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The morpho-mechanical basis of ammonite form

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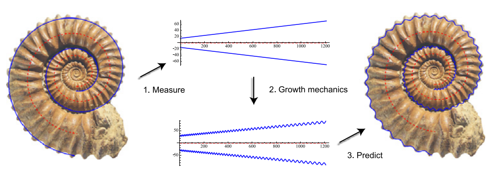
HIGHLIGHTS

- We develop a mechanical model for the formation of ribs in ammonite shells.
- The model is based on fundamental physical principles of the shell growth process.
- All major characteristics of ammonite form and evolutionary trends are captured.
- This work presents the first quantitative model of shell ribbing pattern.
- Enables new understanding of ammonites evolution in evo devo perspective.

GRAPHICAL ABSTRACT



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ABSTRACT

Ammonites are a group of extinct cephalopods that garner tremendous interest over a range of scientific fields and have been a paradigm for biochronology, palaeobiology, and evolutionary theories. Their defining feature is the spiral geometry and ribbing pattern through which palaeontologists infer phylogenetic relationships and evolutionary trends. Here, we develop a morpho-mechanical model for ammonite morphogenesis. While a wealth of observations have been compiled on ammonite form, and several functional interpretations may be found, this study presents the first quantitative model to explain rib formation. Our approach, based on fundamental principles of growth and mechanics, gives a natural explanation for the morphogenesis and diversity of ribs, uncovers intrinsic laws linking ribbing and shell geometry, and provides new opportunities to interpret ammonites' and other mollusks' evolution.

1. Introduction

Ammonites are an iconic group of extinct cephalopods. Characterised by a nearly perfect logarithmic spiral shell with regular ribbing pattern, the mathematical beauty of their form has made them a centrepiece of artistic wonder while their abundance, diversity, and high evolution rate make them a paradigm for biochronology, palaeobiology, and evolutionary theories (Gould, 2002; Eldredge, 1996; Brayard et al., 2009). The two fundamental morphological descriptors of ammonite shells are their coiling and the ribbing pattern known as commarginal ornamentation. This pattern is almost universally present in ammonites and forms along the direction of the accreted shell, appearing as an oscillation in the expansion of the shell cross-section (Fig. 1(a)). However, few authors have considered shell morphogenesis, and no previously proposed models for ammonite ribs (Checa, 1994; Hammer, 2000; Meinhardt, 2009) have produced quantitative and verifiable predictions. The starting point of our study is the notion that mechanical forces generated during growth drive tissue-scale morphogenesis and thus shape developing organisms (Hutson and Ma, 2008; Chirat et al., 2013).

