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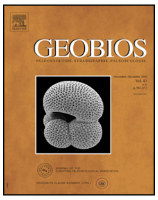

Original article

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 $< 25°$ 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 (~ 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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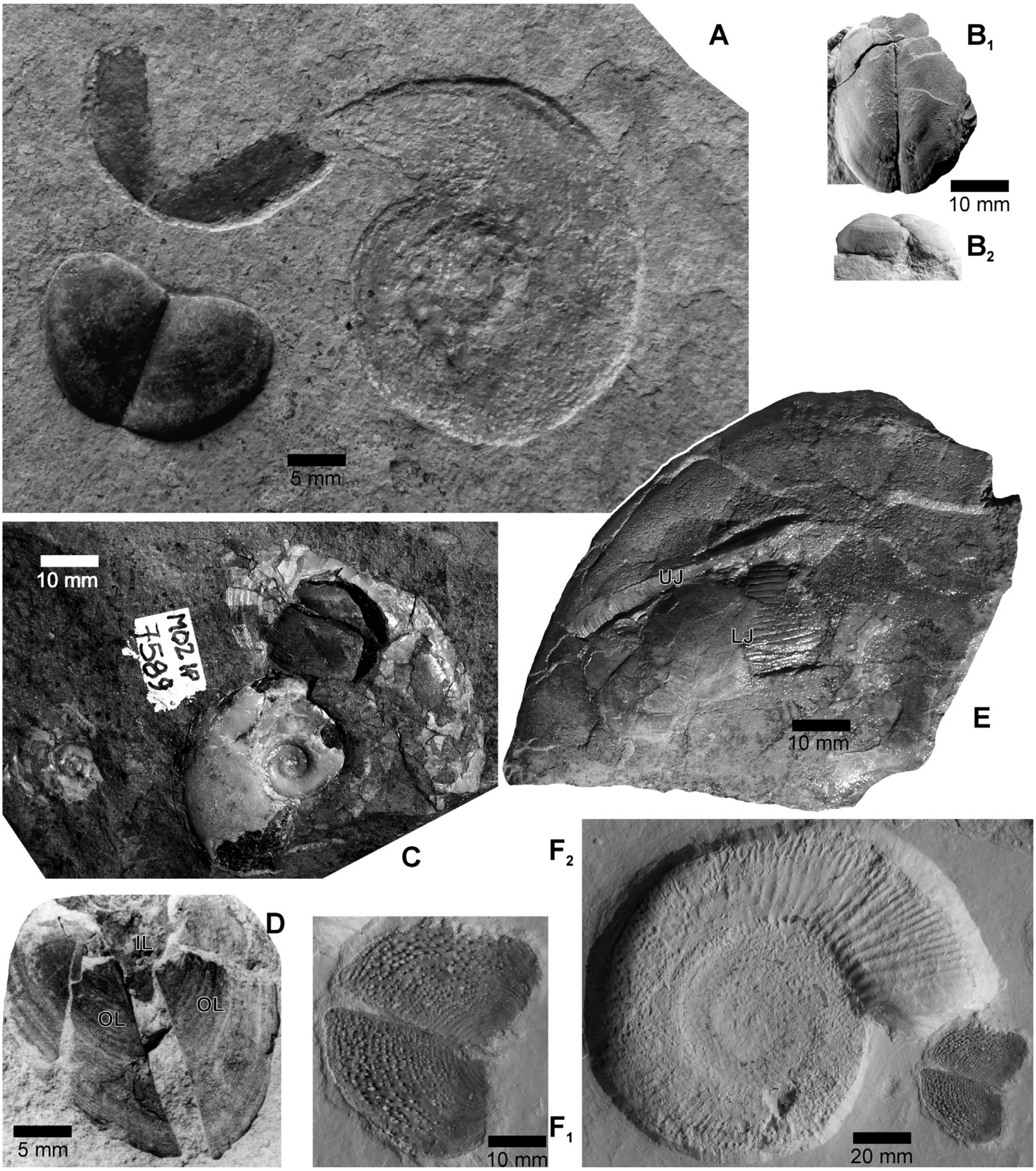


Fig. 1. Aptychi of Aspidoceratidae (**A**–**B**), Haploceratidae (**C**–**D**), Oppeliidae (**E**) and Lithacoceratinae (**F**). **A**. *Physodoceras nattheimense* Schweigert, 1998, a female (macroconch) with its Laevaptychus and upper jaw in front of the aperture; Nusplingen Lithographic Limestone (SMNS 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.

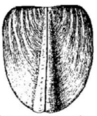
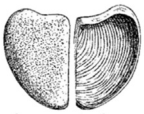
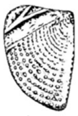
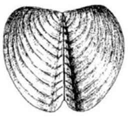
Types of aptychus		Function						
		Lower mandible	Operculum	Ballast	Flushing	Filtering	Pump	Stabilizer
 Cornaptychus	Weakly calcified aptychi with lamellar structure; highly chitinous (black preservation). In hildoceratoids.	●	○			○	○	
 Lamellaptychus	Thick, but spongy inner layer with prominent, concentric lamellae; outer layer very thin. In haploceratoids.	●	●	●	○			○
 Laevaptychus	Especially thick; smooth surface covered with pores; internally sponge-like. In aspidoceratids	●	●	●	○	○		○
 Praestriaptychus	Surfaces only with growth lines. In perisphinctoids and stephanoceratoids.	●	●		○	○	○	○
 Strigogranulaptychus	Thin-shelled; surface with granulation. In perisphinctoids.	●	●		○			
 Granulaptychus	Thin-shelled; surface with concentrically arranged granulation, inside with growth lines. In perisphinctoids.	●	●				○	
 Striaptychus	Surface smooth; valves commonly entirely separate along symphesis. In Cretaceous heteromorphs, e.g. scaphitids and baculitids.	●	●			○		

Fig. 2. Aptychus types characterized by main features, taxonomic association and proposed functions as explained in the text. Our assessment of the likelihood that aptychi performed the functions are as follows: probable (•), possible (o). Illustrations not to scale, modified from Lehmann (1976: fig. 73) and Trauth (1937: pl. 11: 12).

2.1. *Lower mandible (Meek and Hayden, 1864)*

This function probably derived from ammonoid ancestors, and should be regarded as the primary function of ammonite aptychi (Lehmann, 1971, 1976; Dzik, 1981). This hypothesis has become widely accepted, thus, reversing its earlier rejection by Trauth (1927–1938). The mandibles or jaws were part of the buccal mass (Nixon, 1996), which also contained the radula between lower and upper jaws (e.g., Lehmann, 1967, 1979; Doguzhaeva and Mutvei, 1992; Klug and Jerjen, 2012; Fig. 3A). Most likely, the aptychi acted as a more or less rigid board on which the upper mandible retained prey for fragmentation, followed by transport of the fragments by the radula through the oesophagus.

