Cretaceous Research 88 (2018) 46–54

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Suture line complexity as an adaptation to acceleration changes during ammonoid locomotion

Alexander I. Arkhipkin*

Falkland Islands Fisheries Department, FIPASS, Stanley, FIQQ 1ZZ, Falkland Islands

ARTICLE INFO

Article history:
Received 18 January 2017
Received in revised form
23 October 2017
Accepted in revised form 24 October 2017
Available online 28 October 2017

Keywords:
Ammonoid
Suture line
Propulsive movement
Buoyancy
Life style

ABSTRACT

Ammonoids had a great variety in shape of the suture septal lines in their shells that sparked a plethora of hypotheses about the reasons for their complexity; from strengthening the shell wall against implosion to improvement of muscle attachment onto the septal wall and increased retention of the cameral liquid in the phragmocone chambers. In the present study, simultaneous presence of air and water in the last chambers of the phragmocone and change in acceleration during jet propulsive movement were briefly reviewed. As both water and air were present in the same chamber, periodic alternation of acceleration and deceleration should induce subsequent water displacement ('sloshing') due to inertia. This would periodically displace the centre of gravity of the shell making the movement less stable and energy efficient. Analysis of complexity of the suture shape in the dorsal, flank and ventral sides of the shell chambers suggests yet another hypothesis of the suture line variety. More complex suture line in the flank should decrease the water movement at maximum torque when a chamber is half full of liquid. It was hypothesized that the ammonoids evolved a unique way to obstruct the water displacement in the chambers with their fluted septa acting as 'wave breakers' that dissipate the 'wave' on the boundary between water and air. Animals that moved slowly without sudden changes in acceleration had a simple suture line and were either planktonic or grazing predators cruising with more or less constant speed. Complex sutures in advanced ammonoids indicated their ability to sharply change the velocity of their movement when chasing their prey or escaping from predators.

1. Introduction

One of the unique features of ammonoid shell is a winding and convoluted line of septum attachment (suture) to the inner wall of the phragmocone. During more than 300 million years of evolutionary history, various groups of ammonoids evolved a great variety of septal shapes and suture lines, from relatively simple agoniatitic sutures in the Devonian Anarcestida to complex fluted ammonitic sutures in Jurassic and Cretaceous Ammonitida (Hewitt & Westermann, 1997; Klug & Hoffmann, 2015). Possible functions of the fluted septa and their winding sutures in ammonoids have been a subject of some hot debates and arguments among palaeontologists in the last 180 years. The whole array of hypotheses on the reasons for development of the fluted septa and sutures (Kennedy & Cobban, 1976; Hewitt & Westermann, 1997; Keupp, 2000) may be divided into four main groups.

Buckland (1836) put forward a hypothesis which still remains one of the most popular points of view. He suggested that the fluted septa might support the shell wall from the inside against implosion. The buttressing role of fluted septa was seemingly confirmed by the inverse relationship between curvature of the shell wall and interseptal distance. In some ammonoids including oxyconic *Placenticeras*, laterally compressed heteromorphs such as *Hoploscaphites* and even straight shelled *Baculites*, distances between the septa were largest where the curvature of the shell arch was greatest, whereas at the flattened flanks of the shell the foliated sutures of the adjacent septa were located more closely (Jacobs, 1990, 1996). The 'buttressing hypothesis' would indicate that ammonoid species with more complex foliated sutures had an ability to dive deeper than their counterparts with simpler sutures. However, Saunders (1995) failed to find an inverse relationship between the shell and septum thickness and sutural complexity in his analysis of 49 species of Paleozoic ammonoid genera and concluded that his results did not support the argument about deepwater habitats of species with complex fluted septa. Jacobs (1996) counter-argued that both increased shell thickness and

---

* Fax: +500 27265.
E-mail address: aarkhipkin@fisheries.gov.fk.

https://doi.org/10.1016/j.cretres.2017.10.020

more complex septal fluting might contribute to strengthening of the shell against implosion in deepwater ammonoids. Therefore positive correlation was more likely to occur than a negative, between shell thickness and suture complexity, as anticipated by Saunders (1995).

An analysis of pressure stressed onto various geometries of shell septa showed that the ultimate septum was the weakest part of the ammonoid shell, and a more fluted septum yielded higher stresses on the septal surface than the hemispherical septum (Daniel et al., 1997). Thus, it was hypothesized that the ammonoids with more fluted septa had to be adapted to live in shallow water habitats and those with simpler septa in deeper habitats (Daniel et al., 1997; Saunders et al., 1999). Using the finite-element analysis, Hassan et al. (2002) confirmed that the fluted septum was weaker to hydrostatic stress than the hemispherical septum, but contrary to Daniel et al. (1997) revealed that at the same thickness, septa with more fluted ammonitic sutures were stronger than those with simpler goniatitic sutures. Further, Lemanis et al. (2016b) showed that septa with more complex sutures were able to better resist the point load especially directed along the suture line and hypothesized that suture complexity might be developed as a counter measure to predation. That did not explain though the evolutionary phenomenon when some Jurassic ammonoid groups with ornamented (=more protected) shells had more complex sutures than those with smooth shells (=less protected to predation?) but simpler suture lines (Bayer & McGhee, 1984).

