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The gastropod determinate growth

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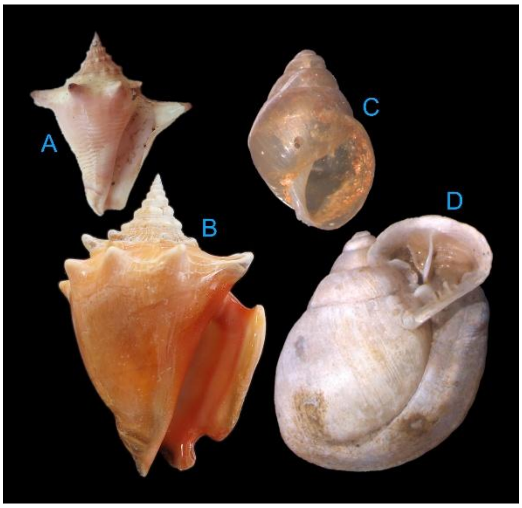
Abstract

Determinate growth in gastropods consists of the formation of a distinct peristome at the end of shell development, representing an adaptation to particular environmental circumstances. This condition contrasts with indeterminate growth, in which the shell maintains a simple, sharp-edged peristome throughout ontogeny. Determinate growth is herein divided into simple and periodic types; the latter is further subdivided into uniform and inconstant forms. A pseudo-determinate condition is also recognized. All these categories are described and discussed, including their distribution and significance in a phylogenetic context.

Keywords: shell, peristome, phylogeny, morphological modifications, anatomy.

Introduction

The term *gastropod determinate growth* was coined by Vermeij & Signor (1992) and subsequently adopted, with minor modifications, in later comparative studies (e.g., Ponder et al., 2007; Simone, 2011). It refers to certain groups of gastropods that develop a differentiated peristome at the adult stage, that is, when growth ceases and the individual reaches reproductive maturity (Fig. 1).



1. Examples of species with determinate growth. **A-B**, *Strombus pugilis*, marine (L 40-60 mm); **C-D**, *Clinispira insolita*, landsnail (L 9-16 mm) (from Simone & Casati, 2013). Above – young, below – mature specimens.

A considerable number of gastropod taxa exhibit determinate growth. In these taxa, the shells of juvenile individuals differ substantially from those of adults; that is, juveniles are not merely miniature versions of the adult shell with fewer whorls. This distinction is illustrated in Fig.

1, where the images above (juveniles) contrast with those below (adults). Juvenile shells are recognizable only as the spire portion of the mature shell.

Gastropods that lack determinate growth instead exhibit indeterminate growth; that is, their shells never develop a clearly differentiated peristome. The outer lip, for example, remains simple throughout ontogeny, presenting a sharp edge that is continuous with, and parallel to, the preceding growth lines.

Determinate growth, in contrast, encompasses a more complex set of patterns and can be subdivided into the following categories:

1. Simple
2. Periodic
   2a. Inconstant
   2b. Constant (or uniform)

Each of these growth patterns is described and discussed below.

All these kinds of shell growth are explained and discussed below.

Gastropod indeterminate growth

2. Examples of species with indeterminate growth. **A**, *Calliostoma gemmosum* (Vetigastropoda) (L 30 mm); **B**, *Pomacea crosseana* (Caenogastropoda, Ampullarioidea) (L 40 mm); **C**, *Notopala essingtonensis* (Caenogastropoda, Viviparioidea) (L 35 mm) (all from Simone, 2011); **D**, *Pugilina tupiniquim* (Caenogastropoda, Neogastropoda) (L 120 mm) (from Abatte & Simone, 2015); **E**, *Buccinanops latus* (Caenogastropoda, Neogastropoda) (L 47 mm) (from Pastorino & Simone 2021).

Indeterminate growth (Fig. 2), as noted above, is characterized by the absence of a distinct peristome in the adult when compared with juvenile or immature specimens. In such cases, there is no reliable conchological criterion to determine whether a specimen has reached full maturity or completed its development to the reproductive stage. The peristome remains simple and aligned with the growth lines (Fig. 2C), which represent successive former peristomes.