The highly porous and exceptionally thick Laevaptychus of aspidoceratids (e.g., Farinacci et al., 1976; Fig. 1A, B) appear to have been ill suited as a lower mandible because its large size relative to the body-chamber implies that it would have occupied a large space within the buccal mass.

2.2. *Protecting the nidamentary glands and/or gonads of females (Keferstein, 1866)*

This idea was proposed a century and a half ago by Keferstein (1866) and accepted by Favre (1873), but immediately cast into serious doubt (e.g., Gray, 1873). Keferstein's proposal has received no attention in recent decades, probably because in the near absence of quantitative evidence on the soft tissue anatomy of ammonites, there is no obvious way to generate arguments for or against it.

2.3. *Operculum (Trauth, 1927)*

The fit of many aptychi to the terminal body-chambers of the shells in which they are found indicates that such aptychi functioned as an operculum to close off the body-chamber and protect the body. An operculum needed to cover only the major parts of the whorl section to protect the soft body from predator attacks. The spaces commonly left open are in the umbilical whorl

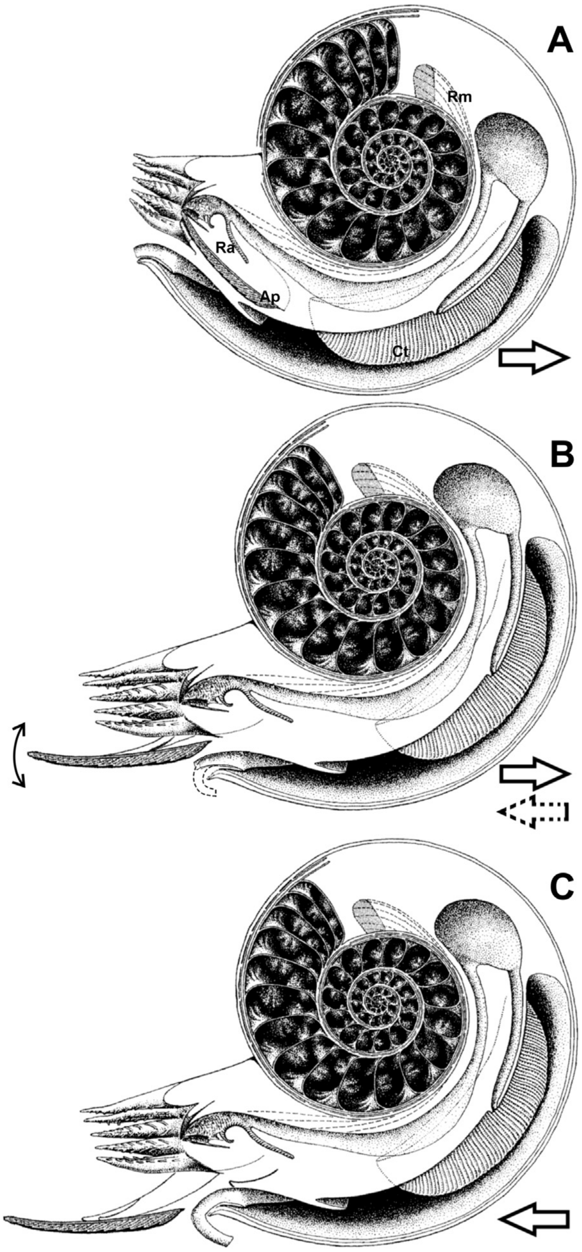


Fig. 3. Reconstruction of an ammonite with thick aptychus (Ap) having various functions. Sagittal section based on modifications from Dzik (1981: fig. 9a). **A**. Partially retracted cephalic complex for resting and backwards swimming. **B**. Projected cephalic complex with independently moving aptychus functioning as stabilizer by flapping in harmony with the jet pulse to prevent rocking, simultaneously acting as ballast and diving plane during forward and backward swimming. **C**. Projected cephalic complex with independent aptychus flushing demersal prey, as well as acting as ballast and diving plane during forward swimming. Ct: ctenidia, Rm: paired retractor muscles, Ra: radula. White arrows indicate direction of swimming.

overlaps, presumably for continuous water circulation required for the gills and at mid-venter, probably for the hyponome (Lehmann, 1990). Among the types of aptychi are the exceptionally thick Laevaptychus and Lamellaptychus of the aspidoceratids and haploceratoids, respectively (subjects of the experiments described below). Protective aptychi are also present in the lappet bearing microconchs of Stephanococeratidae, i.e., the Praestriaptychus of "*Normannites*" (Westermann, 1954: figs. 31–32; pl. 32), where they conform to the whorl section and have growth patterns resembling those of the body-chamber (Hewitt et al., 1993; see also Dzik, 1981).

Observations of Keupp (2000: 113–114) on a specimen of Lamellaptychus from the Upper Jurassic of Regensburg, Germany, show brown, banded colour markings, indicating its visibility from the water, i.e., as an operculum. The same function is strongly supported by a Laevaptychus in a *Physodoceras* from the Upper Jurassic of Wuettemberg, which has healed bite marks.

As an operculum, the aptychus not only prevented direct frontal access to the body, but it also supported the peristome from the radial load applied to the periphery by large predators attempting to crush the flanks of the body-chamber. The outer, lamellar layer on the convex side of the aptychus probably functioned to resist tensile stress when the aptychus was under radial compression from an attack. Thickened aptychi, such as those of aspidoceratids and haploceratoids, would have benefited from the improved bending and buckling strength that thick configurations would provide. Therefore increased thickness for operculum function was the primary adaptation for thick, porous aptychi.

Aptychi in body-chambers are frequently found 90° to 120° behind the aperture, presumably their position after the body had retracted for protection (Trauth, 1927: fig. 7; Hewitt et al., 1993). This implies a tissue volume of no more than two-thirds of the body-chamber volume.

Morton and Nixon (1987) and Schweigert (2009) rejected the operculum function. Schweigert (2009) argued that any protective function of aptychi in microconchs with large lappets as illustrated by Westermann (1954) would have been superfluous because these elaborate apertures provided sufficient protection when the head complex was deeply withdrawn. While this argument could probably be applied to a few special cases, it cannot be generalized: macroconchs and many microconchs (e.g., Cardioceratidae, Eurycephalitinae) have no lappets.

