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The gastropod columella

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Abstract

The columella of coiled gastropod shells is explored, with particular emphasis on its morphological variations. Columellar configuration depends on the angulation of shell growth, which can be negative, producing a zigzagging columella; straight; or positive, producing a wide umbilicus. Shell growth can also occur around an empty central space, resulting in a hollow, tubular columella, a condition particularly evident in shells with negative or straight growth angulation. Some evolutionary trends in shell morphology, such as limpetization, limacization, and lateralization, which have been explored in previous papers, as well as irregular shell growth and the absorption of inner whorls, can modify the columella or even lead to its complete loss. Particular cases recently interpreted as lacking a columella and described as having a "hollow newel" are discussed and regarded as misinterpretations of the shell modifications described above.

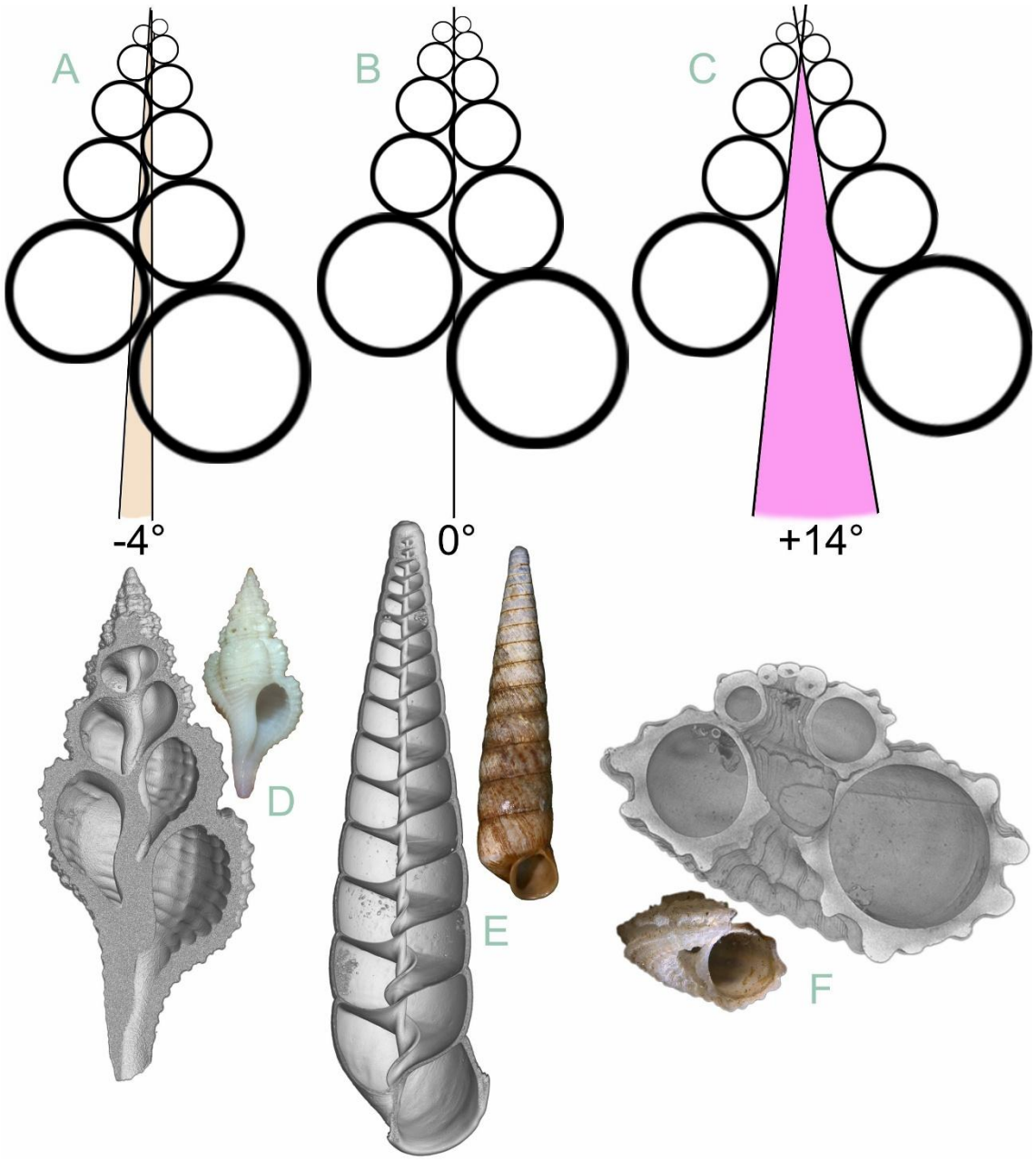
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Introduction

The columella of a gastropod shell is the virtual central axis around which the shell grows. It is present only in spirally coiled shells that develop along an axis. Gastropod shells with other growth patterns lack a columella or have it strongly modified.