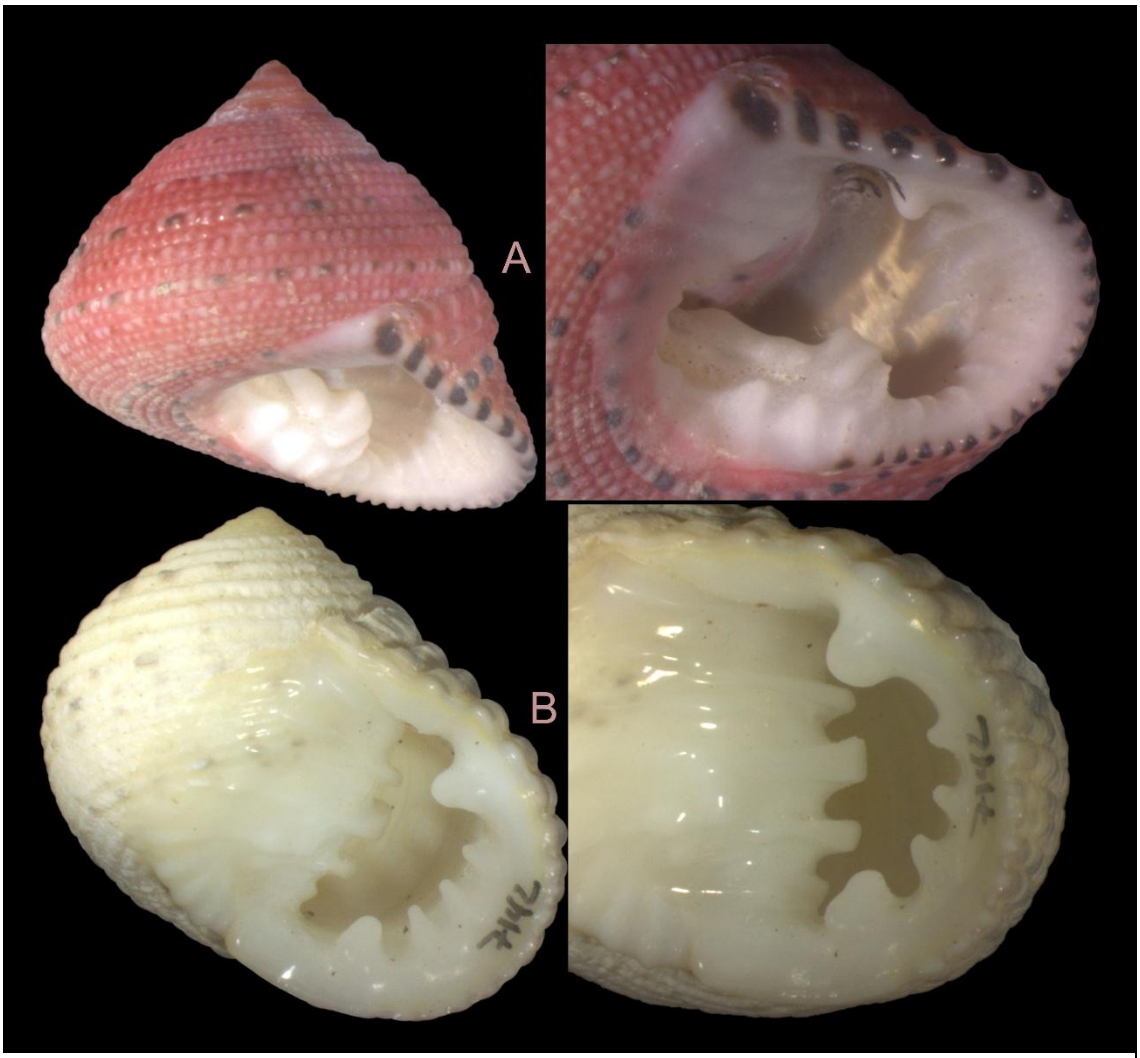
Indeterminate growth is nearly universal among the more basal gastropod clades, particularly in Patellogastropoda and the cocculiniform limpets. In Vetigastropoda, the subsequent major branch, indeterminate growth also predominates (Fig. 2A). There are, however, a few exceptions, such as the genera *Gaza* and *Callogaza*, which exhibit a distinctive deflection of the peristome and the development of an umbilical cover in the adult stage (Simone & Cunha, 2006).

