complete explanations will be, thus, performed in cyrtosoman classes – Gastropoda and Cephalopoda – as well something about the Bivalvia.

Coiled shell in Gastropoda

First of all, it is necessary to make a distinction between coiling and torsion. These are totally different phenomena that are commonly confused. The torsion, a gastropod synapomorphy, is the rotation of ~180° of the body axis, producing a pallial cavity and internal organs (e.g., anus, gills, etc.) located anteriorly (Simone, 2011, 2018a). While the coiling simply is the curling of the shell. The shell can be coiled without the torsion, e.g., the shell-bearing cephalopods; as well as the shell can be uncoiled in a body with torsion, e.g., patellogastropods.



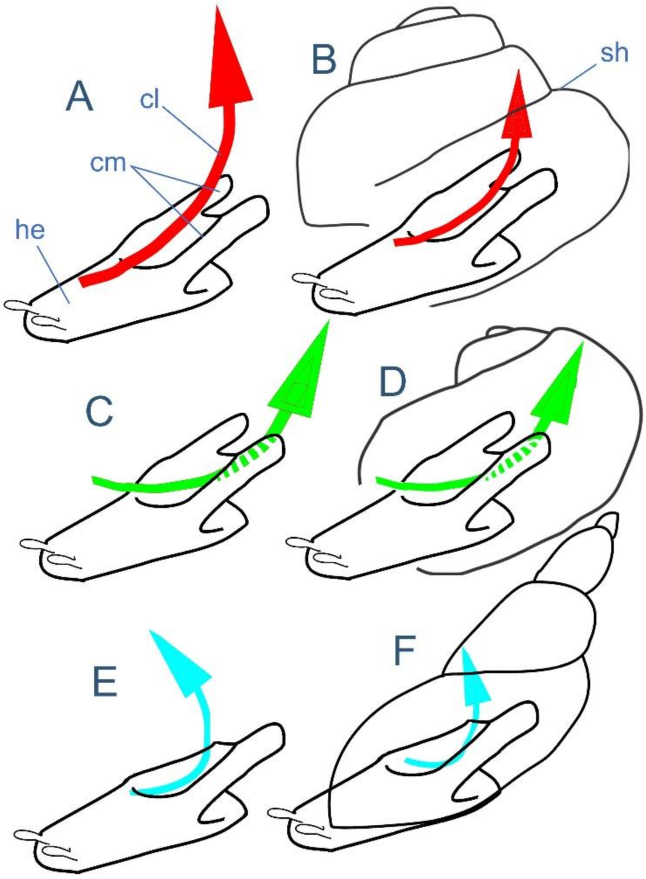
2. Types of coiling shells in Gastropoda. Phylogeny based on Simone (2011) presenting only the main branches, showing with colors the main kinds of shell coiling. The coiling stimulus is in the branch indicated by the large blue arrow.

Checking the phylogeny of the Gastropoda based on morphology (Simone, 2011), summarized in Fig. 2, it is possible to realize that the two first branches of the class are primarily uncoiled shells (Simone, 2018b) – the Patellogastropoda and the Cocculiniformia (black lines). The shell coiling stimulus is present in the following branch, marked by the large blue arrow. After this branch, all shells are coiled, or, if not, are modified from a coiled shell.

However, the coiling stimulus in that branch resulted in 3 different kinds of coiling (Figs. 3-4): 1) a model in such the visceral mass rests dorsal to the columellar muscles (c.m.) (red in Figs. 2-4); 2) a model in such the visceral mass lies between them (green); and 3) another model in such the visceral mass runs to the right of a single (left) columellar muscle (blue). Each of these models are explained below.

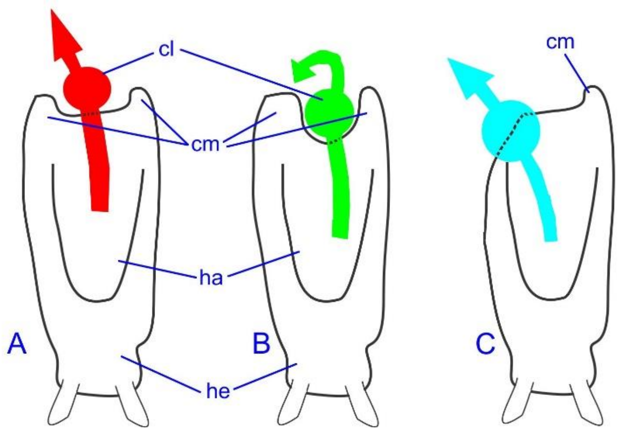
1) Coiling with visceral mass dorsal to columellar muscle

