Editors' choice

Form and formation of flares and parabolae based on new observations of the internal shell structure in lytoceratid and perisphinctid ammonoids

GREGOR RADTKE, RENÉ HOFFMANN, and HELMUT KEUPP

Radtke, G., Hoffmann, R., and Keupp, H. 2016. Form and formation of flares and parabolae based on new observations of the internal shell structure in lytoceratid and perisphinctid ammonoids. *Acta Palaeontologica Polonica* 61 (3): 503–517.

The ultrastructure of pristine shells of Jurassic and Cretaceous lytoceratid and perisphinctid ammonoids indicates that flares and parabolae represent homologous structures. Both mark an interruption of shell growth. We dismiss earlier interpretations of parabolae as actual aperture, relics of resorbed apophyses or superstructure of the musculature associated to a semi-internal shell. Instead we propose an episodic growth model including several growth stops at the aperture during the formation of a frill-like aperture for parabolae and flares. Such an aperture is composed of the outer prismatic layer, the nacreous layer and an apertural prismatic coating. Here, we observed the apertural prismatic coating for the first time as an integral part of flares and parabolae. The apertural prismatic coating covers only the inner surface of the frill and was secreted by a permanent mantle cover indicating a prolonged period without the production of new shell material. Parabolae differ from flares by their general shape and the presence of ventro-lateral parabolic notches and nodes. The notches were formed by folding of the frill and had the potential to form semi-open spines. The corresponding parabolic nodes are caused by an outward swelling of the shell-secreting mantle tissue producing new shell material at the position of the folding. New shell material that belongs to the conch tube is attached to the base of flares and parabolae after withdrawal of the mantle edge representing the continuation of shell growth. Usually, the frilled aperture associated with flares and parabolae were removed during lifetime. This study reports on flares in *Argonauticeras* for the first time. In this genus they are typically associated with varices.

Key words: Ammonoidea, ultrastructure, megastriae, temporary aperture, episodic growth, Jurassic, Cretaceous.

Gregor Radtke [gradtke@zedat.fu-berlin.de] and Helmut Keupp [keupp@zedat.fu-berlin.de], Department of Earth Sciences, Freie Universität Berlin, Malteserstraße 74-100, Building D, Berlin 12249, Germany.
René Hoffmann [Rene.Hoffmann@rub.de], Department of Earth Sciences, Ruhr Universität Bochum, Universitätsstraße 150, Building NA, Bochum 44801, Germany.

Received 23 January 2015, accepted 4 April 2016, available online 11 April 2016.

Introduction

The accretion of ammonoid shells is assumed to be more or less continuous, comparable to the modern *Nautilus* and other shell bearing molluscs (e.g., Martin et al. 1978; Saunders 1983, Cochran and Landman 1984; Ward 1987; Westermann et al. 2004). However, some shell elements, e.g., flares, parabolae, have been suggested to represent temporary apertures indicating growth stops during ontogeny (e.g., Neumayr 1884; Arkell et al. 1957; Bucher et al. 1996). Flares typically occur in Lytoceratoidea while parabolae are reported for Clymeniida, Phylloceratoidea, Lytoceratoidea, and Perisphinctoidea (Wähner 1894; Michalski 1908; Arkell et al. 1957; Keupp 2000; Hoffmann 2010; Hoffmann and Keupp 2010). Both, flares and parabolae are radial linear elements, which encircle the whorl except for the dorsal part (Fig. 1). Flares are prominent, smooth to crenulated rib-, frill-like or sometimes funnel-shaped shell extensions (Fig. 1A) paralleling the growth lines. Flares are underpinned by new shell material, which continues the growth of the conch tube. However, Drushits et al. (1978) describe the flares of *Tetragonites* and *Gaudryceras* only as nacreous thickenings and do not mention an interruption in shell growth. Drushits and Doguzhaeva (1981: fig. 31) demonstrate that the outer prismatic layer is involved in the formation of flares of *Eurystomiceras* (junior subjective synonym of *Nannolytoceras*; see Hoffmann 2010). Hence the outer prismatic layer shows an episodic growth interruption. Recently, it has been shown that the flares of *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al.

http://dx.doi.org/10.4202/app.00154.2015

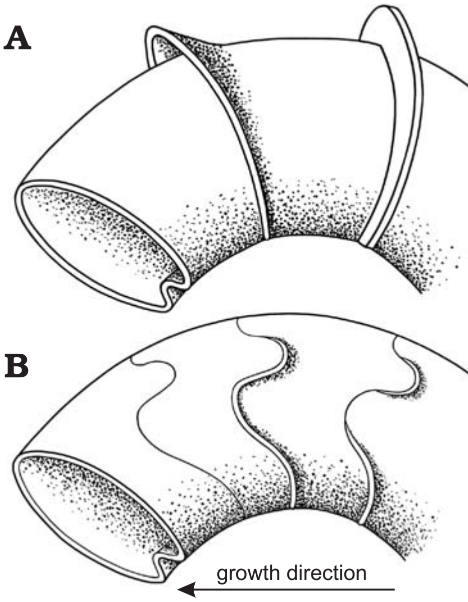


Fig. 1. Different expressions of flares (**A**) and parabolae (**B**).