In Neritimorpha and Heterobranchia, indeterminate growth is likewise almost universal. Marine neritids possess well-developed peristomes; however, this feature remains constant throughout ontogeny and does not represent a true transition at maturity. This condition is herein referred to as "pseudo-determinate growth" (see below). Within Neritimorpha, determinate growth occurs only in terrestrial lineages, as discussed below.

In Caenogastropoda, indeterminate growth is likewise the predominant condition in the more basal lineages. Determinate growth evolved independently in four distinct clades, which are discussed below. Reversions to the indeterminate condition have also occurred in lineages descending from determinate-growth ancestors, for example in xenophorids, in Benthobiidae, in the conoidean clade uniting Raphitomidae, Terebridae, and Conidae, as well as in coralliophilines and rapanines.

Taxa with indeterminate growth apparently never cease shell accretion, although the growth rate likely decreases once the individual reaches a species-specific optimal size. In gerontic specimens, the peristome may become slightly thickened, indicating continued calcareous deposition, albeit at a reduced rate.

Pseudo-determinate growth



3. Examples of species with pseudo-determinate growth (left whole apertural view, right detail od peristome, frontal view). **A**, *Clanculus puniceus* (Vetigastropoda) (L 17 mm); **B**, *Nerita plicata* (Neritimorpha) (L 20 mm).

In these cases, the taxa are in fact characterized by indeterminate growth. However, because their peristomes are elaborate and moderately complex, they may appear to exhibit determinate growth. In pseudo-determinate growth groups, the peristome is simple only during the earliest, minute stages of development. After reaching a certain size, the animal produces the characteristic complex peristome, bearing folds, plicae, canals, and related structures (Fig. 3).

Unlike taxa with true determinate growth, however, these gastropods continue growing by repeatedly resorbing and rebuilding the peristome. In this way, the individual increases from medium to larger sizes while maintaining a distinct and complex peristomal morphology.

Pseudo-determinate growth is relatively common in neritimorphs, especially in intertidal neritids (Fig. 3B). The elaborated peristome typically exhibited by these taxa—bearing teeth on both the palatal surface and the inner surface of the outer lip—develops early in ontogeny and accompanies subsequent shell growth. As the shell enlarges and additional whorls are formed, this complex peristome is periodically resorbed and rebuilt, thereby maintaining protection throughout most of the animal's life.

A similar strategy is apparently present in some trochines (Vetigastropoda) (Fig. 3A). In certain taxa, such as *Clanculus* and related genera, only very minute juveniles lack a complex peristome. The elaborated peristome (Fig. 3A) is already present in relatively small individuals and persists in larger specimens, suggesting that a comparable process of periodic resorption and reconstruction occurs in this group.

Gastropod determinate growth

As outlined above, determinate growth in gastropods refers to the production of a distinct and elaborated peristome at the stage when the animal reaches maturity (Figs. 4, 5). This definition is general and does not include the cases of periodic determinate growth, which are discussed below.

The so-called elaborated peristome in aquatic forms may consist simply of a thickened apertural margin, sometimes flanking well-developed anal and siphonal canals (Fig. 4A), or of a pronounced deflection of the peristome (Fig. 4B). In other cases, it comprises strong folds and teeth, which may be restricted to the inner lip (Fig. 4F) or present on both lips (Figs. 4E, G). The deflection may be directed outward (Figs. 4B, D) or inward (Figs. 4E–G), and the peristome may bear additional expansions and canal-like projections (Figs. 4C, D).

In terrestrial eupulmonates, the typical condition is a simple, thickened deflection of the peristome (Figs. 5A, C, D, F). Nevertheless, a complex mosaic of teeth and folds is not uncommon (Figs. 5B, E, G), a feature examined in detail elsewhere (Simone, 2018c).

The central feature of classical determinate growth is that, after forming the distinct and elaborated peristome, the animal ceases shell growth. The modified peristome evidently serves protective and functional roles; consequently, there appears to be strong selective pressure for the individual to reach this stage of development. Prior to the formation of the definitive peristome, the animal is likely more vulnerable than in the adult condition.