The columella is entirely absent in limpets, in which the evolutionary process of limpetization has occurred. The chain of modifications associated with **limpetization** was explored elsewhere (Simone, 2018a). When this process is of secondary origin, it results in the loss of the columella. Another evolutionary process that tends to result in the disappearance of the columella is shell **lateralization**. This phenomenon was also explored elsewhere (Simone, 2018b) and consists of an evolutionary pathway leading to an involute shell. This shell type represents the endpoint of an evolutionary process in which each whorl envelops the preceding one, so that only the last whorl remains externally visible. This process also tends to result in the loss of the columella. A similar

phenomenon occurs in the evolution of planispiral shells (e.g., in most Planorbidae), which represent a discoidal form of lateralization.



1. Types of columellae considering the angulation of growth. There are all gradations between and beyond these examples. **A**, negative angulation, in which each whorl overlaps previous whorl level, the columella in this case is zigzagging; **B**, straight growth, in which the growth happens along a straight line, in this case the columella is straight; **C**, opened angled growth, in which the growth happens around an opened angle, as a cone, in this case the columella is ample, cone-like; **B-F**, examples of shells with respective types of shell growth, entire shell and tomography image in frontal section; **D**, example with negative angulation, *Lightbournus rendatus* (Fasciolariidae, MNHN) (L 23 mm); **E**, example of shell with straight growth, *Megaspira* sp. (Megaspiridae, MZSP) (L 80 mm); F, example of shell with opened angled growth, *Arene asteria* (Areneidae, MORG 20637) (L 6 mm) (from Cavallari et al., 2026) (courtesy D. Cavallari).

Another gastropod evolutionary process that tends to result in the loss not only of the columella but also of the entire shell is **limacization**. This process was also explored in detail elsewhere (Simone, 2018c) and consists of the reduction and eventual loss of the shell, accompanied by the displacement of the internal organs, particularly the visceral mass, into the head-foot. In the first stage (degree 1), the shell is still present, although a columella is difficult to distinguish. In the

final stage (degree 2), the shell is entirely lost, and the animal becomes essentially a crawling head-foot. Another type of gastropod shell that lacks a columella is that characterized by irregular growth, as seen, for example, in vermetids and siliquariids.

Another condition involves the absorption of the internal whorls of the shell in certain taxa. In these cases, the shell retains a coiled spire, but the internal whorls are absent, leaving the spire totally or partially hollow. The absorption of internal whorls is a synapomorphy of Neritimorpha, in which the visceral mass becomes a broad, uncoiled sac. This phenomenon also occurs in other gastropods, such as *Olivella* (Olividae). In neritimorphs, the shell lacks a columella (Simone, 2011). In *Olivella*, however, because the absorption of the whorls is restricted to the posterior region, a columella is still present in the remaining last whorls.

This paper, therefore, explores several features of the columella, particularly from taxonomic and evolutionary perspectives. The structure exhibits several characters of interest for comparative studies, especially in taxonomy and phylogeny. Some of these attributes have already been explored elsewhere (Simone, 2011, 2024), as well as in a few other studies (Jackiewicz & Koralewska, 2000; Price, 2003; Friend et al., 2024; Vermeij, 2025), which will be discussed in more detail below.

It is interesting to observe that the growth, shape, and other characters of the columella are strongly influenced by two factors: (1) the angle of shell growth (Fig. 1) and (2) the configuration of the growth axis, whether tightly coiled or surrounding a virtual tube (Fig. 2). These factors are explored below. However, shells lacking a columella or having this structure strongly modified as a result of the evolutionary processes mentioned above (limpetization, lateralization, limacization, and irregular growth) are not discussed further here. Detailed discussions of these conditions can be found in the references cited for each case.