2010: fig. 3) are composed of the outer prismatic and nacreous layer. However, none of the above descriptions show complete flares.

Parabolae represent thin raised lines or ribs, which form prominent symmetrical sinuses, the paired parabolic notches (Fig. 1B), at the ventro-lateral edge. Ventrally and laterally parabolae form adorally projecting saddles. Parabolae are oblique to, and hence cut growth lines or other sculptures (e.g., Bucher et al. 1996). Additional structures often associated with parabolae are the parabolic nodes, smooth elevations formed in the parabolic notches. While it is generally accepted that parabolae represent an interruption in shell growth, their primary shape is still under debate. Some authors assumed that parabolae represent the actual moulding of the temporary aperture (e.g., Pompeckj 1894; Keupp 1973), probably formed due to lower growth rates at the position of the parabolic notches (Keupp 1973: fig. 4). In contrast, a secondary state, e.g., resorption of apophyses (Teisseyre 1883, 1889; Siemiradzki 1898–1899; Brinkmann 1929; Hiltermann 1939), or the resorption of semi-closed to closed ventro-lateral, hollow spines with parabolic notches as their former bases (Stieler 1922; Wendt 1968; Guex 1989; Bucher and Guex 1990), or removal of a frill through breakage (Michalski 1908) were assumed by others. Bucher and Guex (1990) supposed that parabolae and flares share a similar ultrastructure (also Bucher et al. 1996; Bucher 1997). Accordingly, flares and parabolae represent different expressions of their concept of megastriae. Both flares and parabolae are assumed to be the result of withdrawal of the shell-secreting mantle. A similar genesis and internal structure (outer prismatic and nacreous layer) suggest that flares and parabolae were homologous structures. A third interpretation was provided by Doguzhaeva (2012). Based on observations of *Indosphinctes,* parabolae were interpreted as a superstructure of the muscular system serving predominantly for the secure attachment of muscles to the inner and outer shell surface. That interpretation points to a semi-internal shell without episodic growth stops during the formation of parabolae.

By comparing concurring hypotheses about the internal structure, formation and shape of flares and parabolae the following questions arise: (i) What was the original shape and potential function of flares and parabolae? (ii) Which processes took part in their formation and/or removal? (iii) Do flares and parabolae represent homologous structures? (iv) Do parabolae indicate a semi-internal shell?

Institutional abbreviations.—BSPG, Bavarian State Collection for Palaeontology and Geology, Munich, Germany.

Other abbreviations.—apc, apertural prismatic coating; ipl, inner prismatic layer; ncl 1/2, nacreous layer of primary/secondary shell; opl 1/2, outer prismatic layer of primary/secondary shell; PI, SEM preservation index; pt, prismatic thickening; sb, shell bulge; var, varix.

Material and methods

The present study is based on pristine shells of *Choffatia* sp. (Perisphinctoidea) from SW Russia, *Argonauticeras besairiei* Collignon, 1949 from NW Madagascar, and *Protetragonites fraasi* (Daqué, 1910) from SW Madagascar (both Lytoceratoidea). All specimens are housed in BSPG (Coll. H. Keupp) (Table 1). According to the SEM preservation index (PI) by Cochran et al. (2010), the examined shell material has a predominantly aragonitic preservation of a good (PI = 3) to fair (PI = 2) state. In all specimens only the phragmocone is preserved. Russian samples show a partial pyritic overprint; the chamber walls are coated with diagenetic pyrite crystals. The remaining hollow spaces are filled with fine loose sediment, which was removed for observation. Madagascan ammonoids are filled with coarse, marly, glauconitic sediment or are completely filled with drusy calcite.

Freshly broken pieces and etched sections of shell material were analysed. Etched sections were prepared by polishing with aluminium oxide and were afterwards treated with 10% formic acid for 5–10 s. All samples were fixed with conductive carbon glue on aluminium stubs and then sputtered with gold. Observations were made and pictures were taken with the scanning electron microscope (Type: Zeiss SUPRA 40VP) of the palaeontological section of the Freie Universität Berlin.

