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## Buoyancy control and growth rates in ammonoids: new preliminary remarks about an old Red Herring\*

by

Jean GUEX<sup>1</sup>

*Abstract*—GUEX J., 2006. Buoyancy control and growth rates in ammonoids: new preliminary remarks about an old Red Herring. *Bull. Soc. vaud. Sc. nat.* 90.1: 41-45. Ammonoid preseptal cavity has been known since a long time and often interpreted as a possible tool for buoyancy control by these animals. This possibility was firmly rejected by D.K. Jacobs (1996) who considered the “cartesian diver” hypothesis as a “Red Herring”. The present paper proposes a re-evaluation of this problem. The relationships between the shell geometry, septal spacing and growth rate of the ammonoids are also discussed herein.

*Keywords*: Buoyancy control, Ammonoids, growth rates, preseptal cavity.

*Résumé*: GUEX J., 2006. Contrôle de la flottaison et taux de croissance chez les ammonoïdés: nouvelles remarques préliminaires sur un «old Red Herring». *Bull. Soc. vaud. Sc. nat.* 90.1: 41-45.

La cavité préseptale des ammonoïdés a été reconnue depuis longtemps et souvent interprétée comme un système de contrôle de la flottaison chez ces animaux. Cette possibilité a été fermement réfutée par D.K. Jacob (1966) qui a considéré le «plongeur cartésien» comme un «Red Herring». Le présent article propose un réexamen de ce problème. Les relations entre la géométrie de la coquille, l'espacement interseptal et le taux de croissance des ammonoïdés sont aussi discutés ici.

*Mots clés*: Régulation de densité, Ammonoïdés, vitesses de croissance, cavité préseptale.

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## INTRODUCTION

Since the publication of Lehmann's fundamental book on ammonoid paleobiology (1976), it is generally admitted that ammonites are biologically much closer to the dibranchiate than to the tetrabranchiate cephalopods. However, we think that the phragmocone of both groups must have been working in a quite similar way. The phragmocone of these ectocochleate cephalopods has two main functions. The first is obviously to serve as a buoyancy apparatus. This necessitates a partial or complete emptying of the residual liquid filling the last completed chambers. We should recall that the osmolarity of this liquid is the same as that of seawater. Extracting it requires an active transport of the  $\text{Na}^+$  and  $\text{Cl}^-$  ions through the siphonal epithelium (DENTON and GILPIN-BROWN 1966; GUEX and RAKUS 1971). This active transfer results in a reduction of the residual liquid salinity which can then leave the chamber passively by simple osmosis. Since the beginning of the 80's it has been clear that nautiloids can also inject liquid into their chambers. This liquid has indeed a high osmolarity and there is a positive correlation between the global density of the extant *Nautilus* and the osmolarity of the residual liquid contained in the last completed chamber of the phragmocone (GUEX 1980). This correlation proves the reversibility of the pumping of the liquid by the siphonal epithelium, a fact experimentally demonstrated by WARD and GREENWALD in 1982. The first goal of the present paper is to show that some ammonites were probably able to continue increasing the size of their shell, even though the phragmocone had ceased its own growth and was empty of any residual liquid, thus restraining its potential use as a density regulator. In the next section, we will briefly discuss the relationships between the growth rate, septal spacing and geometry of ammonite shells.

## THE PRESEPTAL CAVITY: AN OLD RED HERRING

In 1968, Jordan published very important observations on the soft part imprints preserved on internal molds of adult ammonites, located in the posterior part of the living chambers. In this paper, Jordan recognised three types of imprints (Fig.1).

- 1) Very strong dorsal paired structures secreted for permanent muscular attachment.
- 2) A ventral and lunule-like imprint representing the attachment of the siphuncle inside the body-chamber. Note that such an extension of the siphuncle inside the body-chamber does not exist in the *Nautilus*.
- 3) A lateral imprint representing the posterior termination of the mantle adhering to the shell. Jordan called this imprint "Haftband-Struktur" and we

will use his original terminology in the present report. This structure was left by the membrane determining a preseptal cavity between the last septum and the part of the animal lying deepest within its body chamber. The imprint is strongly developed in specimens where the phragmocone has finished its growth. Note that the end of the growth of adult ammonite phragmocones is marked by septal approximation and by the presence, on the internal mold, of strong imprints of the postero-dorsal muscles. At a time when the existence of a preseptal cavity recognizable thanks to Haftband-Struktur was still unknown, MEIGEN (1870) and SCHMIDT (1925) supposed that *Nautilus* were able to secrete or absorb a preseptal gas, thus enabling them to control the animal's density - like a fish's swim-bladder. BIDDER (1962) demonstrated that such a mechanism did not exist in *Nautilus*. More recently, SEILACHER and LABARBERA (1995) took up on Schmidt's ideas (*loc. cit.*). These have been firmly rejected by JACOBS (1996) and KRÖGER (2002). Note in passing that Seilacher and Labarbera did not seem to have been aware of Jordan's 1968 publication. Contrary to Jacobs and Kröger, we think that the existence of a preseptal cavity within the ammonite's definitively terminated phragmocones is undisputable. It is certainly possible that the function of the cavity was to allow adult ammonites to continue to increase the size of their body-chamber, even if the phragmocone did not contain any more residual liquid (i.e. could not be extracted to compensate the excess of weight). At this stage of development, the adhesion of the posterior part of the mantle to the septum was not necessary and it is not unreasonable to think that gas could passively diffuse into the preseptal cavity through the siphonal extension located within the body-chamber, thus increasing the buoyancy of the ammonite. This could allow them to keep a global density equal (or lower) to that of seawater, the shelly weight excess being compensated by the mechanism which is discussed here, without invoking the existence of a "gas gland" or of a gas generating mechanism, an idea which was rightly rejected by JACOBS (1996).

