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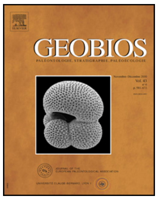

Original article

Ammonite aptychi: Functions and role in propulsion☆

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ABSTRACT

Seven previous proposals of aptychus (*sensu stricto*) function are reviewed: lower mandible, protection of gonads of females, protective operculum, ballasting, flushing benthic prey, filtering microfauna and pump for jet propulsion. An eighth is introduced: aptychi functioned to actively stabilize the rocking produced by the pulsating jet during forward foraging and backward swimming. Experiments with in-air models suggest that planispiral ammonites could lower their aperture by the forward shift of a mobile cephalic complex. In the experiments, the ventral part of the peristome is lowered from the lateral resting (neutral) position by the added "ballast" of a relatively thin Laevaptychus to an angle $< 25^\circ$ from horizontal with adequate stability to withstand the counter-force produced by the jet of the recurved hyponome. However, of the shell forms tested, only brevidomes with thick aptychi, e.g., the Upper Jurassic Aspidoceratidae with Laevaptychus and average whorl expansion rates, were stable enough to swim forward by jet propulsion at about *Nautilus* speed ($\sim$ 25 cm/s). We propose that aptychus function most commonly combined feeding (jaw, flushing, filtering) with protection (operculum), and, more rarely, with locomotion (ballast, pump, diving and stabilizing plane). Aptychi may thus have been multi-functional.

1. Introduction

Aptychi (*sensu stricto*) are calcitic, bivalved plates commonly found singly or in pairs, isolated (Fig. 1B, D) or associated with ammonites (Fig. 1A, F), where they usually occur in the body-chamber (Fig. 1C, E). Aptychi are universally accepted as integral parts of the ammonite organism (e.g., Lehmann, 1981; Dagys et al., 1989; Morton and Nixon, 1987). They are typically wing-shaped, showing a range of morphotypes described and illustrated by Arkell (1957: L437–L440). Six main morphotypes are illustrated by Lehmann (1976: fig. 73); in Fig. 2, we present an expanded list of morphotypes with their characterization.

The numerous records of *in situ* aptychi occurrences include the exceptionally thick-shelled Laevaptychus in aspidoceratids and Lamellaptychus in haploceratoids. Aptychus morphologies (e.g., Lehmann, 1976: fig. 73) commonly differ distinctly among Ammonitina families (Oppel, 1862: pls. 68–74, Trauth, 1927-1938; Lehmann, 1981; Dagys et al., 1989; Tanabe and Landman, 2002) and occur in both sexual dimorphs (e.g., Schweigert, 2009; Parent et al., 2011; Fig. 1C). There is wide consensus that aptychi were part of the buccal mass (e.g., Dzik, 1981; Dagys et al., 1989; Lehmann and Kulicki, 1990; Nixon, 1996).

Interpretations of aptychus function (detailed below) range from protection (operculum) through feeding (lower mandible, flushing out demersal microfauna, filtering) to propulsion (pump for jetting, ballast for lowering the aperture). Historically, the lower mandible hypothesis was the first to appear in the ammonite literature (*fide* Lehmann, 1970). Functional morphologists have argued for and against attributing single or multiple functions of aptychi (e.g., Farinacci et al., 1976; Lehmann, 1981; Lehmann and Kulicki, 1990; Morton, 1981; Seilacher, 1993; Kruta et al., 2009; Trauth, 1927-1938; but see Westermann, 1990 for a wider context). Operculum and lower mandible functions could have been performed alternatively, according to the changing requirements for protection when at rest and for foraging, by moving the aptychus forward and backward past the arms (Schindewolf, 1958).

We support the view that aptychi commonly served more than one function and that functional combinations differed among higher taxa. After reviewing the hypotheses of aptychus functions, we tentatively propose a new function for ammonite aptychi and outline the potential implications for ammonite life-habits. While backward swimming has been by far the most commonly assumed form of ammonite locomotion (Westermann and Tsujita, 1999), we concentrate on forward swimming, which was almost certainly required during foraging and prey capture. We present simple experiments and calculations that indicate that some