Results and discussion

Flares.—*Protetragonites fraasi* and *Argonauticeras besairiei* developed regularly spaced flares. *Protetragonites* has 5–6 and *Argonauticeras* 7–10 flares per whorl. Each flare marks the junction of two shell generations. The older

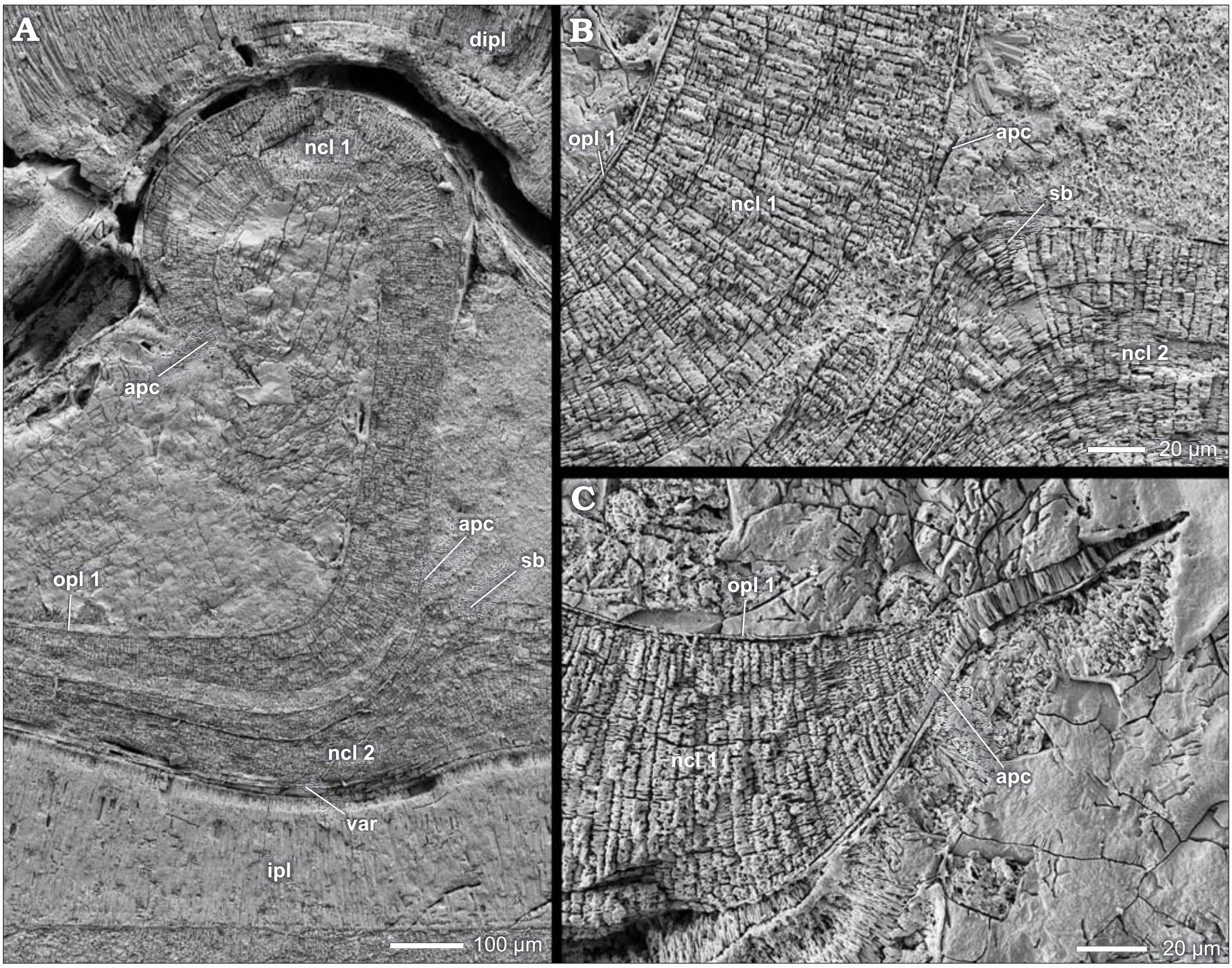


Fig. 2. Internal structure of flares (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 (BSPG MAo-1801) from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. **A**. Complete flare, the primary shell bends outwards and forms a frill. The flare ends in a backward reflection of the shell, i.e., apertural margin. Secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. **B**. Close-up of A, contact of the primary shell and the secondary shell. The interior of the flares is covered by an apertural prismatic coating. **C**. Apertural margin of the flare, the primary shell wedges out. The primary outer prismatic layer and the apertural prismatic coating form a vanishing prismatic wedge. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; sb, shell bulge; var, varix.