This style of coiling is in living taxa exclusive of the Vetigastropoda. It is easier to see in vetigastropods that has a slit preceding the shell aperture, such as pleurotomariids (Fig. 5), haliotids, scissurelids, anatomids and fissurellids (Fretter & Graham, 1962; Voltzow et al, 2004). The shell slit is an indication that the pallial structures are paired, and the water flow coming from both sides must be exteriorized in the middle. Particularly in pleurotomariids and fissurellids, structures of both sides of the pallial hoof are practically symmetric, while in the remaining families some asymmetry is present.



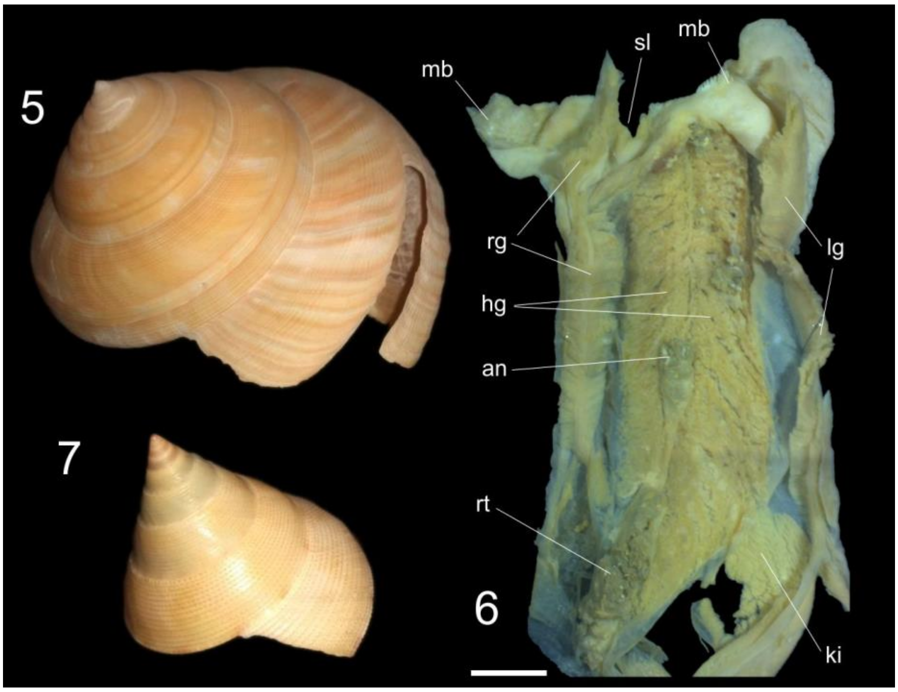
3. Schematic representation of the types of coiling shells in Gastropoda. Left column only head-foot represented, left-slightly dorsal view, with arrow showing the direction of pallial cavity and visceral mass. Right column the same, with average shell overlapped (more explanation in text). Lettering: cl, direction of pallial cavity and visceral mass; cm, columellar muscle(s); he, head-foot. (Not for proportions or scales)

As shown in Figs. 3A-B, 4A, this kind of coiling is highly dorsal, and conducted on a more symmetric manner, in which the plesiomorphic architecture of paired gills, osphradia, hypobranchial gland, auricles, etc., is maintained (Fig. 6). The columellar muscles are clearly paired. They are the floor of the haemocoel, and continue ventrally in the beginning of the visceral whorl. They lie to the right, attaching to the shell's columella, posteriorly to the end of the haemocoel. This is the reason for calling this type of coiling as "dorsal". The typical shell of the taxa that has this type of coiling is usually trochoid, heavy, with relatively small apertures and wide whorls.



