

## CHAMBERED CEPHALOPOD SHELLS, BUOYANCY, STRUCTURE, AND DECOUPLING: HISTORY AND RED HERRINGS

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Hooke articulated the first vision of the buoyancy function performed by the chambered shells of cephalopods. In the 17th century, he argued that the shell went up and down in the water column as pressurized gas filled and emptied the chambers. Although some prescient 19th and early 20th century workers took exception to this view, it was not until the 1960s that Hooke's gas-pressure mechanism was shown to be incorrect. Experimental work by Denton and Gilpin-Brown demonstrated that chambered cephalopod shells are emptied osmotically, generating a partial vacuum in the chambers. Hooke's argument, that cephalopods changed their buoyancy on a daily basis, is not likely to have been true either. Ward (1982) argued cogently that the rate of fluid removal from the chambers, and hence the rate of buoyancy change, is proportional to siphuncular area. In ammonoids the siphuncular area is too small to support rapid change in buoyancy. Thus, ammonoids probably maintained neutral buoyancy throughout life. Despite the evidence for an osmotic pump and low pressures in the chambers, text books continue to refer to gas pressure in cephalopod shells.

Decoupling, the separation of fluid in the chambers from the siphuncle, was thought to shut off the osmotic pump and allow cephalopods to descend below 240m, the osmotic pressure difference between fresh and salt water, without flooding of the chambers. Denton and Gilpin-Brown advanced this concept of decoupling because they did not know that the siphuncle could concentrate salts permitting pumping well beyond the osmotic difference between fresh and salt water. It is now clear that the decoupling explanation was not necessary, it would not have shut off the osmotic pump in the fashion envisioned, and there is no evidence of decoupled water in modern cephalopods. Despite the absence of any supporting evidence, workers continue to invoke decoupling to explain aspects of ammonoid morphology that they find inexplicable on other functional grounds.

As a consequence of the absence of pressurized gas in the chambers, the chambered cephalopod shell must support large hydrostatic forces when the animal is submerged. Workers aware of this structural problem have attempted to explain cephalopod shell form in the context of this hydrostatic load. However, two distinct hydrostatic loading conditions occur sequentially in the chamber formation cycle. Forces operate through the body chamber generating a hydrostatic load on the surface of the last formed septum a phenomenon discussed by Pfaff in 1911. The other septa do not support a load on their surface, but are thought to support loads transmitted from the phragmocone wall an issue associated with Spath's 1919 work. Consequently, the form of septa and sutures in cephalopods cannot be an optimal solution to single mechanical function, but must successfully satisfy these two distinct loading conditions, as well as other selective, and historical constraints on shell form. In 1836 Buckland argued that support of hydrostatic load required a functional relationship between sutural complexity and shell shape. Subsequently, it has been noted that sutural complexity evolves, often iteratively, in response to changes in shell shape. Despite these previous observations it has recently been popular to interpret the function of sutural complexity in terms of a single number without consideration of, the shape of the shell in question, the distribution of complexity along the suture, or the placement of the taxa in an evolutionary context. Such approaches are not likely to resolve issues pertaining to the evolution of sutural function.