2.4. *Ballast for lowering aperture (Gasiorowski, 1960)*

The thick and relatively heavy Laevaptychus of the Aspidoceratidae and Lamellaptychus of the Haploceratoidea, when projected from the aperture with the cephalic mass, would have depressed the aperture of these brevidomes during foraging and feeding episodes (Fig. 3C). Gasiorowski (1960: 70) proposed that thick aptychi functioned as ballast, but did not describe aptychus projection beyond the aperture. This modification, which increased the moment of the ballast, was suggested much later by Morton and Nixon (1987). Mobile aptychi would enable a variety of behaviours (Schweigert, 2009). This hypothesis is treated with experiments (see below).

Keupp (2000: 114) documented some healed Laevaptychus injuries on its inside face, requiring its exposure to the predator. This would support the projection of the aptychus outside the aperture.

2.5. *Flushing benthic prey (Lehmann, 1976)*

In some ammonites, the aptychus (or anaptychus) may have functioned as a hydroplane designed to keep the forward swimming ammonite just above the seafloor, where it produced currents that flushed mainly demersal microfauna into the basal water column for capture (epidemersal ammonite habitat of Westermann, 2013) (Fig. 3C). The static conditions associated with this function are explored experimentally and discussed below.

2.6. *Filtering of microfauna (Morton and Nixon, 1987)*

The aptychus was a stiffening device creating a fine slit between the narrowly separated jaws for filtering microfauna. This function has been supported by Kruta et al. (2011) in *Baculites* from the study of the remains of several small organisms preserved inside the buccal mass.

2.7. Pump for jet propulsion (Westermann, 1990)

The aptychus may have acted as a pump to produce the jet, i.e., as a reciprocating folding board or hinged fan, without moving the entire cephalic complex as in *Nautilus*. The moving mass within the body-chamber was thus much smaller and would compensate for the higher moment caused by its longer stroke in ammonite body-chambers. The force of this jet may have created modest swimming velocity in some ammonites. Aptychi functioning in this way, however, may have produced an almost continuous stream of water for ventilating the gills, homologous to the action of the funnel wings of *Nautilus* (O'Dor et al., 1990), rather than for producing propulsive thrust with the hyponome.

2.8. Stabilizer against pitching (this work)

We propose that some aptychi functioned as active horizontal stabilizers against pitching ("rocking") caused by the pulsing jet (Fig. 3B), mainly during forward swimming. We assume that these ammonites had propulsion systems generated by a jet of water forced by the animal from its body; the tendency of an ammonite to pitch (rotate around the centre of shell stability) would have been stronger than in *Nautilus* because of the lower stability in ammonites resulting from their longer body-chamber. Because foraging and feeding at the substrate probably required a relatively constant shell orientation relative to the substrate, pitching probably had to be minimized during such actions. When projected from the aperture, the aptychus could at the same time have provided vertical steerage when the ammonite foraged just above the seafloor (function of flushing benthic prey, above). Such an aptychus may have had the same functions in backward swimming. This would be another case of multifunction of aptychi: ballasting, steering, and stabilizing.

3. Experiments to test forward swimming

The aim of the experiments is to test two major attributes of planispiral ammonites, especially planorbiconic (formerly "planulate"; see Westermann, 1996) ammonites, as a function of the angular length of the body-chamber:

- **Attribute 1**. Rotation around the centre of shell stability (pitching or "cartwheeling") as it relates to several functions as indicated above. In these experiments, we assume that the centre of shell rotation lies near the centre of buoyancy and centre of mass of the shell. This is not an unreasonable assumption in most cases (Chamberlain, 1980a). We are interested to establish rotations caused by varying the position of the body from entirely within the body-chamber (resting position) to the body extended largely outside the body-chamber. We test such rotations for both mesodomic and brevidomic shells. We also investigate the effect of the presence or absence of aptychi of different thickness, especially thick Laevaptychus and Lamellaptychus. These experiments will inform us on how much "ballast" in the form of aptychus weight is required to rotate the aperture to a lower, near-substrate position which we suggest enhances effective forward swimming, and flushing benthic and demersal prey;
- **Attribute 2**. Maximum potential for forward swimming speed. Our experiments on shell rotation can be used together with measures of the moments due to the application of jet force, drag force, buoyancy, and shell weight to estimate the speed of forward swimming in animals with shell shapes similar to those tested in the experiments.

3.1. Terms and parameters

Variables and parameters used throughout the text and figures are the following (Fig. 4, Table 1):

- B: ballast;
- B_1: soft tissue weight;
- B_2: aptychus weight;
- C_A: centre of shell coiling (coiling axis);
- C_B: centre of buoyancy (C_{B1} for mesodome ammonite; C_{B2} for brevidome ammonite);
- C_M: centre of mass (C_{M1} for mesodome ammonite; C_{M2} for brevidome ammonite);
- D: shell diameter;
- d_{CA}: distance to coiling axis;
- f: distance between C_B and C_M;
- H_2: apertural whorl height; measured from venter to preceding venter;
- J_T: thrust produced by jetting;
- L_{BC}: angular length of the body-chamber;
- OB: aperture rotation angle;
- OB_1: resting aperture angle;
- OB_2: minimum aperture angle;
- OB_3: forward swimming angle;
- OR: aperture angle, *i.e.* angle between the aperture and the vertical;
- OR_1: resting;
- OR_2: minimum;
- OR_3: forward swimming;
- S_T: stability index ($= f/D$);
- V_{BC}: body-chamber volume;
- V_{PH}: phragmocone volume;
- V_P: ventral peristome angle, formed by the peristome from the horizontal;
- W: whorl expansion rate;
- W_T: effective weight, *i.e.*, weight in water;
- α: spiral pitch angle, *i.e.*, angle between the tangent of the circle and the spiral at intersection;
- δ: density.

Forces are given in dynes (1 dyne = 1 $g.cm/s^2$).

3.2. Experimental conditions and assumptions

Due to the distinctly trimodal distribution of angular body-chamber lengths among ammonoids (cf. Westermann, 1996: fig. 3) planispiral ammonoids can be grouped by angular length of the body-chamber (L_{BC}) into three shell types: (1) *brevidomes* with body-chambers about one-half whorl (180–210°); (2) *mesodomes* with lengths about three-quarters whorl (250–300°); and (3) *longidomes* with body-chambers one whorl or longer (350–400°). Body-chamber length determines the angle of the aperture relative to the vertical for an empty shell or when the animal was entirely withdrawn into the shell for protection or resting. This angle is the resting angle, OR_1. For empty shells remaining self-similar throughout ontogeny OR_1 is about 70° from the vertical for brevidomes, and 90–100° for mesodomes (Trueman, 1941; Saunders and Shapiro, 1986: fig. 8; Westermann, 1996: fig. 3). For living animals, however, the higher density of the cephalic complex, compared to the intestinal complex (see below), would have lowered OR_1 somewhat, at least in brevidomes (here assumed as 60°). Projection of the cephalic complex from the aperture while inactive would have lowered the aperture to a near vertical angle, OR_2; when active, it would have risen to the forward swimming angle, OR_3.