Juvenile individuals lacking a fully developed peristome often exhibit less exposed behavior and tend to remain more concealed. This may help explain why collected samples are typically

4. Examples of caenogastropod shells with determinate growth. **A**, *Faunus ater* (Cerithioidea, Pachychilidae; Thailand) (L 74 mm); **B**, *Colobostylus humphreysianus* (Rissooidea, Annulariidae; Jamaica) (L 20 mm); **C**, *Tibia fusus* (Stromboidea, Rostellariidae; Malaysia) (180 mm); **D**, *Lambis scorpius* (Stromboidea, Strombidae; Philippines) (130 mm); **E**, *Leporicypraea mappa* (Cypraeoidea, Cypraeidae; Philippines) (78 mm); **F**, *Bullata bullata* (Volutoidea, Marginellidae; Brazil) (58 mm); **G**, *Macrocypraea zebra* (Cypraeoidea, Cypraeidae; Brazil) (80-120 mm).

composed predominantly of adults. Moreover, because these species appear to undergo relatively rapid growth toward maturity and then remain in a stable adult phase, the proportional abundance of adult specimens in collections is further reinforced.

Although species with determinate growth cease increasing in shell size after reaching maturity, calcareous deposition generally continues. The peristome undergoes additional deposition and becomes progressively thicker, sometimes even more complex in merontic individuals.

In certain taxa, such as *Lambis* (Fig. 4D), this additional deposition may partially cover the characteristic internal folds in older, senescent specimens. In cowries (Figs. 4E, G), gerontic individuals are often rostrate, with unusually elongated anal and siphonal canals. In some pulmonates, continued deposition results in an excessively thickened outer lip. A comparison between Figs. 5A and 5F illustrates this condition, the latter representing a gerontic individual.

Determinate growth is not always indicated solely by peristomal deflection. In some taxa, it is preceded by additional morphological features, such as partial detachment of the final whorl (Fig. 5D), an unusual displacement of the apertural region (Figs. 1D, 5E), or, more rarely, a dent or fold affecting approximately half a whorl immediately before the formation of the definitive peristome (Fig. 5C).

The substantial biological investment required to produce a complex and elaborated peristome likely entails ecological compensation. In some taxa, such as *Strombus* (Fig. 1A), *Lambis* (Fig. 4D), and *Tibia* (Fig. 4C), the expanded and intricate peristome may help stabilize the shell on the substrate, making it more difficult for predators to overturn the animal.

In other cases, narrowing of the shell aperture, as observed in cowries (Figs. 4E, G) and marginellids (Fig. 4F), restricts predator access to the soft body. This protective strategy is particularly significant, dismissing these taxa to have an operculum.

The toothed peristome, a common adaptation—and often a valuable diagnostic feature for taxonomists—also functions as a defense against predation (Figs. 1D, 3A, B, 5B, E, G, 6C). However,

5. Examples of Eupulmonata with determinate growth (all from Brazil except if indicated). **A**, *Megalobulimus helicoides* (Strophocheilidae; Bolivia) (L 83 mm) (from Simone, 2018a); **B**, *Pilsbrylia dalli* (Clausiliidae) (L 16 mm) (from Simone, 2018b); **C**, *Solaropsis caperata* (Solaropsidae) (W 50 mm) (from Silva et al, 2022); **D**, *Habeas corpus* (Urocoptidae) (L 10 mm) (from Simone 2013); **E**, *Anostoma tessa* (Tomogeridae) (W 31 mm); **F**, *Megalobulimus amandus* (Strophocheilidae) (L 79 mm); **G**, *Clessinia coltrorum* (Cyclodontinidae) (L 41 mm) (these 3 from Simone, 2012).

it may impose functional constraints on the animal itself, particularly during withdrawal and emergence from the shell.

In taxa with strongly toothed peristomes, such as *Tomigerus* and *Clinispira* (Fig. 1D), these movements can be performed only with visible difficulty, requiring considerable time and noticeable body contortion.

Periodic determinate growth

Unlike simple determinate growth, periodic determinate growth occurs in taxa that produce multiple differentiated peristomes throughout ontogeny. In this pattern, even juvenile individuals may develop an elaborated peristome, retain it for a certain interval, and then resume shell growth, eventually forming another differentiated peristome—for example, one whorl later.

The former peristomes remain visible on the spire and are referred to as varices or threads. These structures represent the remnants of earlier apertural margins formed during successive phases of shell growth.