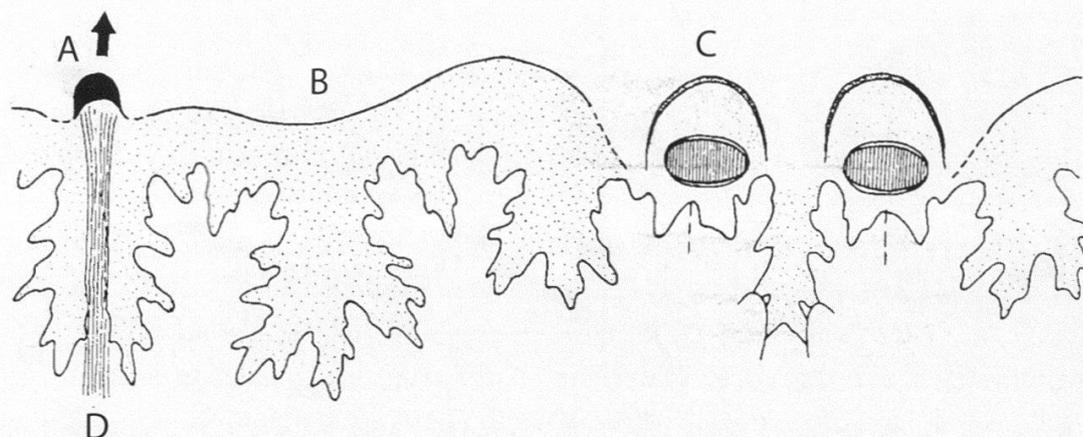


Figure 1.— A) Attachment of the siphuncle. B) Haftband-Struktur. C) Postero-dorsal muscle scars. D) Siphuncle. (From RAKUS 1978).

## SEPTAL SPACING, GROWTH RATE, AND GEOMETRY OF AMMONITE SHELLS

The relative growth rate of ammonites are often evaluated by means of the septal spacings observed in their phragmocone. In general, the author's use the septal approximation, marking the end of the phragmocone's growth, as a proxy to conclude that slow growing ammonites have approximated septa and conversely, that those with a rapid growth have distant septa. In a recent work, we contradicted this widely held opinion. We noted that septal spacing is, on one hand, a function of the complexity and lateral amplitude of the suture line, and, on the other hand, a function of the global weight increase of the ammonite, necessary to compensate the loss of buoyancy. For these reasons we concluded that septal spacing is not a reliable measurement of the growth rate of these organisms (GUEX 1999).

Two criteria suggest that evolute forms have a rapid growth whereas involute forms are slow growing. The first is obvious. At equal growth rate of the tissues, the longitudinal increase of an ammonite body chamber is much more rapid in an evolute form than in an involute one. Our second criteria is indirect. It is also well established that evolute ammonites proliferate during environmental stress episodes (GUEX 2005), which are well-known to be favorable to rapidly growing organisms. As an example we can use again the case of some Middle Liassic Liparoceratidae (*Androgynoceras* in figure 2) where juvenile specimens have a quasi-serpenticone (*Aegoceras*-like) geometry followed by a relatively involute (*Liparoceras*-like) geometry. In this group, the juvenile and fast growing evolute stage has more closely spaced septa than the adult stage of *Liparoceras*-type. The present considerations obviously do not intend to say that widely spaced septa are an indication of slow growth. Some very evolute forms like the *Arietoceras* illustrated by Jordan (*loc. cit.* Plate 5) have very widely spaced septa, indicating a relatively heavy body chamber.

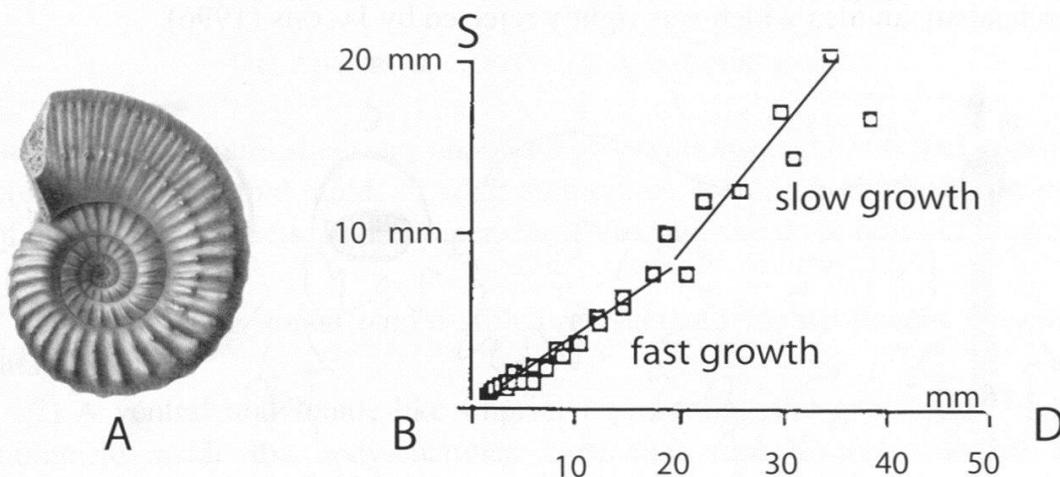


Figure 2.— A) *Androgynoceras*: The *Aegoceras*-like inner whorls are evolute and the *Liparoceras*-like outer whorls are more involute. B) The septa (S) are closely spaced in the juvenile and widely spaced in the adult morphology. (Redrawn from DOMMERMUES 1988).

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