

Abstract

While septa are observed in many Paleozoic gastropod groups, they are often considered rare in modern gastropods. Notable exceptions to this statement in the literature include Turritellidae, Vermetidae, and decollate terrestrial snails. (Septa of Turritella communis were even compared with those found in Nautilus in Lyell's Elements of Geology (1838).) Septation is, however, not rare within these groups and in fact can be found in numerous other Caenogastropod families including Cerithiidae, Muricidae, Batillariidae, Ranellidae, Caecidae and Campanilidae. This wide phylogenetic distribution of septa suggests that septa are either: 1) plesiomorphic for gastropods, or 2) frequently independently evolved, either convergently or through parallelism. Examination of septal microstructure is a first step in understanding how these structures evolved. We have examined the composition, microstructure, and patterns of septal insertion in 11 turritellid species, both fossil and Recent. Septa were found to be very thin (0.14-20 mm), with thicker septa (up to 0.80 mm) composed of multiple thin septa fused together. Number and spacing of septa was found to be highly variable among species. Septa also appear to be generated in continuity with secondary thickening of the shell wall in many species. Septa within both Turritellidae (Cerithioida) and Ranellidae (Littorinimorpha) (Bandel, 1990) appear to exhibit crossed lamellar microstructure, indicating significant energy investment by the animal. Functional significance of gastropod septa remains unclear, but possibilities include prophylaxis against apical breakage, defense against predation, response to excess calcium, or ballast. In any case, septa are not rare in gastropods.

Introduction

Here we consider a septum to be a non-pathological wall of shell material which completely closes off the adapical portion of the shell and leaves a void space sealed off from the body cavity (in contrast to cephalopod septa which are penetrated by a siphuncle). While it is acknowledge to be commonin several living different groups in isolation, particularly turritellids, septation is often considered uncommon in extant gastropods generally (e.g. "only in benthic gastropods with a very long shell" (Ray, 2008), "uncommon chambered gastropods" (Majewske, 1974) "septation is not common in Mesozoic and **Cenozoic gastropods**" (Cook et al., 2015). In contrast septation is considered to be relatively common in Paleozoic gastropod groups, whether high or low spired (Cook, 1993, Gubanov et al., 1995) and generally "not an unusual phenomenon" (Yochelson, 1971).

This dichotomy is not universal, with some authors (e.g. Fretter and Graham, 1962) considering septation to be "not uncommon" in gastropods and even common in high-spired forms. Here we argue that this formulation more accurately describes the phylogenetic distribution of septation in gastropods, both Recent and fossil. Cook et al. (2015) note that septation occurs in Paleozoic Omphalocirridae, Omphaalotrochidae, Raphistomatidae, Vetigastropoda, Murchisoniidae and Heterobranchia. The Caenogastropoda represent 60% of extant gastropods (Ponder et al., 2008) and our analysis suggests that septa are either primitive for this clade or evolved independently within several different member groups.



Figure 1. Examples of septation in Turritellids. A. A dome shaped septum visible in the apex of *Turritella altilira* with the protoconch and earliest teleoconch whorls absent. B. Multiple dome shaped septa present within Vermicularia recta (wooden mount approximately 1 cm wide). C. Septa present near the apex of T. communis. D. Extensive septation in T. robusta.