The logarithmic spiral extends the diameter (D) with each whorl defined by a factor called the whorl expansion rate (W) by

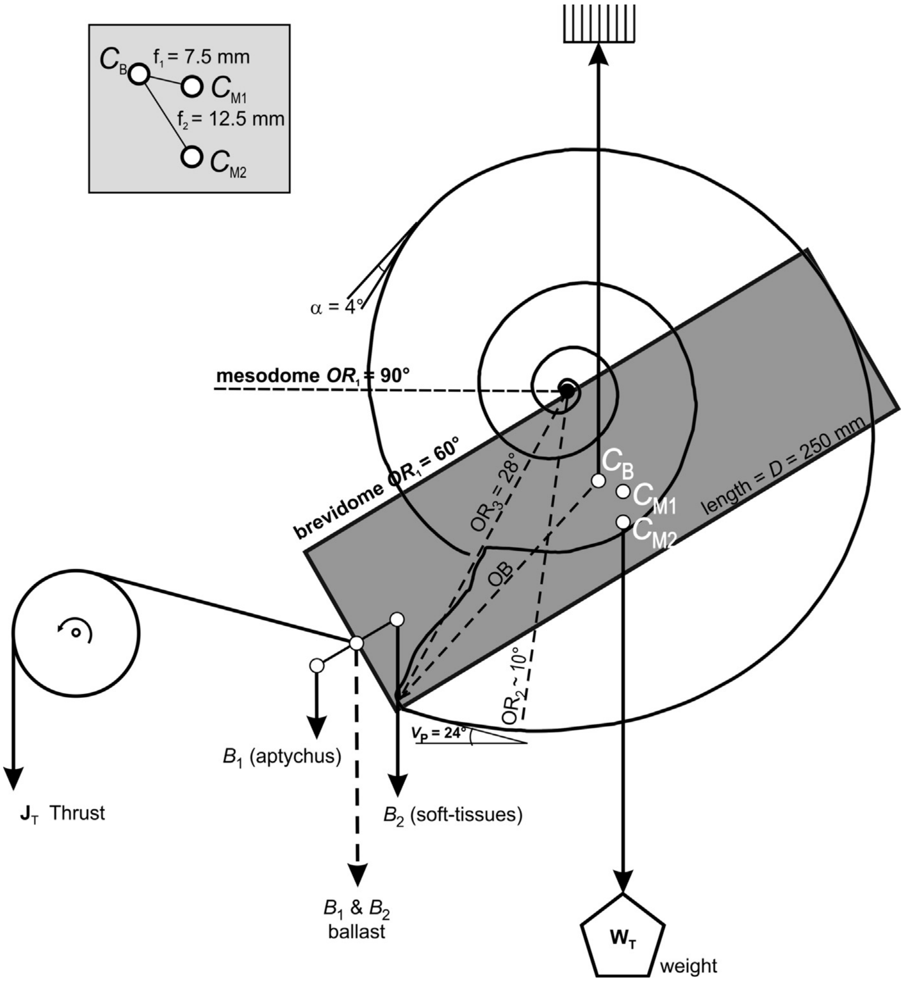


Fig. 4. Designs for the in-air experiments with mesodomic and brevidomic, planorbiconic Ammonitina with a diameter D = 250 mm, a volume of 2000 cm^3 and tissue mean density of 1.65 g/cm^3. The left half of the batten-shaped bar represents a torsion balance with the pivot at the buoyancy centre C_B, where the apparatus in suspended. Under water weight, mass W_T, is attached at the mass centre, C_M. Torque is produced by the ballast B attached at the left end of the bar representing the body protruding from its resting orientation OB_1 partially out of the aperture to OB_2. B includes tissues only (B_2) or in addition a variety of Laevaptychus (B_1). Their masses are combined and calibrated to a single mass (B_1 and B_2). The restorative moment on f opposes the moment of W_T. This measures the ballast required for lowering the aperture from its resting angle OR_1 (shown for a mesodome at 90° and a brevidome at 60°) to the angle OR_2. Forward swimming by jet thrust J_T requires a low ventral peristome angle $V_P < 25°$ for the recurved hyponome and sufficient stability S_T to counter opposing force produced by J_T. Increasing W_T enlarges the spiral pitch angle (α) and lowers V_P. Inset: detailed view of f_1 (mesodome) and f_2 (brevidome).

Raup (1967), or by the apertural whorl height relative to corresponding diameter (H_2/D) of Parent et al. (2010, 2012), i.e., the dorso-ventral or internal whorl height. Reducing L_{BC} and enlarging W increases the relative distance between the centres of mass (C_M) and buoyancy (C_B), i.e., the stability index $S_T = f/D$. This parameter is a measure of the static restorative moment due to the buoyant force of the shell acting upward and the deadweight of the animal acting downward which counters disruptive forces acting to rotate the animal away from its resting orientation (Raup and Chamberlain, 1967, 1980a; Saunders and Shapiro, 1986). It is this restorative moment due to buoyancy and shell deadweight that limits the moment (and hence force) of jet propulsion (see experiments below) in forward swimming. In other words, the moment produced by the jet force must be matched by the moment created by buoyancy and weight of the mass; otherwise the animal would spin out of control (see Discussion).

The stability index S_T is about 0.03 for mesodomes and 0.05 for brevidomes (Saunders and Shapiro, 1986: fig. 8). The high stability of *Nautilus* ($S_T \approx 0.09$) is due to its extremely short body-chamber and high W, which among Mesozoic ammonoids is probably matched only by some lytoceratines and exceptional ancylocer-atines, e.g., Scaphitidae (Landman et al., 2010) or *Pictetia* (Hoffmann et al., 2009). Short body-chambers and/or high W are more frequent in Palaeozoic ammonoids (e.g., Klug, 2001).

Rotation away from an animal's resting position due to the application of a disruptive force would usually occur around a

Table 1
Weight of the soft tissue ballast for the two models of a 250 mm-diameter and 2000 cm^3-volume hypothetical ammonite, with volume ratios of body-chamber (V_{BC}) and phragmocone (V_{PH}) indicated.