4. Schematic representation of the types of coiling shells in Gastropoda. Head-foot in dorsal view. **A**, dorsal type; **B**, between columellar muscles model; **C**, right model (more explanation in text). Lettering: cl, direction of pallial cavity and visceral mass; cm, columellar muscle(s); he, head-foot; ha, haemocoel. (Not for proportions or scales)

The dorsal kind of coiling apparently evolved to preserve the paired architecture of the pallial and pericardial structures, present in other non-gastropod mollusks. However, the evolution within Vetigastropoda also was in the direction of atrophy of the right side of pallial organs. Vetigastropods, such as Trochoidea (Fig. 7) and Seguenzioidea,

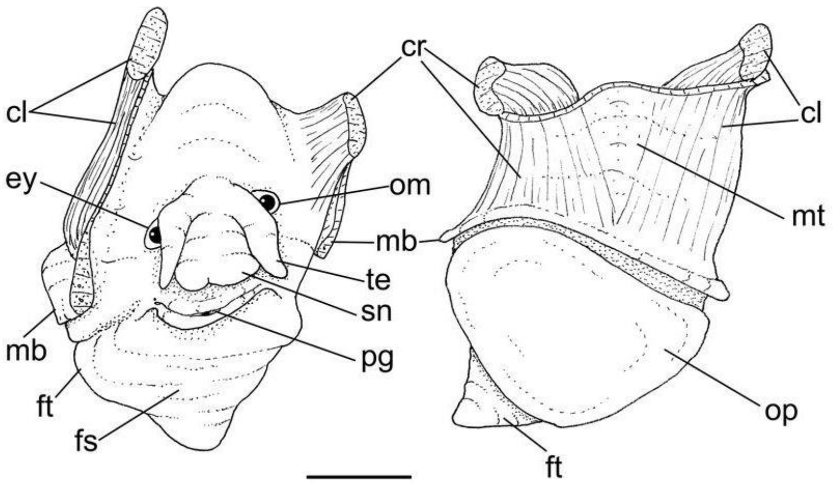


5-7. Examples of Vetigastropoda. **5**, shell of *Bayerotrochus teramachi*, Plerotomariidae (Japan, MZSP 306619) (W ~150 mm); **6**, pallial cavity of *Perotrochus atlanticus* (Brazil, MZSP 32026), ventral view, scale= 5 mm; **7**, shell of *Tristichotrochus haliarcus*, Calliostomatidae (Japan, MZSP 321857) (W ~40 mm). Lettering: an, anus; hg, hypobranchial glands; ki, kidney; lg, left gill; mb, mantle border; rg, right gill; rt, rectum; sl, slit.

lost the right pallial structures and lost the shell slit. The pallial water flow inside the pallial cavity became U-shaped as the remaining more derived neritimorphs and apogastropods. However, even in these slit-lacking vetigastropods, the dorsal type of coiling is realized. They usually still have a pair of columellar muscles, auricles, and kidneys.