As noted above, periodic determinate growth can be subdivided into: (1) inconstant and (2) constant (or uniform) forms. Both patterns are discussed below.

6. Examples of caenogastropods with inconstant periodic determinate growth, all from Brazil. **A**, *Cerithium atratum* (Cerithioidea-Cerithiidae) (30 mm); **B**, *Charonia variegata* (Tonnoidea-Charoniidae) (245 mm); **C**, *Distorsio clathrata* (Tonnoidea-Personiidae) (60 mm). Arrows indicating presente and previous peristomes.

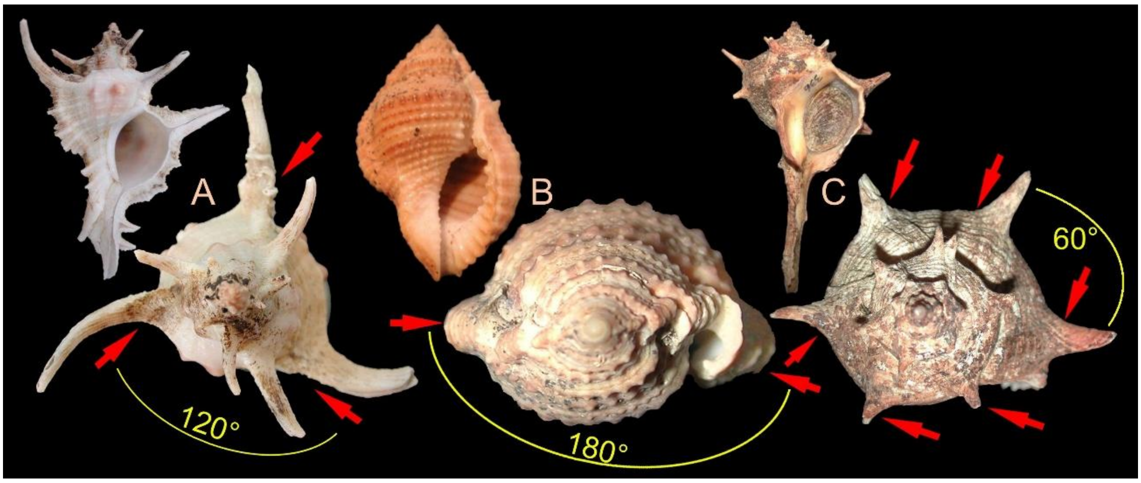
Inconstant periodic determinate growth

Periodic determinate growth is termed *inconstant* when the appearance of distinct peristomes is apparently irregular and unpredictable, and may even be undetectable in some specimens. When the shell is examined in apical view, there is no consistent angular position or fixed proportion of the whorl at which successive peristomes occur during growth (Fig. 6, arrows).

As shown in Fig. 6, previous peristomes can be recognized as axial threads along the spire whorls (arrows). The distribution and number of these threads typically vary among specimens within the same population.

Constant or uniform periodic determinate growth

Constant (or uniform) periodic determinate growth is generally similar to the inconstant pattern described above. Its defining feature, however, is the regularity in the formation of differentiated peristomes. In this condition, successive peristomes are produced at relatively uniform intervals, either as a consistent proportion of a whorl or at a constant angular position when the shell is viewed apically (Fig. 7).



7. Examples of caenogastropods with uniform periodic determinate growth, from Brazil. **A**, *Siratus senegalensis* (Muricoidea, Muricidae) (L 70 mm); **B**, *Marsupina bufo* (Tonnoidea, Bursidae) (L 35 mm); **C**, *Bolinus brandaris* (Muricoidea, Muricidae) (L 90 mm).

In the examples illustrated, the muricid genus *Siratus* produces a differentiated peristome at intervals of approximately one-third of a whorl, corresponding to about 120° when the shell is viewed apically (Fig. 7A). The bursid genus *Marsupina* forms a new peristome at roughly half a whorl, or 180° (Fig. 7B), whereas the muricid genus *Bolinus* does so at intervals of about one-sixth of a whorl, or 60° (Fig. 7C).

Across gastropods, the number of peristomes formed per whorl varies widely, ranging from several dozen per whorl, as in some muricids such as *Trophon* and *Nucella*, to fewer than one per whorl, as observed in certain cymatiids, such as *Cymatium*.