V_{BC}:V_{Ph}	Mesodome 4:1	Brevidome 3:1
V_{BC}	2000 cm^3 × 0.8 = 1600 cm^3	2000 cm^3 × 0.67 = 1333 cm^3
Mobile tissue	1600 cm^3 × 0.55 = 880 cm^3	1333 cm^3 × 0.55 = 733 cm^3
Mobile mass	880 cm^3 × 1.065 g/cm^3 = 937 g	733 cm^3 × 1.065 g/cm^3 = 788 g
Weight in sea water	937 × 10^3 dynes × (1.065 – 1.025) = 37.5 × 10^3 dynes	788 × 10^3 dynes × (1.06 – 1.025) = 32 × 10^3 dynes

point on a line joining the centres of buoyancy and mass, probably about half-way between the two centres. Since the animal is untethered and free to rotate in any direction, and since in a swimming animal subject to instantaneous variations in thrust and drag, one can expect this point to shift slightly, but continuously, with time so that the centre of rotation defines a random walk around the midpoint of the buoyancy-mass couplet. However, in constructing the experimental test apparatus, we assume for simplicity that a shell will rotate around its centre of buoyancy. In the shell morphologies investigated here, the centres of buoyancy and mass lie very close to one another; this assumption does not introduce significant error in our results.

Forward swimming of ammonites required that the ventral margin of the peristome be at a ventral peristome angle V_P, here considered to be $< 25^\circ$ from the horizontal. An angle of this magnitude is needed to provide space for the hyponome to bend backward beneath the shell and to produce a horizontal jet stream. Brevidomic and, especially, mesodomic ammonites required their high aperture resting angle ($OR_1 \sim 100^\circ$; Saunders and Shapiro, 1986: fig. 8) be lowered by adding extra "ballast" to the mobile cephalic complex (head with arms and buccal mass). But even the most brevidomic ammonites ($L_{BC} \sim 180^\circ$, $W \sim 2$, and $OR_1 \sim 60^\circ$; Saunders and Shapiro, 1986 and above) needed extra ballast to hold the aperture down against the thrust at modest forward speed. Jet propulsion in longidomic ammonites at best produced very low swimming velocities due to minimal stability (Chamberlain, 1980a: fig. 8; $S_T < 0.01$, Saunders and Shapiro, 1986: fig. 2). V_P equals OR_2 minus the spiral pitch angle, which at $W = 2$ is 4° (compared to 9–12° in *Nautilus* at $W \sim 3$). For example at $W = 2$ and $OR_3 = 28^\circ$, $Vp = 24^\circ$ (Fig. 4).

Soft tissue probably comprised maximally two-thirds of the body-chamber volume, as pointed out above. Three-quarters of the tissues may have been mobile; they could be advanced to project partly from the aperture to gain the attitude required for foraging from the substrate, and withdrawn into the body-chamber for protection from benthic predators during rest periods. The remaining, roughly one-quarter, tissues would have belonged to the fixed intestinal complex. The overall density (δ) of *Nautilus* soft tissue is 1.055 or 3% denser than seawater, and for the mobile parts 1.065 or 4% denser than seawater (Ward, 1988). In coleoids, now known to be the closest relatives of ammonoids (Engeser, 1996), the homologous parts are more muscular (arms and tentacles) and somewhat denser, $\delta = 1.075$ or 5% denser than seawater (Hewitt et al., 1999). Ammonoid arms, however, were weakly muscular at best as indicated by their complete lack of preservation in contrast to coleoid arms (Engeser, 1996: p. 14). The median value of $\delta = 1.065$ (4% denser than seawater) is therefore accepted here. The volume of the phragmocone relative to the entire organism was an essential variable for neutral buoyancy. Table 1 shows the parameters for body-chamber/phragmocone volume ratios (V_{BC}:V_{Ph}) of 4:1 for mesodomes and 3:1 for brevidomes, with difference in body-chamber mass probably compensated by varying shell thickness. During forward movements of the mobile parts, partly out of the body-chamber, mantle cavity volume would have changed from about 10 to 40% of V_{BC}, and vice versa.

Experimental data and calculations are based on a hypothetical planorbiconic ammonite of 250 mm diameter and *ca.* 2000 cm^3 volume. Under water weight of body-chamber with body is 499×10^3 dynes, including soft tissue with a weight in water of 32×10^3 dynes. To this we added a hypothetical series of Laevaptychi ranging from 20×10^3 to 80×10^3 dynes. We concentrate here on brevidomes, which carry Laevaptychi. Volume estimates of Laevaptychi of Tithonian Aspidoceratidae were based on specimens from Argentina and Spain.

A Laevaptychus is highly porous, with tissue-filled tubes, so that its density is much less than that of the constituent calcite, i.e., 1.65 g/cm^3 (Hewitt et al., 1993). The volume of the thick aptychi of Aspidoceratidae relative to body-chamber volume ranges in our data from 1% to 4% (in part quantified for us by Roger Hewitt). When the ammonite was submerged in seawater, however, with the resulting buoyancy forces and relative volumes, the estimated weight of this Laevaptychus is 1 to almost 3 times that of all soft tissue, i.e., about 20×10^3 to 90×10^3 dynes for our aspidoceratid model with 250 mm diameter and *ca.* 2000 cm^3 volume.

3.3. Experiment design

Since experimentation is often more difficult under water than in the air, G.E.G.W. developed a simple apparatus that works in air but gives results applicable to water. The device simulates planorbiconic ammonites and is diagrammed in Fig. 4. It is based on the application of buoyancy and effective weights of objects suspended in water from a modified torsion scale, of the kind formerly used for weighing letters, by using a batten-shaped bar. The weight of this bar is small compared to the forces used in the experiment. The scale acts like a pendulum with the static restorative moment represented by the pivot-arm, above, and the weight, below. Bar length of 250 mm represents the ammonite shell diameter *D*, with values for the centres of buoyancy C_B and mass C_M, and for the stability index S_T derived from the mathematical analyses of Saunders and Shapiro (1986: figs. 2, 8). The bar is suspended at C_B, the point of action of the uplifting buoyant force. The most common, mesodomic ammonites have $S_T = 0.03$ and near horizontal OR_1 (90–100°). To represent them, a small hole is drilled perpendicular to the bar for C_{M1}, at $f = 7.5$ mm (shell diameter × 0.03) from C_{B1}, which allows for the attachment of the weight (W_{T},), representing the downward force of the shell and body. The weight of any "ballast", such as a Laevaptychus added to the system, is deducted from $W_{T.}$ This preserves the overall neutral buoyancy. Mobile ballast *B* is attached at the end of the bar. This represents the extended body projected to different distances outward from the body-chamber. Small weights representing an aptychus may also be added. This setup results in rotation producing the aperture angle *OR*. For brevidomes, we used a resting angle of about 60° and $S_T = 0.05$, where another small hole is drilled for attachment of various W_T at 12.5 mm ($f = 200 \times 0.05$) and a 40° angle below C_{B2}. Varying the positions and magnitudes of the weights representing body and aptychus produced different angles of the bar relative to the vertical. In this way, we can estimate the effect of an aptychus on the orientation of a living ammonite with shell, body, and aptychus characteristics similar to those of the experimental model.

