Chambered Cephalopod Shells, Buoyancy, Structure and Decoupling: History and Red Herrings

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PALAIOS, 1996, V. 11, p. 610–614

The chambered shells of cephalopods have inspired scientists for over 3 centuries. However some of these imaginative interpretations, of both historical and more recent vintage, have proved to be “red herrings”, distracting, or having the potential to distract, researchers from more fruitful avenues of inquiry. The gas pressure hypothesis of Hooke is the original granddaddy of the cephalopodous red herrings. More modern red herrings include the decoupling hypothesis originated by Denton and Gilpin-Brown (1966), the use of historical straw men by Saunders (1995) and the cartesian diver hypothesis of Seilacher and LaBarbera (1995). These last two, in that they are relatively new, have yet to significantly mislead. Herein this list will be explored in order of publication, the gas pressure hypothesis first and the cartesian diver notion last.

GAS PRESSURE

Hooke presented scientific work before the Royal Society on a regular basis in keeping with his contract as secretary and demonstrator of the society. In meeting this regular deadline he advanced the science of Microscopy and discovered the law of springs- the regular behavior of most materials- that bears his name. Giving the requirement for constant productivity his role of demonstrator entailed, it was perhaps inevitable that Hooke should turn to the fascinating subject of the chambered shell of cephalopods. His discourse presented to the Royal Society on the 16th of December in 1685 treated this subject:

...for the solution of such a Phaenomenon as this, of floating and sinking of Nautilus. ... It seem’d indeed, very strange, how that Creature could so, at his Will fill, and empty, the Cavities of the Shell with Water... how (when there, at such a Distance from the Air) he could evacuate the Water, and fill the Cavities with Air, that was difficult to comprehend, especially being under so great a Pressure of Water: But if Nature had furnish’d him with a Faculty of producing and artificial Air, then the riddle would be quickly unfolded. I found, therefore, that by Art it was possible to make an artificial air... which might have as much power of expansion as might counterpoise, nay, nay out-power both the pressure of the Air... and also the Water too, though 100 times greater than that of the Air. It will be a difficult matter... for me to prove that the Nautili have such an owner for that I could never yet get Sight of the Fish that inhabits those Shells. [Derham 1726, pp. 309–310]

Thus was born the concept of gas pressure, the concept that the chambers are emptied of water (cameral liquid) much as a modern submarine empties its rigid tanks, through the use of compressed gas. Hooke was incorrect, there is no gas generating mechanism in cephalopods. However, the gas pressure explanation held sway for over 250 years. It misled all but a few skeptics (including Owen, Buckland, Pfaff, to a certain extent Spath, and Westermann; see Jacobs, 1992) keeping the hounds of science off the scent for a quarter of a millennium- a red herring of considerable impact.

Owen in 1829 obtained the first Nautilus soft parts preserved in spirits available to a western scientist. Thus Owen was the first to get a “Sight of the Fish” that Hooke laments not having. His dissection, reported in his monograph on the Pearly Nautilus in 1832, called into question the gas pressure interpretation. In Owen’s view the siphuncular artery was insufficient to generate gas:

...it must be admitted... that the size of the artery seems barely adequate to support the vitality of the membrane much less to effect a secretion (of gas), for which in fish an ample gland appears to be indispensable. [Owen, 1832, p.47]

In the 1832 monograph, and again in 1878, Owen advocates an experimental program that would resolve the gas pressure issue:

It would be advisable, in the event of another fortunate capture of the Nautilus, to lay open the chambers under water, when the presence of gas in any of them would be ascertained... [Owen, 1832, p.47].