Angulation of growth

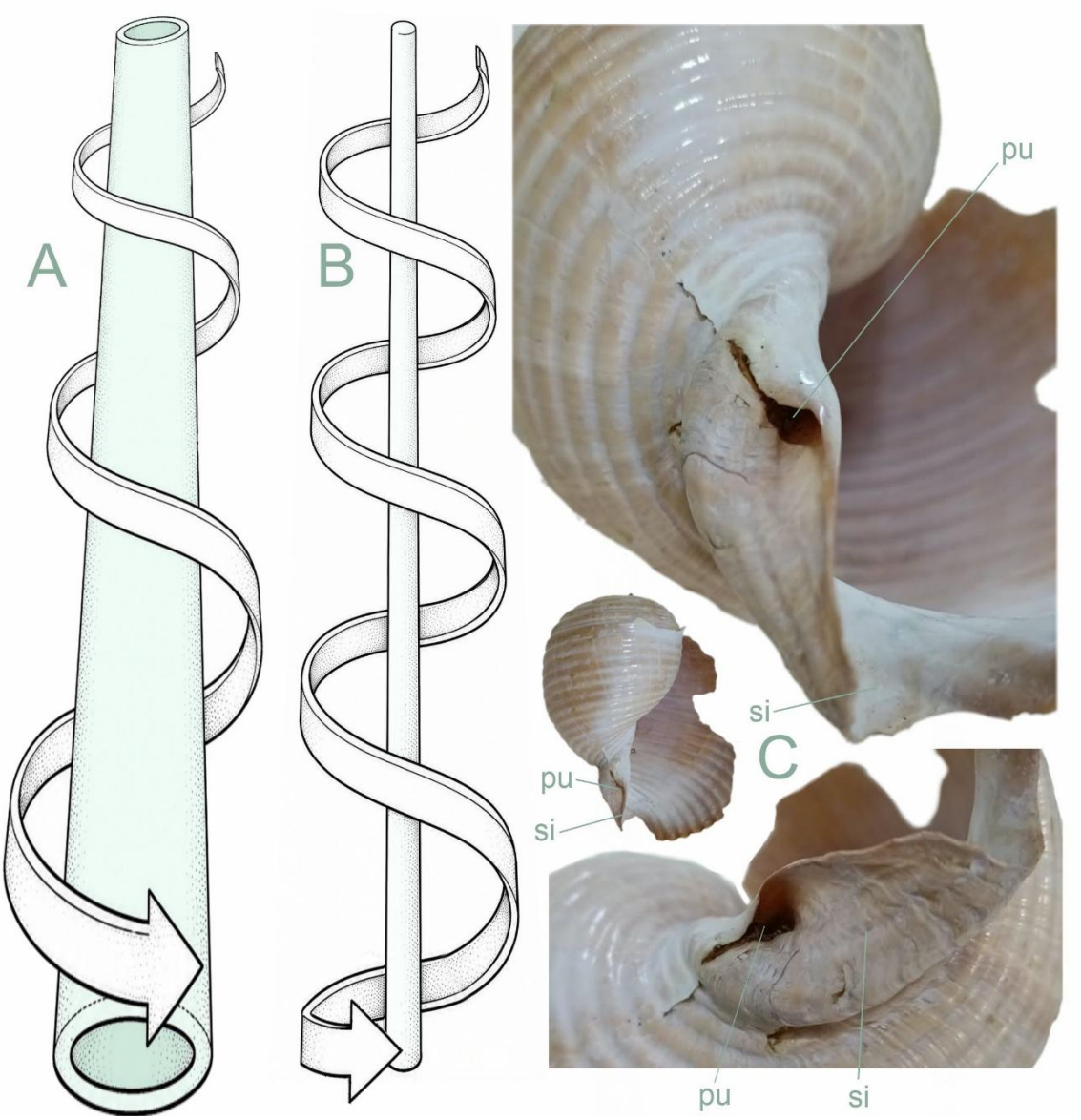
Schemes and examples of the different types of growth angulation are shown in Fig. 1. It is important, however, to keep in mind that a continuous range of variation occurs, both between and beyond the examples illustrated.

As mentioned above, the columella is the axis around which the coiled shell grows. This axis can be straight (Fig. 1B), producing a straight columella (e.g., Fig. 1E), around which the whorls are arranged. The growth axis can also have a negative angulation (Fig. 1A). In this case, each whorl is positioned slightly below the preceding one, overlapping the vertical space occupied by the preceding whorl. This arrangement produces a zigzagging columella, as seen in longitudinal section (Fig. 1D). The opposite condition can also occur, with shell growth proceeding at a wide, positive angulation (Fig. 1C). In this case, the shell grows conically, with the inner surfaces of successive whorls becoming increasingly separated. A wide umbilicus is usually present, resulting from the large empty space along the growth axis (Fig. 1F).