The force produced by expelling water through the hyponome drives the animal forward. The movement thus produced generates a drag force acting in a direction opposite to the animal's motion. This jet force and the resulting drag force form a couplet that produces a moment, which acts to rotate the animal (Chamberlain, 1980a). This moment is countered by the animal's hydrostatic stability, i.e., the moment generated by weight and buoyancy. We can take advantage of this relationship to derive estimates of swimming velocities as a function of animal weight and buoyancy in animals with and without aptychi. To do this using the experimental setup described here, we need to assume that the jet-drag moment acts around the centre of buoyancy. This is not strictly true (Chamberlain, 1980a, 1987), but the assumption should not introduce significant error.

We ran two series of experiments aimed at generating figures for swimming velocity: one modelling mesodomes, and the other brevidomes. However, the brevidome experiment is of particular significance with respect to aptychus functioning, because the Laevaptychus-bearing aspidoceratids are brevidomes. Experimental parameters used in testing a planorbiconic, brevidomic ammonite were: D = 250 mm; W = 2; distance from coiling axis d_{CA} = 1.3; S_T = 0.05 (S_T = 0.06, 0.07 and 0.08 were also tested but are not illustrated here). Ballast of 32×10^3 to 105×10^3 dynes was attached close to the end (B_2, for soft tissues) and in front of the end of the bar (B_1 for aptychi), simulating moments produced by forces of 15×10^3, 25×10^3 and 35×10^3 dynes. Simulated forces J_T of 10×10^3 to 80×10^3 dynes were applied by means of a line attached to the end of the bar, thus, countering the stability forces produced by the C_B/C_M (Fig. 4).

3.4. Velocity estimates

The experimental data we developed with regard to rotational moments due to jet force and stability, together with stability-generated limits on thrust, were used to calculate probable swimming velocity limits for animals with body/shell configurations similar to those tested experimentally. We did this by using equation 1 of Chamberlain (1980a):

$$V = \sqrt{\frac{2mg\rho^{-1}A^{-1}C_d^{-1}S\ \sin\theta}{(X/D) - S\ \sin\theta}}$$

where V = swimming velocity; m = total mass of the animal (shell + body + aptychus if there is one); g = the gravitational constant; ρ = density of seawater; A = (total volume displaced by the shell)$^{2/3}$; C_d = drag coefficient; S = hydrostatic stability as defined by Raup (1967: fig. 19); θ = the angle of rotation discussed above, i.e., the angle through which the aperture rotates away from its position when V = 0; X = moment arm of the jet force; and D = shell diameter.

This equation estimates swimming velocity from values for propulsive force, drag force, and the moments resulting from these forces operating over specific distances from their centres of rotation as well as moments due to effective weight and buoyancy. Drag is considered to equal jet force, and is determined in terms of (shell volume)$^{2/3}$ as an area representative of the shell. Drag coefficient (0.8) is taken from data for shells and shell models reported by Chamberlain (1976) that have shapes similar to those of the ammonites tested here. Drag coefficient of such shells are not likely to vary much over at least part of the rotational range investigated here (Chamberlain, 1976), and are not likely to be greatly influenced by extension of the body out of the body-chamber (Chamberlain, 1980b).

It should be emphasized that this approach assumes no secular variation in propulsive thrust, an assumption that departs considerably from the well-known pulsation of the hyponome in cephalopod locomotion and its effect on force production (Chamberlain, 1980a, 1987). Our approach does not consider the effect of acceleration and deceleration of water in the jet or around the animal or the influence of these phenomena on instantaneous velocity of the animal. Nevertheless, when applied to *Nautilus*, this equation produces results that are equivalent to the observed swimming speed of this animal (Chamberlain and Westermann, 1976; Ward et al., 1977; Chamberlain, 1987). This suggests that our approach is reasonable.

4. Results

Our experimental results are given in Fig. 5. This figure reports data for a simulated inflated, planorbiconic, brevidome ammonite resembling aspidoceratids (D = 250 mm, volume = 2000 cm^3, W = 2, S_T = 0.05). The figure is intended to show the effect on orientation (aperture angle relative to the vertical) of body extension out of the aperture with and without an aptychus of different weight. It also shows the thrust, or jet force, that such an extension of the body would permit without inducing excessive static instability, i.e., cartwheeling. In all cases, neutral buoyancy is maintained (i.e., tissue weight is reduced as aptychus weight is increased).

The x-axis plots the effect of a series of "ballasts" in the form of an aptychus added to the animal as a function of the weight of the aptychus. At its origin, the plot shows the orientation of such an animal with its body not extended from the aperture. With the