In fact, the experimental program advocated by Owen was not carried out until the work of Denton and Gilpin-Brown: first on Sepia (Denton and Gilpin-Brown, 1961a, b, c; Denton et al., 1961); then on Nautilus (Denton and Gilpin-Brown, 1966); and lastly on Spirula (Denton et al., 1967). These researchers did acknowledge Owen as a source of inspiration for the research they conducted, and their efforts took place over 125 years after he first suggested the experimental program. This should give us pause as to the directness of scientific progress and the dangers in not understanding the history of one’s discipline.
Despite the simplicity of Denton and Gilpin-Brown’s observations, they led to significant advances in cephalopod biology, including rejection of the long standing gas pressure model. Their observations and conclusions can be briefly summarized as follows. Observations of Denton and Gilpin-Brown:

1. Fluid flows into the shell, gas does not burst out (the chambers are in a partial vacuum).
2. The fluid in the chambers is less salty than sea water.

Conclusions:

1. An osmotic pump operates in cephalopods removing water from the chambers without active changes in gas pressure.
2. The shell supports the hydrostatic load of the overlying water and shell structures must be of sufficient strength to resist implosion.

DECOUPLING

Even as Denton and Gilpin-Brown (1966) advanced our understanding of cephalopod shell function, they unwittingly introduced another “red herring” that has confounded cephalopod work for a generation. This is the concept of decoupling. Denton and Gilpin-Brown were not the first to consider an osmotic pump in cephalopods—Bruun (1943, 1950) considered the possibility of an osmotic pump in the internal chambered shell of *Spirula*. However, living *Spirula* is nearly always recovered from considerable depth, often in excess of 1000 meters. Bruun felt that this was too deep for an osmotic pump to function and, with some regret, rejected the osmotic pumping mechanism. In an osmotic pump the attraction of water to the salts in solution, and the ability of the pump to work against pressure, is a function of the difference in ionic concentration between two solutions. Given a solution of fresh water and sea water the concentration difference is only sufficient to pump against 250 meters of water pressure. Denton and Gilpin-Brown followed Bruun’s argument and similarly felt that an osmotic pump could only function down to 250 meters, otherwise, they felt, water would be forced back through the pump. To reconcile this conflict (between the observed habitat depth of modern cephalopods and the apparent limit to pumping imposed by the difference in salt concentration between fresh and sea water) Denton and Gilpin-Brown (1966) invented the concept of decoupling. The notion of decoupling advanced by Denton and Gilpin-Brown involved a mechanism, such as a change in orientation of the shell, that isolated fluids inside the chamber preventing them from contacting the siphuncle. This isolation from contact with the cameral liquid was presumed to “decouple” the pump, preventing reverse flow from the siphuncle to the chamber when the external pressure was in excess of the 250 meter osmotic pressure difference. However, there is no obvious reason to think that change in contact with fluid on the inside of the chamber would materially change the operation of the osmotic pump.

In fact, this notion of decoupling is a fallacy based on the perceived need to reconcile conflicting data. Subsequent work has documented that there is no conflict of the sort envisioned by Denton and Gilpin-Brown, between habitat depth and an operational osmotic pump. Starting with Diamond and Bossert (1968) it became apparent that salts could be concentrated in minute intracellular channels, permitting an osmotic pump to operate at depths greater than 250 meters. Greenwald et al. (1982) conducted an ultrastructural study of the *Nautilus* siphuncle confirming that all the features of a hyperosmotic pump are present. Thus the concentration of salt in the sea no longer can be viewed as providing a limit to the osmotic pumping function.

Depth limits to evacuation of cephalopod shells may ultimately involve aspects of ultrastructural design, the size of the siphuncle, and/or the energy demands of pumping at great depth. Thus the concept of decoupling associated with the osmotic limits on pumping as originally advocated by Denton and Gilpin-Brown was convincingly routed in 1982. Nevertheless, workers interested in the function of fossil cephalopod morphology continue to invoke decoupling to explain the features of the shell that they observe. Decoupling is usually invoked in the face of novel structures (Weischat and Bandel, 1991), or the perceived failure of other functional explanations (Saunders, 1995; Saunders and Work, 1996). However, all such references to decoupling invoke an explanation that has been refuted in its original form, a fact not lost on Denton and Gilpin-Brown (1973) themselves who referred to the work of Diamond and Bossert (1968) as a possible alternative explanation to decoupling. Thus decoupling is an historical red herring that lives on to confound our understanding of cephalopod shell function. Any reference to decoupling in the current cephalopod literature must be carefully scrutinized to determine the intended meaning of the author.