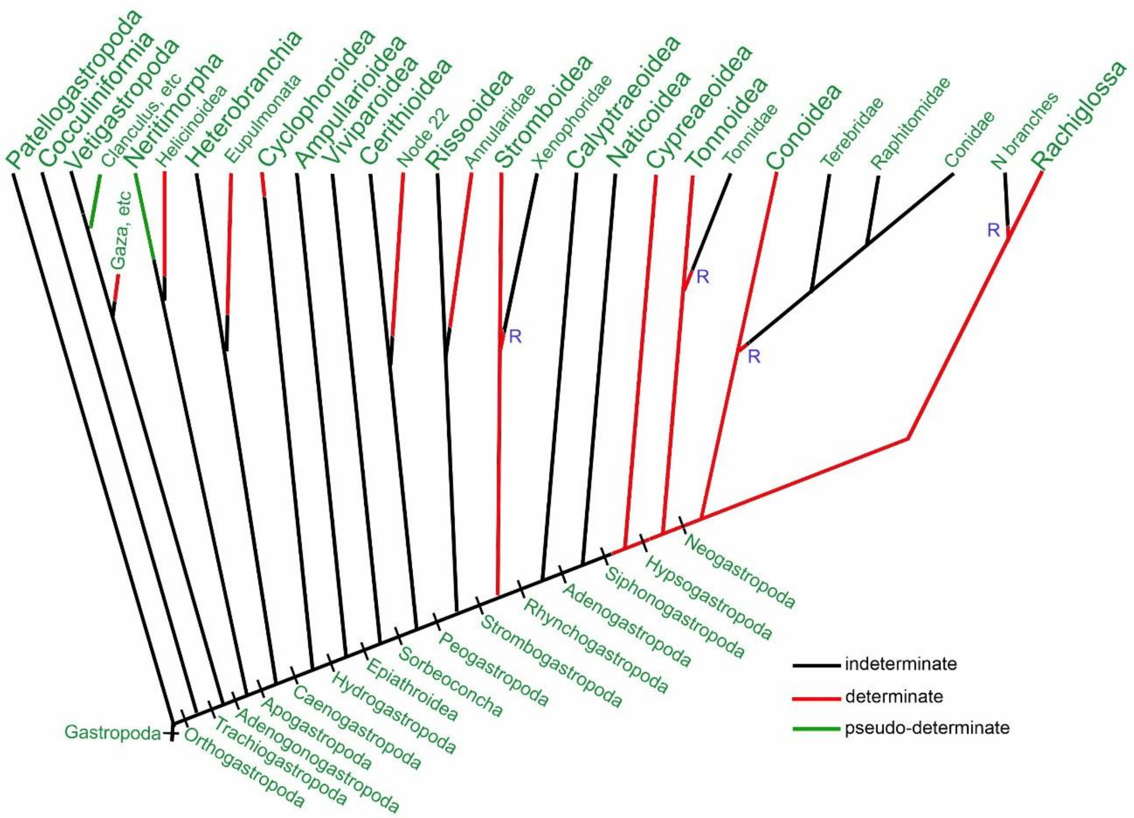
Naturally, gastropods are biological organisms rather than mechanical systems, and some variation occurs in the positioning of successive peristomes during shell growth. Consequently, even in taxa exhibiting uniform periodic determinate growth, the axial threads (varices) along the spire rarely conform to perfectly geometric standards.

For example, in Fig. 7B, the varices are not aligned in an exact plane corresponding to precisely 180° at each half whorl. The angular values provided above should therefore be understood as approximations rather than exact measurements.

Phylogenetic inferences

As discussed above, determinate growth in gastropods, along with its various modifications, has evolved multiple times independently across the class. The phylogenetic relationships of Gastropoda are summarized in Fig. 8, based primarily on MolluscaBase (2025), with additional influence from Simone (2011, 2021, 2024).

In the dendrogram presented (Fig. 8), relationships among the major gastropod clades are depicted chiefly on the basis of phenotypic characters, with selected less inclusive taxa incorporated for strategic representation. Branches shown in black correspond to taxa exhibiting indeterminate growth, a condition that appears to be basal within Gastropoda (Figs. 2A–C) and is also shared with other molluscan classes.