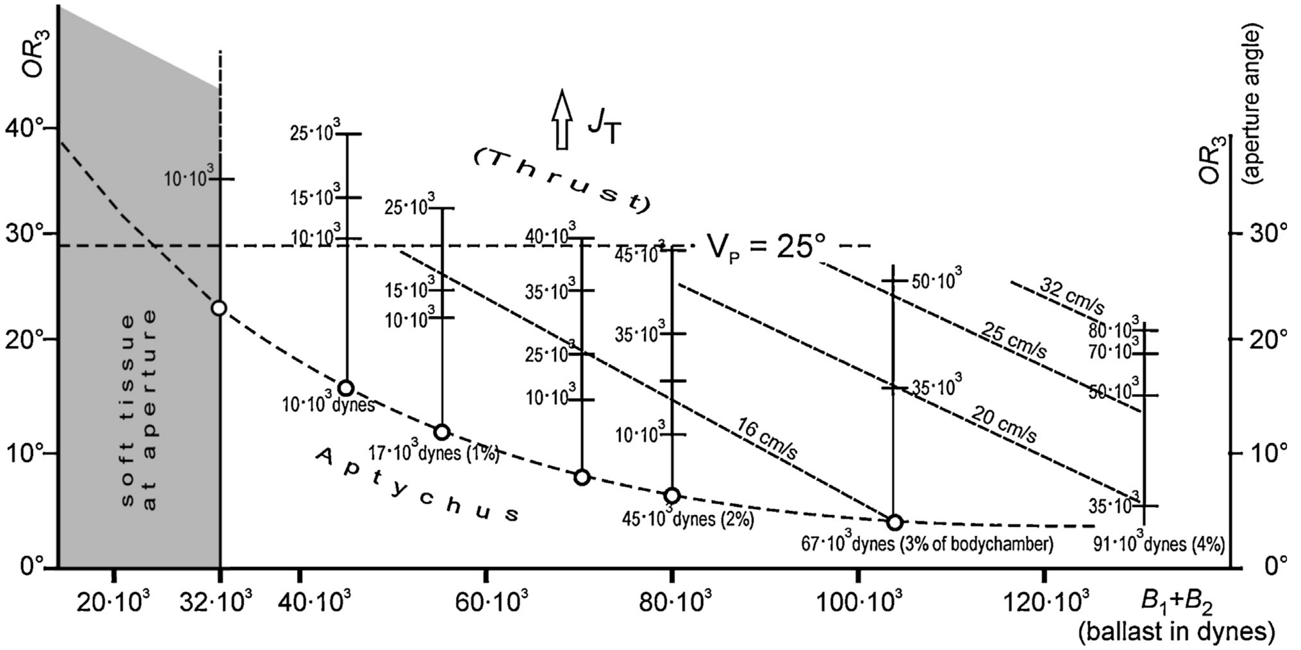


Fig. 5. Stability against backward rotation by thrust of a hypothetical aspidoceratid with variables and parameters as in Fig. 4, with OR_1 = 60, OR_2 = 5 to 15°, and OR_3 = 20 to 40°. Aperture ballast B of soft tissue is augmented with Laevaptychus varying from $5 \cdot 10^3$ to 91×10^3 dynes (up to about 4% of body-chamber volume V_{BC}; shown by the broken line with circles), which reduces the aperture angle OR_3. Various jet thrusts J_T are then applied countering B for each Laevaptychus ballast (vertical scales in dynes from the dashed line with circles). The assumed maximum of the ventral peristome angle (V_P = 25° at OR_3 = 29°) required for forward swimming by the hyponome limits J_T. When the Laevaptychus is moderately thick (45×10^3 dynes, about 2% of V_{BC}), this 250 mm-diameter hypothetical ammonite can withstand a hypothetical thrust of 45×10^3 dynes, equivalent to the force producing a modest forward speed of 20 cm/s (broken diagonal lines), sufficient for foraging.

protrusion of about one-half of the body (under water weight = 32 × 10^3 dynes) out of its chamber the aperture is lowered from the resting angle of about 60° (OR_1; not indicated) to the minimum angle (OR_2) of about 20° (right margin of gray area in plot). This is low enough for the hyponome to bend beneath the aperture, but not for effective jetting action involving flushing demersal prey during forward swimming. Adding a 10 × 10^3 dynes weight, simulating a 10 × 10^3 dynes forward thrust, marked along the *y*-axis, will elevate the aperture to 35° (OR_3), which we consider too great for effective flushing of prey while moving forward. Increasing ballast in small steps by adding an aptychus with increasing under water weights (10 × 10^3 to 91 × 10^3 dynes) is shown by the dashed line labeled "Aptychus" in which the open circles give points on the line actually determined experimentally. The lines drawn vertically from each such point show the aperture orientations (read on the *y*-axes) that would be produced by a jet force of the magnitude indicated on these "thrust" lines drawn vertically from each tested aptychus point. In order to function effectively during forward foraging, the ventral peristome angle (V_P) produced by such jet forces should be less than about 25° (horizontal dashed line). The potential maximum forward swimming velocities associated with these jet forces are shown by the inclined dashed lines, each one labelled with the speed it represents. These "speed" lines terminate at the upper limit of likely acceptable foraging orientations.

4.1. Angle of the ventral peristome

The low angle of the ventral peristome ($V_P < 25°$) we suggest was needed for the hyponome to bend beneath the shell to produce a horizontal jet stream, was achieved in all experiments by moving the cephalic complex (without aptychus) forward and half-way out of the aperture. But swimming potential varied greatly (Fig. 5).

4.2. Brevidomic aspidoceratids

The simulated brevidomic aspidoceratids, the main subject of our experiments, have higher stability ($S_T \sim 0.05$) and an exceptionally thick and heavy Laevaptychus acting as extra ballast. With 32 × 10^3 dynes of soft tissue only, OR_2 becomes 25° (Fig. 5), then reduces to near verticality with increasing Laevaptychus ballast. Fig. 5 shows that a thin aptychus (17 × 10^3 dynes, *ca.* 1% of the V_{BC}) would counter thrust producing a swimming velocity of about 16 cm/s. A medium-thick Laevaptychus (30 × 10^3–60 × 10^3 dynes) increases the thrust limit and allows swimming velocities of about 20 cm/s. Finally, a thick aptychus of ~ 4% of the V_{BC}, (80 × 10^3–90 × 10^3 dynes), which are fairly common, may allow enough thrust for swimming velocities between 25 and 35 cm/s. Thus, even when the protruding body has only thinly calcified aptychi, the aperture rotates to a near vertical orientation. By adding increasing weights of simulated Laevaptychus (10 × 10^3–91 × 10^3 dynes, 0.5–4% of body-chamber volume) to the soft tissue ballast (32 × 10^3 dynes), the potential jet force, and swimming speed increases considerably (Fig. 5).

4.3. Mesodomic ammonites

The simulated mesodomic ammonites (not illustrated) rotate below $V_P < 25°$, but their low stability against rotation ($S_T \sim 0.03$) reduces the potential propulsive forces required for swimming. Similarly, jetting backward would have been strictly limited and only in the precise direction towards the centres of mass and buoyancy. Additional "ballast" in the form of aptychi is unavailable in the majority of aptychus-bearing ammonites, because the majority of aptychi are only thinly calcified.

5. Discussion

5.1. Ontogeny and aptychi function

Our study of aptychi function is based on planispiral ammonites without significantly modified body-chambers or on ephibic growth stages (outer preadult whorls; see Westermann, 1958). The last three to four subadult whorls of ammonites typically grew 8-fold in diameter with only minor deviations from isometry, usually with expansion rates of about $W = 2$ (or $H_2/D \sim 0.3$) so that these juvenile and immature growth stages comprised over 99% of total subadult volume. It has been known for a long time that the earliest four to five whorls ($D = 5$ to 10 mm) commonly differed significantly in coiling and whorl section (Westermann, 1954; Bucher et al., 1996; Parent, 1997), and presumably also in many of the aptychi functions discussed above. Hydrostatic conditions depended strongly on body-chamber length, which may have changed through ontogeny. Ontogenetic variation may have produced differences in the distribution of the soft tissues and internal fluids, which altered the relative positions of the centres of buoyancy (C_B) and mass (C_M), critical parameters for stability and propulsion. The few studies on the ontogeny of body-chamber length (e.g., Westermann, 1971) and personal observations indicate that in many Ammonitina, body-chambers were longest in the juvenile stage and shortened gradually towards the adult stage. The aptychus was developed no later than post-nepionically in the perisphinctids (Kulicki and Wierzbowski, 1983) and other ammonites (Hewitt et al., 1993). We conclude that aptychi functions may have changed during growth, but more research is required to determine if these changes would produce significantly different orientations and rotational potential, and thus, swimming ability, and its concomitant influence on mode of life, during the life cycles of many ammonites.