The last fluted septum might provide additional anchoring abilities to the mollusc body in the living chamber, serving as a temporary attachment site to soft tissue of the body that might penetrate to the folds and lobes of the septum (von Buch, 1829; Spath, 1919). Lewy (2002) further suggested that these soft body appendages might stiffen in the corresponding folds of the ultimate septum. He hypothesized that improved anchorage of the body allowed the ammonoids with fluted septa to better withstand the ‘dragging’ forces between the body and shell during movement and to be more ‘aggressive’ in their behaviour. However, stiffening of the soft tissue adjacent to the ultimate septum would make it difficult to unlock the posterior part of the body during its translocation to form a new septum, and soft tissue connection would not be that strong (Klug & Hoffmann, 2015). It has been also suggested that the fluted surface of the ultimate septum might reinforce the major adductor attachment (Seilacher, 1975; Henderson, 1984). However, attachment of these muscles is always to the anterior from the ultimate septum both in modern *Nautilus* and in ammonoids with noticeable adductor muscle scars (Doguzhaeva & Mutvei, 1996; Klug et al., 2008).

Besides the above groups of ‘mechanical’ hypotheses, there are also ‘physiological’ hypotheses that assumed that fluted septa helped to enhance the buoyancy regulation. Mutvei (1967) assumed that the septal surface in ammonoids was covered by the organic conchiolin membrane that provided transport of cameral liquid to the siphuncle for buoyancy regulation. Barskov (1999) suggested that cameral deposits found within the phragmocone chambers may constitute a system of organic membranes in live animals that were capable of absorbing and retaining significant amounts of cameral liquid. Both Weitschat & Bandel (1991) and Saunders (1995) hypothesized that the presence of organic membranes helped to empty and refill the chambers. Based on their findings, it was suggested that ammonoids with more fluted septa were capable of rapidly changing their buoyancy for vertical migrations. This assumption was not supported by recent studies of morphology of phragmocone chambers using micro-computed tomography (Lemanis et al., 2016a). It showed that the ratio between the surface area and volume of a chamber was quite similar in the Paleozoic goniatite *Arnsbergites* with simpler suture lines and Jurassic ammonitid *Kosmoceras* with complex suture line. Due to the fact that all modern cephalopods with calcified phragmocone (*Nautilus*, Sepiida and *Spirula*) have an osmotic mechanism to regulate their buoyancy, these ‘physiological’ hypotheses were strongly criticized and even rejected by many authors (Westermann, 1992; Jacobs, 1996; Hewitt and Westermann, 1997).

Finally, Kulicki (1979) suggested that folding of septal margins should result in the retention of the cameral liquid that should be kept in place by the action of surface tension forces, therefore preventing the overflow of liquid in the chambers. Contradictory, he also indicated that a fluted septal surface with retained liquid in its folds should somehow ‘improve the liquid exchange’ that facilitated vertical migrations of ammonoids. Hewitt and Westermann (2003) further noted that secondary to providing shell strength, the fluted suture line also served as water storage preventing the cameral liquid in the last chambers from ‘slopping about’ which could potentially damage the siphuncle and destabilize the movement in large ammonoids such as *Lytoceras*. Whilst reviewing functions of the fluted septa in ammonoids, Klug & Hoffmann (2015) presented eight additional hypotheses which were to a certain degree related to one of the four major groups shown above.

In the present study, yet another hypothesis on the reasons for suture line variety in ammonoids is suggested, addressing an unresolved question about ‘a myriad of patterns’ in suture geometry in ammonoids that seems to evolve largely independently of shell morphology (Saunders, 1995). It is based on peculiarities in the movement of recent cephalopods with an external shell (*Nautilus*) as well as coleoids with internal phragmocones, as advised by Jacobs & Landman (1993). Mechanics of movement of the cameral liquid in the last chambers of the phragmocone has been analyzed, taking into account the acceleration change during propulsive movement of the animal. Particular attention has been paid to possible shift of the center of gravity during displacement of various quantities of cameral liquid within the chambers. Finally, the movement of the boundary between the cameral liquid and air at different liquid quantities has been related to the complexity of suture line shapes in the dorsal and ventral parts of the shell as well as the flanks between them.

2. Propulsive movement – alternation of acceleration and deceleration

Practically nothing is known about soft parts of ammonoid bodies, as fossil shells show hardly any traces of the mantle and funnel (hyponome) musculature (Mironenko, 2015). Their modes of locomotion and swimming are mostly assumed to be similar to those of *Nautilus*, the only survivor of ectocochliate cephalopods (Jacobs & Chamberlain, 1996; Naglik et al., 2015). Modern *Nautilus* has two types of propulsive movement. “Piston jet propulsion” involves the movement of the head down into the shell aperture by the massive head retractor muscles, then displacing water from the mantle cavity which consists of about 15% of the total body volume. The water jet is directed by the funnel formed by two overlapping muscle folds (hyponome), hanging down from either side of the head. There is a flap valve inside the funnel preventing water being drawn back into the mantle cavity. This type of jet propulsion is mainly used as an escape mechanism from a predator (Wells & O'Dor, 1991). The second type of propulsion, peristaltic jet propulsion is produced by the hyponome itself for respiration and cruising. Two large funnel folds move peristaltically and press water forward and down through the gills and out through the spout. Contractions of the funnel folds are timed providing an almost continuous flow of water which produces the jet that slowly drives the animal backwards at a speed of few cm/s (O'Dor & Webber, 1991).