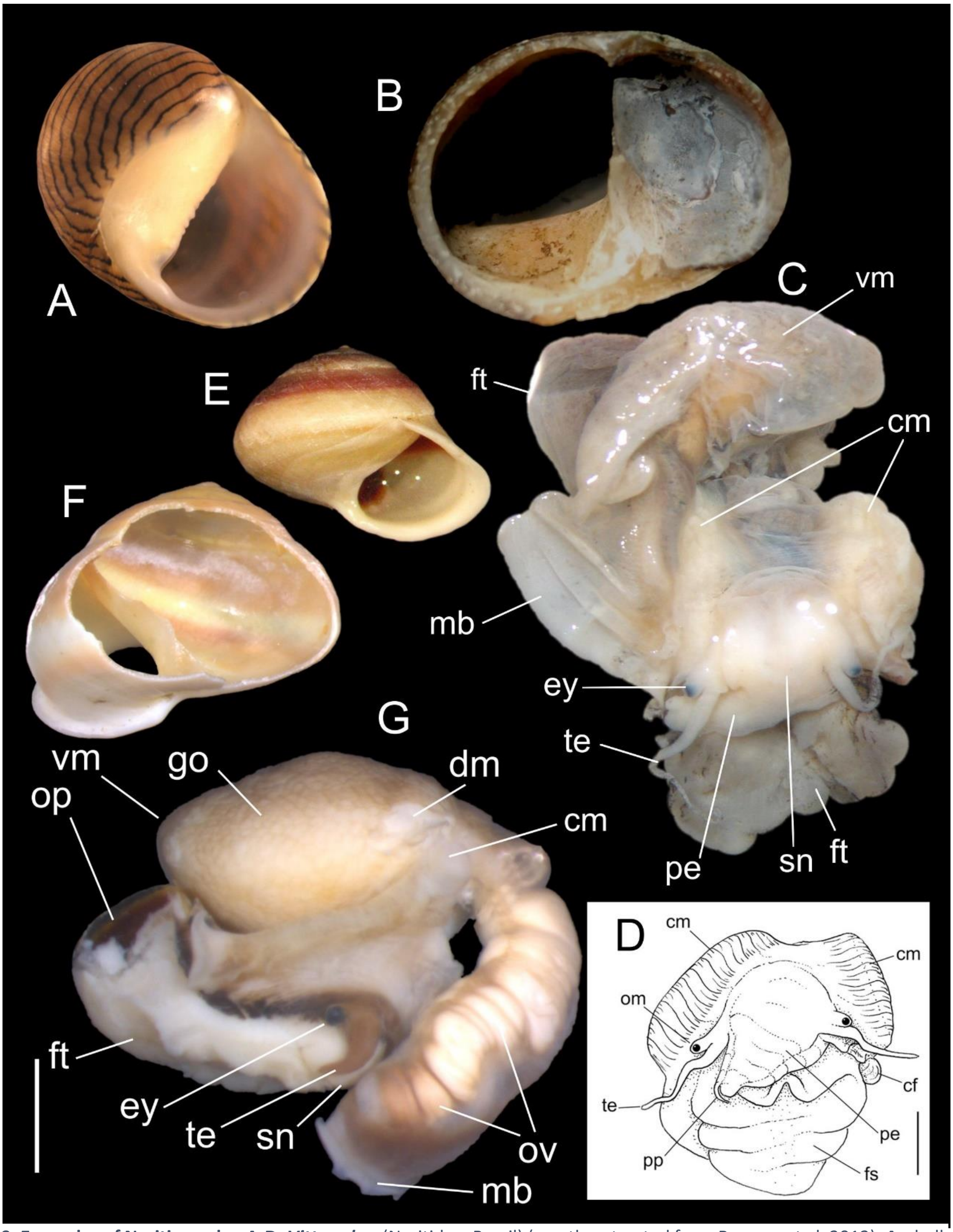
2) Coiling visceral mass between both columellar muscles

The coiling type between both columellar muscles is, in living taxa, exclusive of Neritimorpha (Fig. 2C-D, 3B). In this conformation, both columellar muscles became divergent from each other, in a V-shape (Fig. 8). The posterior end of haemocoel and the anterior end of the visceral mass lays between both columellar muscles, in level they attach to both sides of the shell, in region just posterior to inner apertural lip (Fig. 8, 9C, D, G).



8. *Helicina variabilis* (Helicinidae). Head-foot in anterior (left) and posterior (right) views. Lettering: cl, right columellar muscle; cr, left columellar muscle; ey, eye; fs, foot sole; ft, foot; mb, mantle border; pg, pedal gland; sn, snout; te, cephalic tentacle; om, ommatophore (extracted from Simone, 2018c).

This divergent conformation of the columellar muscle is



9. Examples of Neritimorpha. **A-D:** ***Vitta zebra*** (Neritidae, Brazil) (mostly extracted from Barroso et al, 2012); **A**, shell, apertural view (W 18 mm); **B**, same, dorsal view, transverse section just dorsal level from inner lip showing visceral cavity; **C**, dissected male, mostly dorsal view, pallial cavity longitudinally opened and deflected, saccular visceral mass deflected upwards; **D**, drawing of head-foot, male, anterior view, scale= 2 mm; **E-G:** ***Helicina variabilis*** (Helicinidae, Brazil) (extracted from Simone, 2018c); **E**, shell MZSP 106171, frontal view (W 13 mm); **F**, same, dorsal view, with part of shell wall removed in order to expose visceral cavity; **G**, specimen removed from shell, mostly frontal view, pallial cavity removed and deflected downwards, Scale= 2 mm. Lettering: cm, columellar muscles; dm, diaphragm muscle; ey, eye; fs, foot sole; ft, foot; go, gonad; mb, mantle border; om, ommatophore; op, operculum; ov, pallial oviduct; pe, penis; pg, pedal gland; pp, penis papilla; sn, snout; te, cephalic tentacle; vm, visceral mass.

the result of absorbance of the shell's columella, typical of the Neritimorpha (Figs. 9B, F). Lacking columella, the "columellar" muscle must attach to the lateral regions of the aperture, in order to promote the retraction of the head-foot. Despite the absence of the columella, these muscles remain to be called “columellar” in the usual literature (e.g., Barroso et al., 2012; Simone, 2018c) indicating its homology with other gastropods.