HISTORICAL STRAW MEN

Saunders (1995) has recently presented evidence that Paleozoic ammonoid suture complexity does not vary inversely with thickness of the shell or septum. He argues that this is a test of a general structural hypothesis, which he refers to as the “Buckland Hypothesis”. There are two misleading aspects to Saunders’s argument. First, he implies that a concept known as the “Buckland Hypothesis” is current among cephalopod paleobiologists. Second, he implies that Buckland predicted an inverse relationship between sutural complexity and shell, or septal, thickness. There is no such generally known hypothesis called the “Buckland Hypothesis”, and Buckland (1836) did not predict the relationship Saunders (1985) explored. By invoking history in the fashion he does, Saunders connects his own hypothesis to the research tradition of other cephalopod workers exploring functional questions. Thus he casts his result as a general test of the whole discipline, but Saunders
(1995) tests his own hypothesis, a hypothesis never seriously considered by other cephalopod workers.

In addition to my own (Jacobs, 1990, 1992; Jacobs and Chamberlain, 1996) and Saunders's (1995) citations of Buckland, there are two additional citations of Buckland's contribution to the Bridgewater Treatise by cephalopod workers documented in the Science Citation Index. Denton and Gilpin-Brown (1973) cite Buckland as regards his ideas of siphuncular expansion and contraction to change density, not in terms of his shell structure ideas. Denton (1961) discusses the beauty of God's Creation evidence in ammonite shells, not the functional or adaptive aspects of Buckland's arguments. When other cephalopod workers refer to earlier ideas involving shell function they most frequently allude to the "Pfaff" (1911) problem, which involves support of the hydrostatic load born through the body chamber and acting on the last formed septum, or the ideas of Spath (1919) which can be thought to involve the hydrostatic load born on the outside of the phragmocone and potentially supported by the complex suture (Westermann, 1971; Jacobs, 1992). Although Westermann (pers. comm.) was aware of Buckland's work, he and other workers did not cite him. Thus the "Buckland hypothesis" as construed by Saunders (1995) has not been current, nor is it representative of the ideas of workers who have recently examined the functional morphology of modern or fossil cephalopod shells.

The Rev. Buckland using the pre-Darwinian adaptationist paradigm of Paley generated a number of insights into fossils and the fossil record that parallel modern interpretations (Jacobs, 1992). He made a general Paleyean claim of perfect adaptation of lightness and strength of shell construction in ammonites. Sutural "sinuosity", as well as other aspects of the cephalopod shell contributed to this general argument. However, Buckland did not make any precise prediction about inverse relationships between sutural complexity and shell, or septal thickness. In fact, Buckland explicitly emphasized the relationship between sutural complexity and shell shape, not shell or septal thickness.

Thus on the back or keel . . . where the shell is narrow, and the strength of its arch greatest, the intervals between the septa are also greatest, and their sinuosities comparatively distant; but as soon as on the flattened sides of the same shell . . . assumes a form that offers less resistance to external pressure the foliations of the edges of the transverse plates approximate more closely; as on the flatter forms of gothic roof . . . [Buckland, 1836, p. 348].

Thus Buckland's most precise "hypothesis" pertaining to the structural function of cephalopod shells bears little resemblance to what Saunders (1995) represents as the "Buckland Hypothesis".

The relationship between sutural proximity and shell curvature first observed in ammonoids by Buckland, is also an element of subsequent work. Checa (1966) and Westermann (1971, 1973) both observe that sutural elements are introduced in the flank region as lineages evolve more compressed involute forms with flatter flanks. In 1990 I expressly tested the notion that shell curvature was inversely related to the proximity of sutures as argued by Buckland (Jacobs, 1990). In that paper I demonstrated that there was a strong statistically significant inverse relationship between the spacing between the size of the vaults or spaces in the complexly associated sutures of Baculites. This result quantitatively supported Buckland's argument of a relationship between sutural "approximation" and shell curvature. As Buckland (1836), and the previously cited workers note, this relationship is also evident in a number of coiled cephalopods, and, evidently, responds to evolutionary change in shell shape. However, the extent of this relationship in fossil shelled cephalopods, such as the Paleozoic ammonoids has yet to be determined. The inception of this relationship between shell shape and sutural complexity has also not been assessed in the context of evolving lineages.