The angulation of growth is, therefore, a fundamental parameter for understanding the gastropod columella. There are, however, several cases in which shell growth changes its angulation during development, resulting in irregularly coiled shells. One example is *Cerion* (Eupulmonata, Cerionidae), in which the first whorls exhibit wide coiling angulation, whereas the remaining whorls have a straight arrangement. Another example is *Distorsio* (Caenogastropoda, Personiidae),

in which whorls with variable angulations occur along the shell. These cases are also not treated in this issue.

The distance of the growth axis



2. Schemes of columellae and pseudoumbilicus. **A**, A hollow columella, the central tube represents the columella (abstracting the whorls' insertion), and the coiled arrow represents the shell growth, which happens at certain distance from a middle point, forming a hollow axis, in negative angulation growth (tube zigzagging), this forms the pseudoumbilicus; **B**, a solid, rod-like columella, with remaining parameters like Fig. A; **C**, *Tonna galea* (Tonnoidea, Brazil, MZSP), showing the pseudoumbilicus, frontal-inferior, frontal and anterior views (L 120 mm) (partially broken shell). Lettering: pu, pseudoumbilicus; si, siphonal canal.

In addition to the angulation of growth, another important parameter is the distance of the growth axis from a virtual central point. When this distance is zero, the columella is solid, forming a simple rod or pillar (Fig. 2B). When the growth axis is displaced from this virtual central point, the shell grows around a central hollow tube (Fig. 2A, C).

This parameter applies only to shells with negative angulation (Figs. 1A, D) and straight growth (Figs. 1B, E). In shells with open-angle growth (Fig. 1C, F), the successive whorls are already positioned away from the central axis.

Thus, when shell coiling occurs at a distance from the virtual central point, both in negative-angulation and straight growth, a hollow tube is formed (Fig. 2A), enclosing a central lumen. The columella is therefore hollow, consisting of a zigzagging tube in the first condition and a straight tube in the second.

The inferior end of this tubular columella, i.e., the end closer to the peristome, is called the **pseudoumbilicus** (Fig. 2C). This designation is clear in shells with negative-angulation growth, but its use is questionable in shells with straight growth, in which the structure is usually referred to simply as the **umbilicus**. This question arises because a hollow, straight columella can be considered a narrow variant of open-angle growth. The difference between a hollow, straight columella and the columella of an open-angle shell is that the former remains relatively uniform in width along its length, whereas the latter progressively widens during shell growth. In practice, however, this distinction is not usually made.

Shell umbilicus and pseudoumbilicus



3. *Gaza compta*, shell, as example of covered umbilicus. A, adult shell with occluding umbilicus by a flap from peristome (holotype MZSP 40324) (W 26 mm); **B**, immature shell with umbilicus still opened (MZSP 40325) (W 20 mm). More details in Simone & Cunha (2006).

Another feature associated with the shell columella is the presence or absence of an umbilicus. This shell attribute was partially explained in the previous section. When shell growth proceeds around a virtual line, both in negative-angulation and straight growth (Fig. 2B), no umbilicus is formed, resulting in what is called an **imperforate shell**. However, when growth proceeds with positive angulation (Figs. 1C, F), or when the shell grows around an axis displaced from the central point, forming a hollow tube (Fig. 2A), an opening is present adjacent to the inner lip of the peristome. This opening is usually called the **umbilicus**, and the shell is consequently described as **perforate**.

The umbilicus can become occluded during the final stages of shell growth by a callus or by a calcareous flap extending from the inner lip of the peristome (Fig. 3). In these cases, the umbilicus is present but secondarily occluded, a condition also referred to as *covered*. An interesting example is the genus *Gaza* (Vetigastropoda) (Simone & Cunha, 2006). Immature specimens have a typical open umbilicus (Fig. 3B), which becomes occluded by a calcareous peristomal flap at the end of shell development (Fig. 3A).

This posterior occlusion of the umbilicus may serve to prevent the invasion of organisms into its interior. In large shells with an open umbilicus, it is not uncommon to find other organisms living inside it, such as polychaetes and small mollusks. An example is *Angaria delphinus* (Vetigastropoda) (personal observation), in which many specimens have another organism living within the umbilicus.