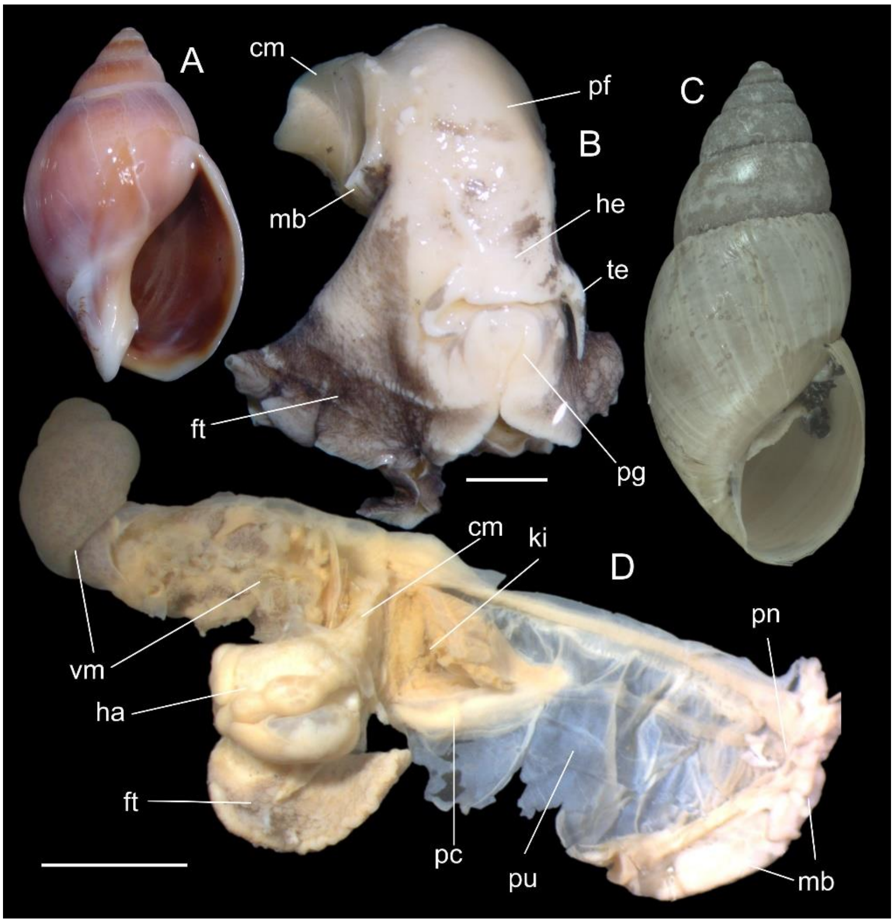
The shell coiling of this type usually produces a globose shell, with ample aperture and usually minute, inlaid spire. Despite externally the shell spire is clear, internally it is only the roof of a wide chamber (Figs. 9B, F) that bears a saccular visceral mass (Figs. 9C, G: vm).

Neritimorphs typically have a single gill, despite having a pair of auricles (Fig. 9C), subjects of future Malacopedia issues. However, the evolution along the neritimorphs was to the loss of the gill and one of the auricles, becoming monotocardians just like the apogastropods. This happened in land taxa, such as Helicinidae (Figs. 8, 9E-G). However, even in these terrestrial neritimorph branches, the divergent columellar muscle and the lack of columella are present.

3) Coiling with visceral mass to the right of the columellar muscle

This kind of shell coiling is the commonest amongst the gastropods, as it occurs in Apogastropoda (Fig. 2: blue), a taxon that encompasses the caenogastropods (Figs. 10A, B) and heterobranchs (Figs. 10C, D), the vast majority of the Gastropoda diversity.