Saunders' (1985) argument, that shell thickness or septal thickness should be inversely related to sutural complexity, has not been previously advocated by Buckland, or cephalopod workers. Other workers may have recognized that other variables are involved making it unclear, at least a priori, whether a positive or negative relationship should be expected. For example, ammonoids living at depth might be expected to have both thicker shells and more complex sutures, as both could be conceived of as adding strength to the shell. This would lead to an expectation of positive correlation between thickness and sutural complexity, rather than the negative one anticipated by Saunders (1995). Additional, potentially explanatory, factors include the issues of shell shape advanced by Buckland (1836) and myself (Jacobs, 1990) as well as issues of lineage history. Thus the situation is complex and requires multivariate analysis of a suite of both sutural and shell characters as well as explicit tests of precise functional hypotheses. Saunders has been very active recently collecting much potentially very useful data on Paleozoic ammonoid morphology (Saunders 1995; Saunders and Work 1996). Hopefully these data can be brought to bear in testing the ideas of shell function developed by other cephalopod workers.

**CARTESIAN DIVER**

Seilacher and LaBarbera (1995) recently advocated a cartesian diver buoyancy compensation mechanism in the soft tissues of ammonites. They envision a muscular diaphragm enclosing a bubble of compressed gas at the end of the body chamber of ammonoids. The volume of this bubble could then be adjusted by muscle to change buoyancy. This mechanism, if it were to exist, would require the de novo evolution of two morphologic structures, a gas generating mechanism, and the muscular contraction apparatus. These deve-
opments would be startling in any animal. Speculations regarding their presence in fossil cephalopods are especially surprising; cephalopods have already evolved a chambered shell to achieve neutral buoyancy, and this chambered shell is known to operate in the absence of pressurized gas. The cartesian diver argument consists of two parts: 1) a suite of taphonomic observations that are purported to be more easily explained if there were a Cartesian Diver in the unobserved soft tissues of ammonoids; and 2) a set of theoretical calculations purporting to document how a cartesian diver might work in an ammonite.

No direct evidence for the existence of the cartesian diver mechanism is available in the morphology of any cephalopod, living or fossil. References to siphophores notwithstanding, it has yet to be established that a cartesian diver system operates in any metazoan. Thus the Seilacher-LaBarbera argument is very similar in form to Hooke’s gas pressure argument of three centuries earlier (see above), “A mechanical system can operate this way so maybe an organism does as well.” However in Hooke’s case the argument was presented in the absence of information about Nautilus. Unfortunately aspects of Seilacher and LaBarbera’s cartesian diver argument are contraindicated by observed fact or fail in the conceptual/mechanical realm of their own proposal.

1. Observed muscles: No one has observed a band of muscle scars or attachment adjacent to the sutures in ammonite shells as is envisioned in Seilacher and LaBarbera’s work. Small pairs of muscle scars are observed dorsally and ventrally in ammonoids near the suture. They are not continuous around the shell, but appear to run at a low angle toward the aperture. Such muscles even occur in the heteromorph Baculites (Crick, 1898), an important point in that heteromorphs play a large role in the Seilacher-LaBarbera argument. These muscles are thought to be homologues of the funnel and head retractors of coleoids (Jacobs and Landman, 1993). The observation of these muscle scars appears to preclude the existence of those envisioned in the cartesian diver model.