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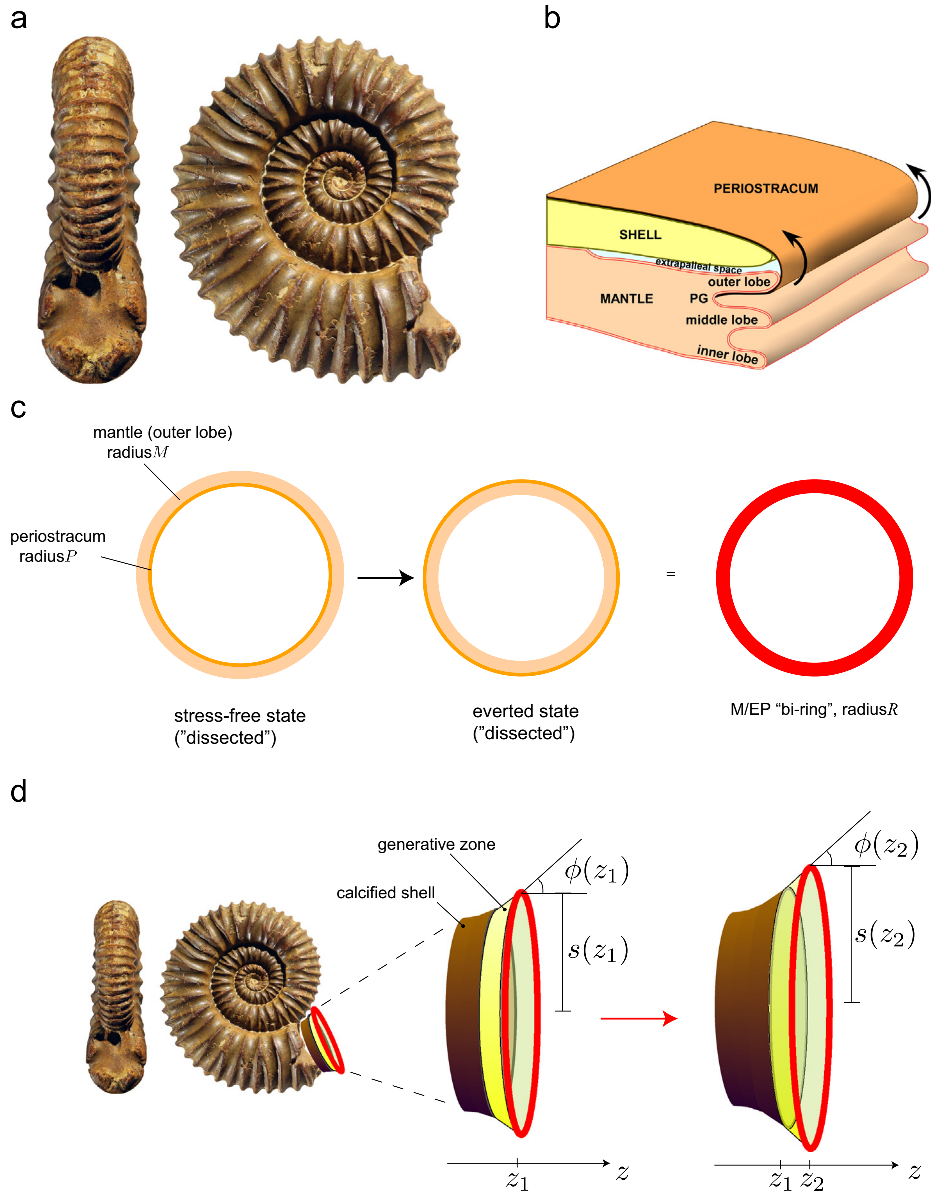

Fig. 1. Ammonite ribs and model setup. (a) Commarginal ribs in *Peltoceras schroederi*. (b) Schematic of mantle/periostracum anatomy and eversion of periostracum (PG: periostracal groove). (c) The mantle and everted periostracum (M/EP) act mechanically as a single elastic bi-ring with radius $R(z)$ when dissected from the shell. (d) Primary variables for model. The shell has radius s and orientation angle ϕ with respect to the growth axis z.

By focussing on the mechanical structure of the shell secreting system, we propose a model for ammonite morphogenesis that captures all basic features of morphological diversity and phenomenological laws observed in ammonite shell form and uncovers an intrinsic link between the shell expansion and the ribbing pattern. Many authors have argued about the functions of this ornamentation, as related to buoyancy control, camouflage, hydrodynamic efficiency, or strengthening the shell against predators (Chamberlain and Westermann, 1976; Ward, 1981; Westermann, 1996; Cowen et al., 1973; Vermeij, 1993). While these functionalist interpretations have been central within evolutionary theories, our theory provides the first predictive and *quantitative* mechanistic explanation of their form and presents new opportunities for interpreting the evolution of their shell in an evolutionary developmental biology perspective.

All modern mollusk shells are composed of an outer organic layer, called periostracum, and underlying calcified layers, all being secreted by the mantle, a thin elastic membrane lining the inner shell surface (Simkiss and Wilbur, 1989) (Fig. 1(b)). During growth, the mantle moves forward slightly beyond the calcified shell edge while secreting the periostracum, which isolates the extrapallial fluid from which the calcified shell is precipitated (Saleuddin and Petit, 1983). The periostracum is secreted in the periostracal groove, between the outer and middle mantle lobes, and is extruded between the two mantle lobes, where a stiffening process of sclerotisation takes place (Waite, 1983). It is subsequently turned inside out around the outer mantle lobe, and reaches its external position where no further thickening occurs. When calcification occurs, the periostracum becomes fixed on the outer shell surface. The unfixed periostracum surrounds the outer mantle lobe and is attached at both extremities along the calcified shell edge and inside the periostracal groove. The shape of the generative zone, namely the stiff periostracum surrounding the softer outer mantle lobe, is therefore incrementally recorded and fixed in the calcified shell during growth. In turn, the calcified shell edge acts as a template for the new growth increment. This basic structure of the mantle edge–periostracum complex has been also described in *Nautilus* (Westermann et al., 2005) and it is