The apogastropods are also called Monotocardia, a taxon that has as character the total loss of the right auricle. The single remaining auricle raised that name. Jointed to the loss of the auricle, several other right structures also atrophied, such as the kidney and columellar muscle. These are notorious characters (synapomorphies) Thus,



10. Examples of Apogastropoda. **A-B:** ***Buccinastrum deforme*** (Caenogastropoda, Nassariidae, Argentina) (see Pastorino & Simone, 2021 for more details); **A**, shell, apertural view (L ~40 mm); **B**, head-foot, dorsal view, scale= 5 mm; **C-D:** ***Bulimulus sula*** (Heterobranchia, Bulimulidae, Brazil) (see Simone & Amaral, 2018, for more details); **C**, shell of holotype, frontal view (L ~19 mm); **D**, dissected specimen, mostly ventral view, pallial cavity deflected to right and visceral mass to right, head-foot in middle still attached, scale= 5 mm. Lettering: cm, columellar muscles; ft, foot; go, gonad; he, haemocoel structures; ki, kidney; mb, mantle border; pc, pericardial structures; pg, pedal gland; pn, pneumostome; te, cephalic tentacle; vm, visceral mass.

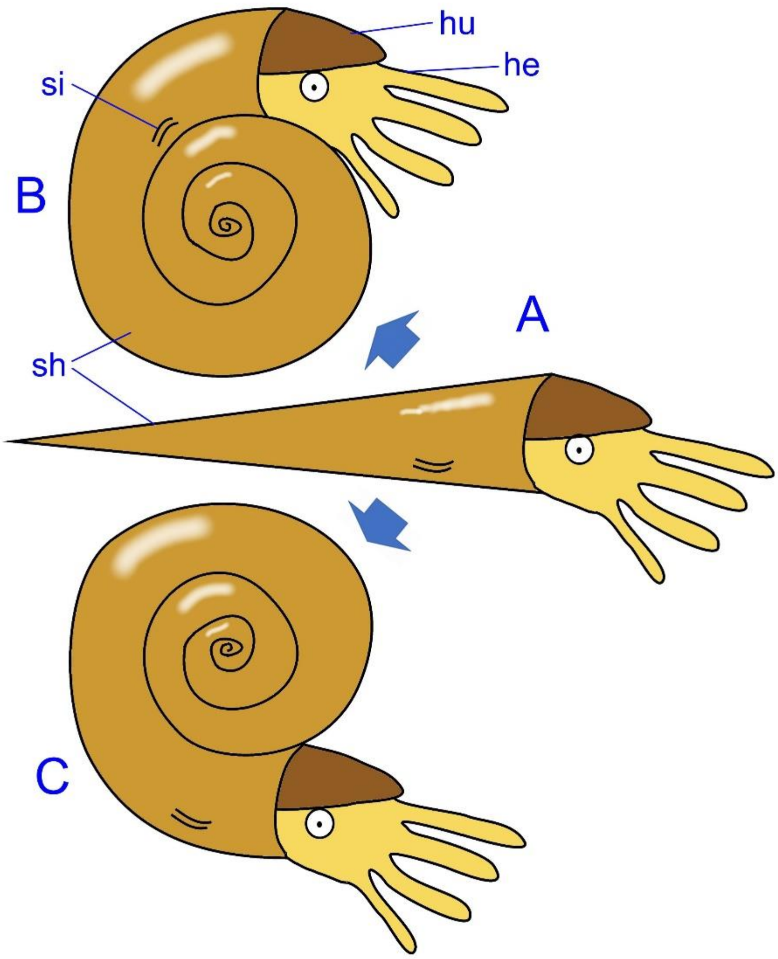
the apogastropods only have a single (left) columellar muscle. It usually is very well developed, hypertrophied, to add the function of the two original muscles.

Despite being the left remaining columellar muscle in apogastropods, it is strongly curved to the right (Figs. 10 B, D) dislocated by the presence of the pallial cavity and visceral mass in its left side. Of course, this basic plan has been modified to all kinds of conformations in the myriad of forms of this huge taxon, loss included (e.g., in slugs – Simone, 2018a). For sure, these descriptions are related to dextral shells. Sinistral ones usually have the contrary modifications.

As explained in the Introduction, the coiled shell form apparently evolved to facilitate its transportation. Beyond the shell coiling itself, the coiling evolution also produced an asymmetric somatic conformation, usually compressing the right structures in pallial cavity and anterior end of visceral mass. This phenomenon causes the atrophy of these right organs, and consequent hypertrophy of the remaining left ones. This is particularly important in apogastropods, being one of their synapomorphies. However, the same evolutive pathway occurred, as convergence, in the remaining kinds of shell coiling, of the vetigastropods (dorsal) and neritimorphs (between columellar muscles). The paired, plesiomorphic conformation is found only in the most basal branches of these taxa as explained above. Additionally, it is not clear which, or if one of these 3 coiling types is the most basal. This question remains unanswered.