5.2. Foraging and anatomy

The arms and tentacles of coleoids are sometimes preserved due to their high muscular content (Fuchs et al., 2013). In contrast, the appendages of ammonites are never found. This suggests that appendages of ammonoids were anatomically different from those of coleoids and very likely contained little musculature. Ammonoid appendages would therefore have been unable to act as effective steering devices (Seilacher, 1993). The hyponome (divided or not; cf. Westermann, 2013) may have sufficed to direct the animal in a general direction, but maintaining position near the sea floor for benthic foraging may not have been possible with the hyponome or appendages. The horizontally flattened aptychus, resembling the bow planes of submarines, could have accomplished the vertical control necessary for this mode of feeding. Lehmann (1976), however, did not state explicitly that such aptychi (*sensu lato*) were steering devices and his use of the term "shovel" referred to its shape, not its function. The aperture angle did not change with each vertical directional change. The ammonite could have foraged up a sloping seafloor or steering in the water column by re-directing the hyponome.

Flushing of epifaunal microfauna from the seafloor into the water above the substrate surface provides for the capture in the basal water column of prey by filtration of the water. This activity should be greatly improved by forward swimming at the moderate velocities estimated above (Fig. 5). Ostracods and foraminifers in the crop content of some ammonites (Lehmann, 1975) indicate that this kind of activity may have been possible in at least some ammonites. Other ammonites seem to have been capable of feeding also on macrofauna, by biting with the aptychus acting as lower mandible (see above). This function is supported by crop contents that include fragments of ammonite shells (e.g., Lehmann, 1973: pl.

11, fig. 5). Michael (1894) has described the crop contents of a *Neochetoceras* with shell fragments and small aptychi (possibly from males) of similar or even conspecific ammonites (Günter Schweigert, pers. com. Dec., 2012). Moreover, when acting as hydroplane, a thick aptychus, like Laevaptychus, would have acted simultaneously as ballast, reducing the angle of the aperture to enable forward swimming.

5.3. *Multifunctionality of aptychi*

There seems to be no barrier against double, triple or even quadruple functions of aptychi. The most frequent combination probably alternated between those of operculum and lower mandible (Fig. 2). Possible ways of the positional change of the aptychus required to serve one or the other function were discussed by Schindewolf (1958), Lehmann and Kulicki (1990) and Seilacher (1993). Possible additional functions of the same aptychus would be steering and stabilizing, as discussed above.

Most likely only some of the total range of apytchi functions were developed in a single ammonoid species or perhaps even family. The phylogenetic changes from one function or set of functions to another in different ammonite lineages must have involved modifications of shape, structure and microstructure of the different aptychi. For instance, the thin Cornaptychus of some hildoceratoids would not have been particularly useful as ballast, but may well have combined the functions of operculum and lower mandible, possibly even adding pumping and/or filtering functions (Fig. 2). The thin, usually dissolved calcitic layer of the Striaptychus of *Hoploscaphites* would have stiffened it, possibly for either improved crushing or biting, or it may have served the secondary function as operculum (Landman et al., 2010).

The propulsion system required by nektonic ammonoids is unknown; no remains of hyponome or pumping organs have been found. The absence of *Nautilus*-like large retractor muscle scars indicates that a *Nautilus*-like "piston pump" was most probably missing. Furthermore, if the short stroke typical of *Nautilus* would be extended to a long stroke more in line with the much longer body-chambers of ammonoids, the well-known "rocking" typical of *Nautilus* would become unstable "cartwheeling". Ammonoid pumps for jetting would most probably have differed from that of *Nautilus*. Possible pumping systems include a coleoid-like muscular mantle (Jacobs and Landman, 1993), and the aptychus function listed above (pumping for propulsion). Another possibility (Westermann, unpublished) is a rapidly pulsating internal part of the hyponome, with a valve controlling the intake from the mantle cavity. This would also provide continuous ventilation of the gills.

General comparisons between *Nautilus* and normally coiled Mesozoic ammonoids are usually restricted to internal shell structures, which tell us less about basic habitat differences than body-chamber length and aperture. Nautilidae are extremely brevidomic. During activity their hyponomic sinus forms a ventral peristome angle (V_P) of only 5–15° allowing their hyponome to bend beneath the shell during forward-jetting, i.e., clear adaptations to their scavenging and carnivorous, nekto-benthic habits. Mesozoic ammonoids vary from brevidomic to longidomic and consistently lack a hyponomic sinus indicating basically different propulsion systems ranging from moderate forwards and backwards swimming potential, including the possibility of medusa-like slow propulsion by modified arms and twin-nozzle hyponomes (Westermann, 2013), to vertically migrating or drifting megaplankton, planktivorous habits (Westermann, 1996; Kruta et al., 2009).

6. Conclusion

Our experiments on mesodomic and brevidomic ammonites quantify the ballasting effect of protruding bodies with thick aptychi on: (1) lowering of the aperture so that the hyponome could bend backwards beneath the shell to produce horizontal forward jet propulsion; and (2) providing static stability in this lowered aperture position against the counter-forces produced by the jet. The potential maximum speeds in forward swimming for planispiral subadult animals or for adults without mature body-chamber modifications are estimated from these data (Fig. 5). Functions of filtering microfauna, ballast, pump for propulsion and stabilization against pitching require that the aptychus moved independently from the buccal mass.

At least some ammonites were potentially able to swim forward, especially the Aspidoceratidae and Haploceratoidea with thick, protruding aptychi. Besides lowering and stabilizing the aperture, these protruding aptychi could have acted as diving planes for vertical steering, stabilizing against the pitching produced by the pulsating jet and for flushing demersal micro-fauna into the open bottom waters for capture. Thus, a mobile aptychus could have been involved in several functions, e.g., feeding, locomotion and protection.

Aptychus diversity appears low when compared with the large variety of Mesozoic ammonite morphologies, but with a consistent association between aptychus type and ammonite taxon. Kruta et al. (2009) have stressed that the differentiation in the development, structure and microstructure of aptychus types likely indicate differences in the mode of life and feeding habits. These differences are in accordance with the proposed differences in functions and their combinations discussed above. Multi-functionality would have constrained the ontogeny and evolution of aptychi, as reflected in their conservative morphology. Thus, aptychi might be considered of high taxonomic value in Ammonoidea systematics.

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