8. Cladogram representing relationships of main groups of Gastropoda, based on MolluscaBase (2025) and Simone (2011, 2021, 2024). As indicate in the below-right corner, the branches color indicates the presence of determinate growth (red), pseudo-determinate growth (green) or indeterminate growth (black). Some less inclusive branches are also schematically shown. "R" represents reversions. The branch "Node 22" is based on (Simone, 2011) and is explained in the text, as well the rachiglossan branch "N branches".

The determinate growth condition is represented by red branches in Fig. 8. It can be observed that this condition evolved independently, representing convergent events, at least eight times. These include: (1) in the vetigastropod Margaritidae, specifically in the genera *Gaza* and

Callogaza (Simone & Cunha, 2006); (2) in terrestrial neritimorphs of Helicinoidea (Bandel & Frýda, 1999; Simone, 2018d); (3) in Heterobranchia, particularly within Eupulmonata, including most representatives of the group (Figs. 1D, 5); and (4) in certain lineages of Cyclophoroidea, such as Diplommatinidae and related taxa, as well as in larger forms with deflected peristomes (e.g., *Cyclotus*, *Cyclophorus*) and even species bearing a snorkel-like extension (e.g., *Rhiostoma*).

Within Caenogastropoda, determinate growth arose independently in several additional lineages. It appears (5) at node 22 of Cerithioidea (Simone, 2011), a clade that includes Batillariidae, Pachychilidae, Cerithiidae, Potamididae, Planaxidae, and Thiaridae, and most likely also Cerithiopsidae, Triphoridae, Eulimidae, and Epitoniidae. This cerithioidean lineage exhibits a mixture of simple determinate growth and periodic determinate growth, both inconstant and uniform (e.g., in epitoniids). Owing to this complexity, these subcategories are not differentiated in Fig. 8.

In the Rissooidea/Littorinoidea lineage, determinate growth appears (6) in the terrestrial Annulariidae (Fig. 4B) (Simone, 2004, 2006). It also arises (7) in Stromboidea, where it represents a basal synapomorphy of the superfamily. Furthermore, this condition constitutes a synapomorphy of Siphonogastropoda (Simone, 2011, 2024).

Within Caenogastropoda, the determinate growth condition reverted to an indeterminate state at least four times (indicated by "R" in Fig. 8): (1) in the stromboidean Xenophotidae; (2) in the tonnoidean Tonnidae; (3) in the conoidean clade comprising Terebridae, Raphitomidae, and Conidae; and (4) in several rachiglossan lineages, such as, e.g., Buccinanopsidae (Fig. 2E), Melongenidae (Fig. 2D), Babyloniidae, Olividae, Mitridae, and Volutidae.

Figure 8, however, does not depict the branches exhibiting periodic forms of determinate growth, as this condition appears in several internal nodes. Including all such occurrences would render the cladogram excessively complex and detract from the didactic purpose of this essay. The occurrence of periodic determinate growth in cerithioideans (node 22) was briefly explained above.

Within Rachiglossa, several examples can be cited, particularly in Muricidae, some of which were also mentioned above. Another noteworthy case of uniformly periodic determinate growth occurs in Harpidae, Busyconidae, and some Buccinidae.

Among tonnoideans, uniformly periodic determinate growth is typical of most Bursidae, whereas inconstant periodic determinate growth is more characteristic of other families, such as Cassidae, Charoniidae (Fig. 6B), Cymatiidae, Personiidae, and Ranellidae.

Figure 8 also depicts, in green, the branches representing taxa with pseudo-determinate growth, such as Neritimorpha (including several Neritidae; Fig. 3B) and, tentatively, some vetigastropods, such as Clanculus and related forms (Fig. 3A).

In cases of periodic determinate growth, the preceding peristomes remain externally preserved along the spire. Internally, however, they are partially resorbed, as the mantle is capable of dissolving shell material, thereby freeing space for the expanding body of the animal. These shell regions thus function as a calcareous reserve. The varices also serve to reinforce the shell: a shell bearing multiple axial varices along the spire (e.g., in *Epitonium*) is mechanically more resistant than a comparable shell lacking such structures (e.g., *Turritella*).

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