2. The use of catch muscle in calculations: LaBarbera’s calculations are based on the stresses sustained by the catch muscles and byssal attachment muscles of bivalves. Under isometric contraction conditions catch muscles are able to resist stresses of 1.2 to 1.4 M-Nm⁻². These “isometric” forces were measured in, and pertain only to, muscles that are not actively shortening. However when the cartesian diver rises to its minimum depth of operation the pressure difference between the gas in the vessel and the external pressure is maximal. Against this maximal pressure the muscle must contract dynamically or else the cartesian diver will never be able to sink. Forces generated by muscles in dynamic contraction are substantially less than those measured in isometric contraction.

Muscles also fatigue. A starfish can open a bivalve, not by overpowering the bivalve catch muscle, but by exerting a lower force over a long time period, waiting for the catch muscle to fatigue. Although fatigue in catch muscles occurs more slowly than in other muscles, force does decline over a period of hours and energetic costs of muscle contraction occur throughout contraction (Bauger and Gillis, 1968). In that catch muscles are metabolically active it is not at all clear that a cartesian diver will be energetically more efficient than a slowly swimming neutrally buoyant organism.

These issues would appear to require that the cartesian diver operate at much lower forces than advertised, and probably intermittently as a consequence of fatigue. In addition, LaBarbera’s calculations are based on a hemispherical cap of muscle at the end of the body chamber. In that this chamber constitutes the forming chamber of the shell, septal geometry must constrain morphology and preclude it from being the perfect cap envisioned. Given these factors, muscle contraction-strength, fatigue, and geometry, we must conclude that the Cartesian diver mechanism has not been advocated in an appropriately conservative manner. Thus the vertical depth limits on this particular thought experiment are likely to be at least an order of magnitude less than those published by Seilacher and LaBarbera (1995).

3. Circulatory constraints: Seilacher and LaBarbera assume a blood-vascular rete would be able to supply gas to initiate the pressurized gas chamber. They use analogy to the gas bladder of fish in this regard. However, the gas bladders of fish have roughly the same pressure on the inside as the ambient water pressure. This is not the case in the envisioned system. Again when the organism is at the shallow end of its depth range there will be high pressure inside and low pressure outside of the gas filled muscular chamber. For the rete to function blood must be delivered to the inside of the muscularized bladder where diffusion through a membrane can release it. Thus the pressure inside the bladder will be born directly on the vessels of the rete. If the pressure in the bladder is greater than the pressure in the blood vessels, then the blood vessels associated with the rete will simply collapse and no filling of the bladder will be possible. It is possible to imagine solutions to this problem. Either the rete can operate only near the greatest operational depth where pressures would be more equal, or the organism could develop a high pressure cardiac pump that could generate pressures equal to the pressure in the gas bladder (A high pressure cardiac pump was invoked by Buckland (1836) to dilate the siphuncle in his improbable mechanism of buoyancy adjustment.

Hopefully the above arguments will convince many readers that the cartesian diver mechanism in ammonites is not mechanically plausible. However there are additional philosophic issues at stake. Concepts of function, such as the cartesian diver mechanism, are a joy for the researcher to conceive of, however if not testable they are not scientific. The gas pressure mechanism of Hooke became a red herring not because it was untestable but because
the test, advocated first by Owen, was not performed for a long time. Once the absence of gas pressure was demonstrated in modern cephalopods the inference could then be extended to fossil forms (e.g., Denton and Gilpin-Brown, 1973). Seilacher and LaBarbera claim that there is a “potential weakness” in using the nearest relatives of extinct taxa to constrain hypotheses. However, when preserved evidence of the functional features in question are lacking, as is the case in the cartes- sian diver argument, analogy to modern relatives is the remaining constraint on speculation. Without such phylogenetic constraint all mechanically plausible explanations are equally admissible and untestable.

There are many kinds of red herrings, misuses of history, untestable hypotheses, hypotheses that are accepted without test, concepts that persist out of context. However, I have pursued these colorful fishes long enough. Someone else will have to provide a more complete taxonomy.

ACKNOWLEDGMENTS

I thank Dave Bottjer, Dan Miller, Jenny Schwenke, and Tom Roos for their assistance with the manuscript.

REFERENCES