Columellar muscle

The gastropod columellar muscle is obviously associated with the columella. However, a more appropriate designation would be the **foot and head retractor muscle**. This is because a columella is not always present, whereas the muscle is retained. Nevertheless, by tradition, it continues to be called the *columellar muscle*.

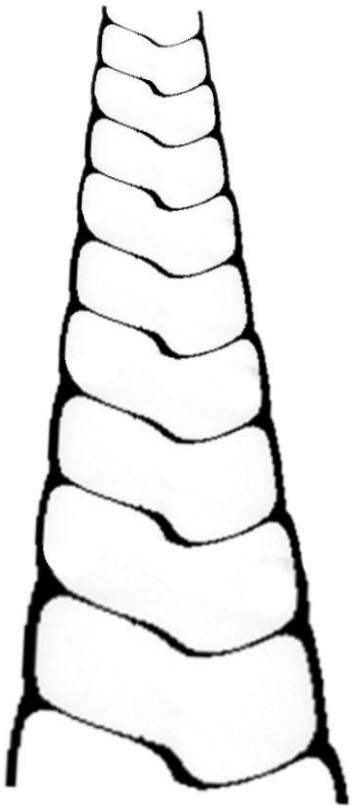
The columellar muscle usually originates in the ventroposterior region of the head-foot and runs anterodorsally, spreading into the head integument and also extending along the foot. Its contraction promotes the retraction of the head and foot into the shell. Since, in coiled gastropod shells, the columella occupies a ventral position within the last whorl, this retractor muscle originates along the terminal portion of the columella. This anatomical relationship explains its traditional name.

There are, however, gastropod shells that lack a columella, as mentioned above. In particular, shell lateralization is an evolutionary pathway leading to the formation of involute shells (Simone, 2018b). In highly lateralized taxa, the columella is absent because each whorl covers the preceding one. Nevertheless, the muscle is usually still referred to as the *columellar muscle*. A similar condition occurs in gastropods with irregular shell growth, such as vermetids and siliquariids (Caenogastropoda), as well as planispiral shells.

During the process of limpetization, however, the columellar muscle becomes strongly modified from the earliest stages (Simone, 2018a), and the head-foot retractor muscles are rarely referred to as columellar muscles. The more usual designation is *shell muscle*. In degrees 1 and 2 of limpetization, corresponding to what are usually called *ear shells*, the head-foot retractor muscles originate from discrete regions of the shell. In degree 3, corresponding to true limpets, these retractors have a horseshoe-shaped origin on the shell, forming the typical *shell muscle* (see Simone, 2018a, for further details).

As limacization progresses the shell tends to disappear (Simone, 2018c), the columellar muscle undergoes corresponding modifications and may eventually disappear as well.

Discussion



4. *Megaspira sp*, the same specimen represented in Fig 1E. However, the tomography section is done in a region preceding columella, simulating the Friend et al. (2024) concept of a coiled shell lacking columella. This condition actually does not exist.

As mentioned above, the shell columella has been addressed in several published studies (Jackiewicz & Koralewska, 2000; Price, 2003; Simone, 2011, 2024; Friend et al., 2024; Vermeij, 2025), which provide interesting additional information. However, the scope and objectives of those studies differ from those of the present contribution. None of them provides the comprehensive synthesis of information presented here.

Particularly, Friend et al. (2024) presented an interesting synthesis of conclusions regarding columellar structure. However, their failure to distinguish among the phenomena discussed herein led to some distorted or misleading conclusions. The most interesting example is the category they termed "absence of columella," which they attributed to some turritellids. This condition, however, does not occur in any coiled gastropod and is therefore nonexistent (Fig. 4). The figure illustrating this condition (Friend et al., 2024: fig. 4B) actually shows a longitudinal section taken anterior to the columella, as demonstrated in Fig. 4 herein.

The actual absence of a columella, examples of which were identified by those authors, is related to other phenomena discussed above, such as limpetization, lateralization, irregular shell growth, and shell reduction. These evolutionary pathways tend to result in the modification or eventual disappearance of a clearly defined shell columella (Simone, 2011, 2018a, b, c, 2024). Thus, contrary to what these authors stated, the columella had in fact been studied previously, as had the evolutionary pathways that tend to modify its structure. The concept introduced by Friend et al. (2024), termed "hollow newel," can be explained by the shell modifications described above; it is therefore neither an isolated category nor a novelty.

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