Coiling in Cephalopoda

Another important mollusk taxon that has coiled shell are the cephalopods. Despite the vast majority of the living cephalopods having small, internal shells or even lost it at all (e.g., octopuses), belonging to the subclass Coleoidea, the diminishment of it does not allow coiling conformations. The single exception is *Spirula*, the only living coleoid with a spiral shell, despite being internal.



11. Schematic representation of Ammonoidea or Nautiloidea cephalopods, right view, living position: **A**, uncoiled shell, e.g., *Orthoceras*, possible ancestor of the other forms; **B**, form with shell coiled ventrally; **C**, form with shell coiled dorsally.. Lettering: he, simplification of head, arms and siphon (hyponome); hu, hood; sh, shell; si, siphuncle (seen if shell was transparent).

The remaining cephalopod subclasses – the Ammonoidea and the Nautiloidea – have heavy, external shells, and the coiling phenomenon is clear. The main problem in them is they are mostly fossils, i.e., extinctic. Ammonoidea is totally extinct since the Cretaceous, while Nautiloidea was much more abundant in the past, but still has 5 species in 2 genera in Recent, belonging to the family Nautilidae.

One of the more basal cephalopods are *Orthoceras* (Nautiloidea), a common genus of the beginning of the Paleozoic. As usual for cephalopods, its shell is internally divided by successive hollow chambers, separated by calcareous septa. Most of the animal's organs lay in the last chamber. However, the shape was a straight cone (Fig. 11A). Two other kinds of coiling are found in cephalopods, both in ammonoideans and nautiloideans: shells with spire ventral to the head (Fig. 11B) as, e.g., *Engonoceras*; and, much more common, shells with spire dorsal to the head (Fig. 11C), as, e.g., *Nautilus*. Although most of these shelled cephalopods are fossil, the position of the spire is relatively easy to infer because of the siphuncle (Fig. 11: si). The siphuncle is an internal tubular connection between the chambers, and it is ventrally positioned. As schematized in Fig. 11, the position of the siphuncle helps the determination of the coiling way.

The huge diversity of the fossil ammonoidean and nautiloidean branches of course raised several additional modifications, including the reversion to straight shells, and strange other coiling ways, as in heteromoph ammonites. However, they are not the usual rule. Characteristically, the cephalopod shell coiling is planispiral, i.e., growing in a plane. The typical cephalopod shell is enantiomorph (mirror images) in both halves. Some branches even evolved the shell design for fast swimming (Monnet et al 2011). Other kinds of non-planispiral coiling were experimented by the enigmatic heteromorphs. Some of them even look like sinistral gastropods, e.g., *Turrilites*.

Coiling in Bivalvia

The most notable are the ostreoidean Gryphaeidae (Fig. 12), a mostly fossil group in some genera that have the right valve coiled, while the left valve becomes operculum-like (Fig. 1-left). Similarly, the enigmatic extinct bivalve branch called Rudista (Hippuritoidea) also has some spiral valve and high valves' asymmetry, e.g., genera *Diceras*, *Ichthyosarcolites* and *Toucasia*.

12. Example of spiral bivalve. *Exogyra arietina* shell (Cretaceous, USA, MZSP 300816) (L ~35 mm), left and right views.

13. Example of slightly spiral bivalve. *Spinosipella agnes* shell (Verticordiidae, Brazil, holotype MZSP 36917) (L ~23 mm), posterior and left views.

In living bivalves nothing truly spiral is found in the same level as that of the cyrtosomans. Some modern bivalves have the umbos slightly coiled, weakly spiral-like, and symmetric. An example is the famous *Glossus humanus* (Venerida – Mediterranean). Another example is *Spinosipella* (Anomalodesmata) (Simone & Cunha, 2008a, b) (Fig. 13). The species of this genus, as well other verticordiids, have relatively highly coiled umbos. These umbos are so far apart that they need a calcareous, saddle-shaped reinforcement called lithodesma. Nothing special is allocated in these coiled umbos, only lobes of the gonad are found inside (Simone & Cunha, 2008a).

Acknowledgments

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