Physics determined ammonite shell shape

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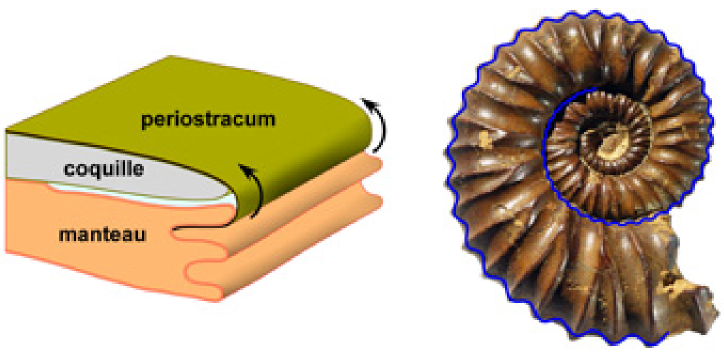

Left: Diagram representing the shell's production area. The mantle secretes calcified shell and periostracum, an organic layer that covers the outside of the shell. It is there that mechanical interactions spontaneously generate oscillations that produce the ribs. Right: A theoretical prediction (blue line) produced by the model is superimposed on an ammonite dating from the Jurassic. Credit: Derek Moulton, Alain Goriely and Régis Chirat

Ammonites are a group of extinct cephalopod mollusks with ribbed spiral shells. They are exceptionally diverse and well known to fossil lovers. Régis Chirat, researcher at the Laboratoire de Géologie de Lyon: Terre, Planètes et Environnement (CNRS/Université Claude Bernard Lyon 1/ENS de Lyon), and two colleagues from the Mathematical Institute at the University of Oxford have developed the first biomechanical model explaining how these shells form and why they are so diverse. Their approach provides new paths for interpreting the evolution of ammonites and nautili, their smooth-shelled distant "cousins" that still populate the Indian and Pacific oceans. This work has just been published on the website of the *Journal of Theoretical Biology*.

The shape of living organisms evolves over time. The questions raised by this transformation have led to the emergence of theories of evolution. To understand how biological shapes change over a geological time scale , researchers have recently begun to investigate how they are generated during an individual's development and growth: this is known as morphogenesis. Due to the exceptional diversity of their shell shapes and patterns (particularly the ribs), ammonites have been widely studied from the point of view of evolution but the mechanisms underlying the coiled spirals were unknown until now. Researchers therefore attempted to elucidate the evolution of these shapes without knowing how they had emerged.

Régis Chirat and his team have developed a model that explains the morphogenesis of these shells. By using mathematical equations to describe how the shell is secreted by ammonite and grows, they have demonstrated the existence of mechanical forces specific to developing mollusks. These forces depend on the physical properties of the biological tissues and on the geometry of the shell. They cause mechanical oscillations at the edge of the shell that generate ribs, a sort of ornamental pattern on the spiral.

By examining various fossil specimens in light of the simulations produced by the model, the researchers observed that the latter can predict the number and shape of ribs in several ammonites. The model shows that the ornamentation of the shell evolves as a function of variables such as tissue elasticity and shell expansion rate (the rate at which the diameter of the opening increases with each spiral coil).

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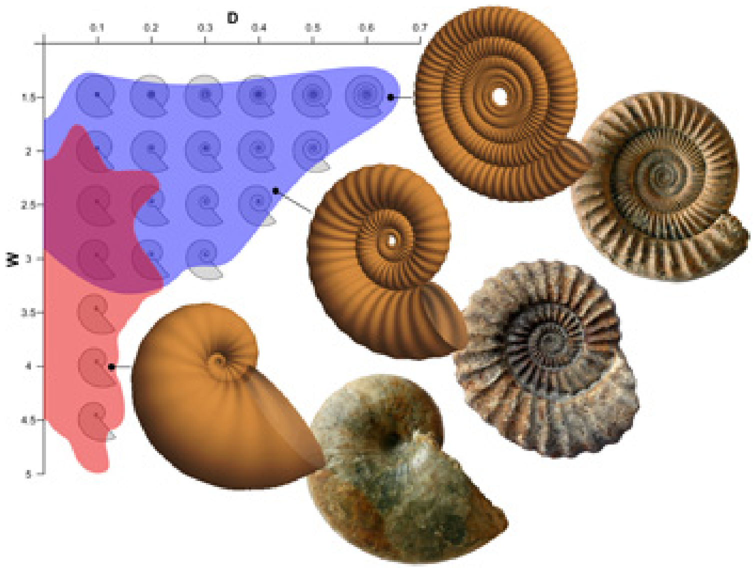

The mechanical model predicts the correlations observed between rib frequency and amplitude and the shell's general shape in ammonites (blue morphological space) and nautili (red morphological space) The 3D-views produced by the model are juxtaposed with fossil specimens, ammonites and nautili, that have a similar shape. The ribs tend to disappear for the broadly open shell shapes that have characterized nautili for almost 200 million years. W = expansion rate D = coiling tightness. Credit: Derek Moulton, Alain Goriely and Régis Chirat

By providing a biophysical explanation for how these ornamentations form, this theoretical approach explains the diversity existing within and between species. It thus opens new perspectives for the study of the morphological evolution of ammonites, which seems to be largely governed by mechanical and geometric constraints. This new tool also sheds light on an old mystery. For almost 200 million years, the shells of nautili, distant "cousins" of ammonites, have remained essentially smooth and free of distinctive ornamentation. The model shows that having maintained this shell shape does not mean that nautili - wrongly referred to as "living fossils" - have not evolved, but is due to a high expansion rate, leading to the formation of smooth shells that are difficult to distinguish from one another.

More generally, this work highlights the value of studying the physical bases of biological development: understanding the "construction rules" underlying the morphological diversity of organisms makes it possible to partially predict how their shape evolves.

More information: "The morpho-mechanical basis of ammonite form;" D.E. Moulton, A. Goriely, R. Chirat; *Journal of Theoretical Biology*; Vol. 364; January 7, 2015 (date for paper publication; article already available online). DOI: 10.1016/j.jtbi.2014.09.021

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