Materials and Methods

All taxa examined were part of the collections at the Paleontological Research Institution. Taxa were from the recent collection except for *Vermicularia recta* (Pliocene), and the Miocene T. altilira and T. robusta. For several taxa septa were visible in broken specimens. Specimens from several turritellid species were sectioned using a wafering saw so that septa could be examined. These include Recent Maoricolpus roseus, Turritella banksi, communis, duplicata, gonostoma, terebra, and Zeacolpus fulminatus as well as the Miocene T. altilira, gatunensis and robusta and Pliocene Vermicularia recta. CT scans of Terebra subulata and Bithynia sp. were performed with a GE CT-120. Nano-CT scans of Mitra mitra, Strombus pugilis, Cerithium nodulosum, *Cenchritis muricatus, Opalia* sp., *Pomatias elegans* and *Cenchritis muricatus* were performed with a ZEISS-Xradia Versa 520. Description of four taxa as possessing internal septa were taken from the literature, *Athleta tuomeyi*, Caecidae, *Campanille*, and Ranellidae. Additionally septal microstructure was characterized using a Jeol Scanning Electron Microscope. No specimens were coated. Where specimens are marked as etched, etching was performed using 1% glacial acetic acid for 20 s. Chemical composition of septa was determined through Raman spectroscopic imaging utilizing a Renishaw InVia microRaman system with a 785 nm laser as this technique is non-destructive and has a spatial resolution of $\sim 1 \,\mu m$.

Vermicularia recta

B. Turritella terebra septa appear to form in continuity with this inner shell layer (etched).

C. Other turritellids also have crossed lamellar microstructure in septa (V. recta etched).

Figure 5 A.Soft anatomy of *Turritella bacillum*. Note that the apical edge of mantle tissue is located 4.5-5 whorls from the apical end of the animal. B. CT scan of T. altilira. In turritellines, septa appear to always be $\sim 150 \ \mu m$ thick, with thicker septa consisting of multiple thin septa fused along the edges. It is not known whether this pattern extends to other cerithioid taxa with thin, apically convex septa.

Discussion

Septa appear to be present in all cerithioidean taxa examined, and appear to be universally apically convex and thin (Figure 2). *Campanile* also has thin, apically convex septa. In other Caenogastropoda septa may be either apically convex and thin or be thick. Some taxa do appear to lack septa, (e.g. *Bithynia*), but this was in fact rare in the Caenogastropods examined here. If septa are not primitive for Caenogastropoda then they very frequently occur in both high and low-spired gastropods. Limpet-like taxa may be the exception. This suggests that either septa are adaptive for higher-spired forms or are a spandrel, a structural by-product of another feature (Gould and Lewontin, 1979).

Within turritellids, septa appear to form in continuity with internal secondarily deposited shell material. Both this secondary material and the septum itself exhibit crossed-lamellar microstructure. This microstructure is the most common aragonitic microstructure in molluscs and is more resistant to breakage than microstructures with less biological control. Wherever the dominant shell structure is crossed lamellar, including pulmonate gastropods, septa begin as spherulitic prismatic transitioning to crossed-lamellar microstructure (Bandel, personal communication). While Bandel suggests that the mantle is directly responsible for septum deposition, with the transition to crossed lamellar from spherulitic prismatic microstructure corresponding to increased mantle control, we belive the anatomy of Turritella precludes this (Figure 5). If this is the case, then this would be the first example of which the authors are aware of crossed lamellar microstructureformed without direct contact with the mantle.

onclusions

As septa are not uncommon in Paleozoic gastropods and may be primitive for the largest extant clade of gastropods it seems inappropriate to consider septa uncommon in gastropods. As crossed lamellar microstructure is more energy intensive to construct than homogenous or spherulitic microstructures these features are not likely to be a response to excess calcium. Septa therefore are either adaptive, providing 1). protection against infection/parasitic infestation of the animal when the apex is broken or 2). structural support against crushing. Alternatively septa may be spandrels, the result of; 3). incomplete filling of the apex when it is filled to provide balast or protection or 4). accidental by-products of internal thickening of the shell. It is possible that septa are not homologous among all taxa and that different explanations may be represented in different taxa.

For turritellids, septa can occur in high numbers and in shells with substantial apical filling (e.g. T. robusta, Figure 1D), suggesting they are not always adaptations to the loss of the apex, although they may be exapted for this purpose. An observed trend towards higher numbers of septal insertion in taxa with more substantial shell thickening (excepting whorls that are completely filled) indicates that in these organisms dome-shaped septa may be spandrels.

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