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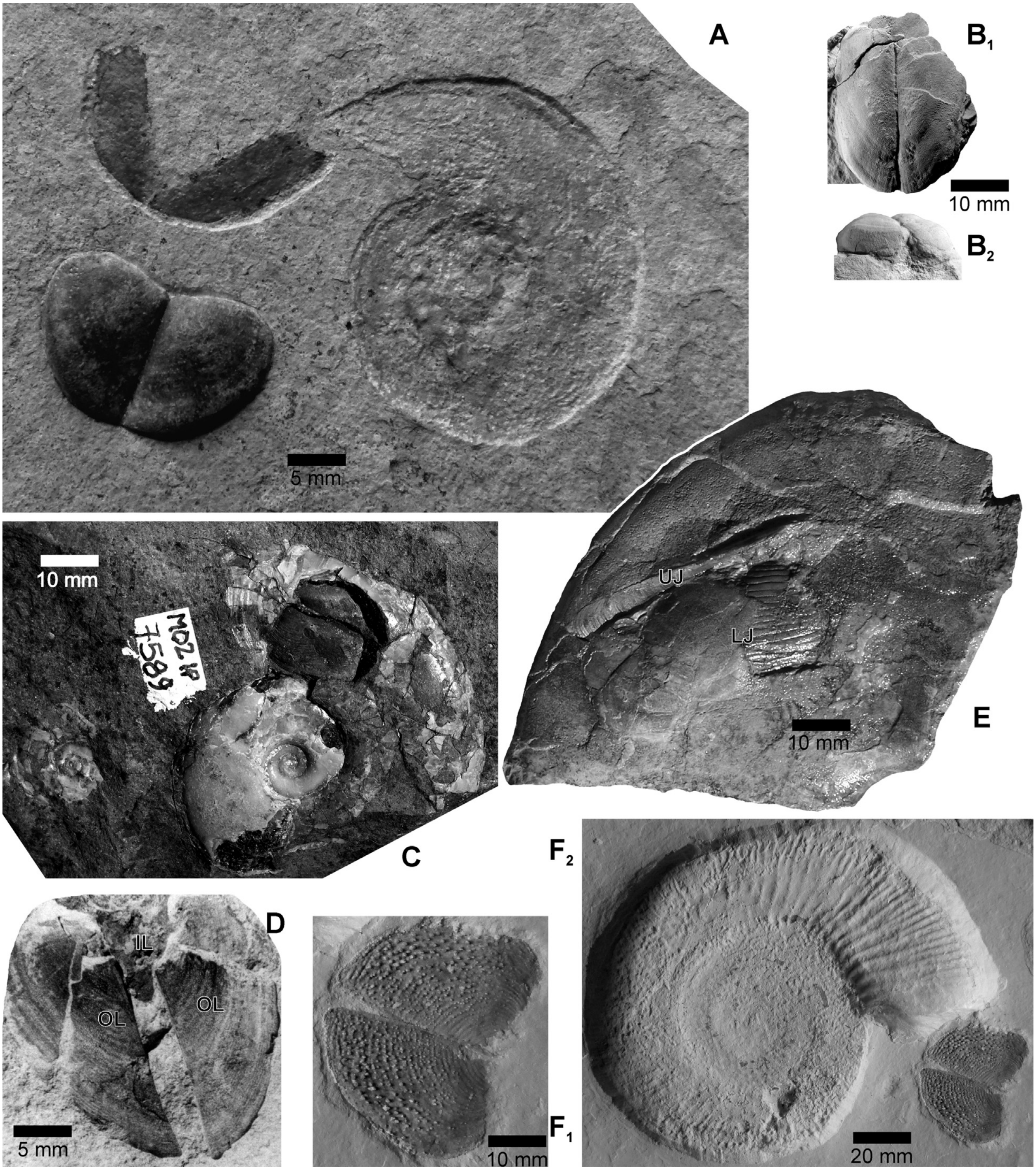

Fig. 1. Aptychi of Aspidoceratidae (**A**–**B**), Haploceratidae (**C**–**D**), Oppeliidae (**E**) and Lithacoceratinae (**F**). **A**. *Physodoceras nattheimense* Schweigert, 1998, a female (macroconch) with its Laevaptychus and upper jaw in front of the aperture; Nusplingen Lithographic Limestone (SMNS 63232, courtesy G. Schweigert). **B**. Laevaptychus of an Aspidoceratidae indet., Zitteli Zone (Tithonian) of Picún Leufú, Neuquén-Mendoza Basin, Argentina, lower (B_1) and frontal (B_2) views; modified from Parent et al. (2011). **C**. Complete adult female (macroconch) of *Pseudolissoceras zitteli* (Burckhardt, 1903) with complete Lamellaptychus in body-chamber; in the lower left a complete male (microconch) with Lamellaptyhcus covered by shell remains, Zitteli Zone of Cerro Lotena (Neuquén-Mendoza Basin), Museo Olsacher, Zapala, MOZPI-7589. **D**. Complete Lamellaptychus of a macroconch female *P. zitteli* from the Zitteli Zone of Cerro Lotena, with inner lamella (IL) and outer lamella (OL) preserved. **E**. Complete adult body-chamber (L_{BC} = 120°) of a female (macroconch) of *Cieneguiticeras perlaevis* (Steuer, 1897) with Lamellaptychus (lower jaw, LJ) and upper jaw (UJ), both calcitic, Picunleufuense Zone (Lower Tithonian) of Picún Leufú; refigured from Parent et al. (2011), phragmocone not shown. **F**. *Subplanites* sp., a male (microconch) with its Strigogranulaptychus; Lower Tithonian, Hybonotum Zone, Painten, Bavaria (SMNS 70191, courtesy G. Schweigert).

ammonoids with conventional soft body anatomy and propelled by a coleoid-type hyponome had the potential to swim forward as well as backward. We only consider coleoid-type hyponomes here (but see Westermann, 2013).

2. Functions attributed to aptychi

In this section, we review the various hypotheses of aptychus function in historical order.