shell generation is called the primary shell and the new one is called the secondary shell. The formation of the flares indicates the end of one formation cycle. Two flares of *Argonauticeras* are preserved completely intact, forming a frill (Fig. 2A). They reach a height of up to 800 µm and a thickness of up to 100 µm. The proximal part is straight but slightly adorally inclined, while the most distal part forms a backward inflection that results in a hook-like appearance in cross section. The flare consists of a thin outer prismatic and an underlying thick nacreous layer (opl 1 and ncl 1 in Figs. 2, 3A$_1$, B$_1$, 4A), which is in accordance with the observations of Bucher et al. (1996: fig. 11) and Doguzhaeva et al. (2010: figs. 3, 5). The inner surface of the frilled aperture is covered by a prismatic layer (apc in Figs. 2B, C, 3, 4C, 5A). This layer is called the apertural prismatic coating (apc) here. The flare thins out distally and vanishes forming a delicate prismatic wedge, a product of the opl 1 and the apc (Fig. 2C). In distal parts of flares as well as in non-flared apertural edges the ncl 1 thins out (e.g., Mutvei 2014). Flares at the umbilical edge are less conspicuous and made of a small wedge of the opl 1 (and apc?), which rises slightly (ca. 20 µm) above the shell surface (opl 1/apc in Fig. 4D). The majority of flares have been morphologically altered, i.e., they do not show their original shape. Ventrally, the flares are often preserved as short, rounded stumps projecting above the shell surface (Figs. 3A$_1$, 4A, B), up to 400 µm high, or are completely cut off sub-parallel ending at the level of the shell surface (Fig. 3B), i.e., horizontally cut flare-bases (compare Bucher et al. 1996; Doguzhaeva et al. 2010).

Beneath the actual flare a new shell generation (secondary shell), comprised of a secondary outer prismatic and nacreous layer (opl 2 and ncl 2 in Figs. 2A, B, 3, 4A, C, D), is formed. Thus, the shell seems to be doubled in that area. The new opl 2 begins immediately at the base of the flare and is in direct contact with the apc (Fig. 3A$_2$, B$_2$). The ncl 1 and the ncl 2 can only be separated in proximity to the flare,

Table 1. Ammonoid taxa studied, their locality and age, and occurrence of flares and parabolae. All specimens housed in the BSPG (Coll. H. Keupp). ×, present; –, absent.

Taxon	Specimen number	Locality	Age	Flares	Parabolae
Lytoceratoidea					
Protetragonites fraasi (Daqué, 1910)	BSPG MAn-4530 BSPG MAn-4734	Sakaraha area, Morondava Basin, SW Madagascar	Upper Oxfordian, Jurassic	×	–
Argonauticeras besairiei Collingnon, 1949	BSPG MAo-1705a BSPG MAo-1772 BSPG MAo-1801 BSPG MAo-1802	Ambatolafia area, Mahajanga Basin, NW Madagascar	Lower Albian, Cretaceous	×	–
Perisphinctoidea					
Choffatia sp.	BSPG MAn-4519 BSPG MAn-4520	Dubki near Saratov, SW Russia	Upper Callovian, Jurassic	–	×

because they merge in the aboral direction (Figs. 3A$_1$, B$_1$, 4A, D). Directly in front of each flare, the secondary shell forms a bulge at the base of each flare that vanishes in the adoral direction (sb in Figs. 2A, B, 3A$_1$, B$_1$, 4A, D, 5E). In *Argonauticeras* the bulge and the horizontally cut base of the flare have the same height and form rib-like ridges ventrally (Fig. 3B$_1$). Furthermore, in *Argonauticeras*, the ncl 2 forms an internal thickening beneath the flare, i.e., an internal varix (var in Fig. 3B$_1$). The innermost contributing layer is the inner prismatic layer (ipl), which is uninterrupted, and covers and smoothes the inner shell surface.

Formation of the flares.—During periodic flare formation shell growth ceased and the frilled aperture was presumably covered with mantle tissue, as indicated by the apc (Fig. 5A). In modern *Nautilus*, a probably homologous prismatic coating (mantle adhesive layer secreted by the adoral mantle) appears at the terminal aperture (Erben et al. 1969; Doguzhaeva and Mutvei 1986; Mutvei and Doguzhaeva 1997; Mutvei 2014). The apc occurs also in *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al. 2010: pr in figs. 3, 5), hence we assume a similar genesis for all lytoceratids. Shell growth proceeds with the formation of a new segment of the conch tube at the base of the flare (shell duplication) (Fig. 5D, E). Therefore, the mantle was retracted into the living chamber. It is likely that the mantle edge attaches in front of the flare, since the opl 2 begins in direct contact with the apc. The bulge was probably a reaction to the retraction of the mantle whereby the mantle tissue was compressed and thus was pressed outwards. Similar structures occur in flares of *Anagaudryceras* (Bucher et al. 1996: fig. 11) and *Eogaudryceras* (Doguzhaeva et al. 2010: figs. 3, 5) and can also be seen during shell repair after injuries (e.g., Keupp 1998, 2012). Finally, in the rear parts of the living chamber, the ipl was laid down by the apical mantle as the growth continued (e.g., Kulicki 1979, 1996; Birkelund 1980).

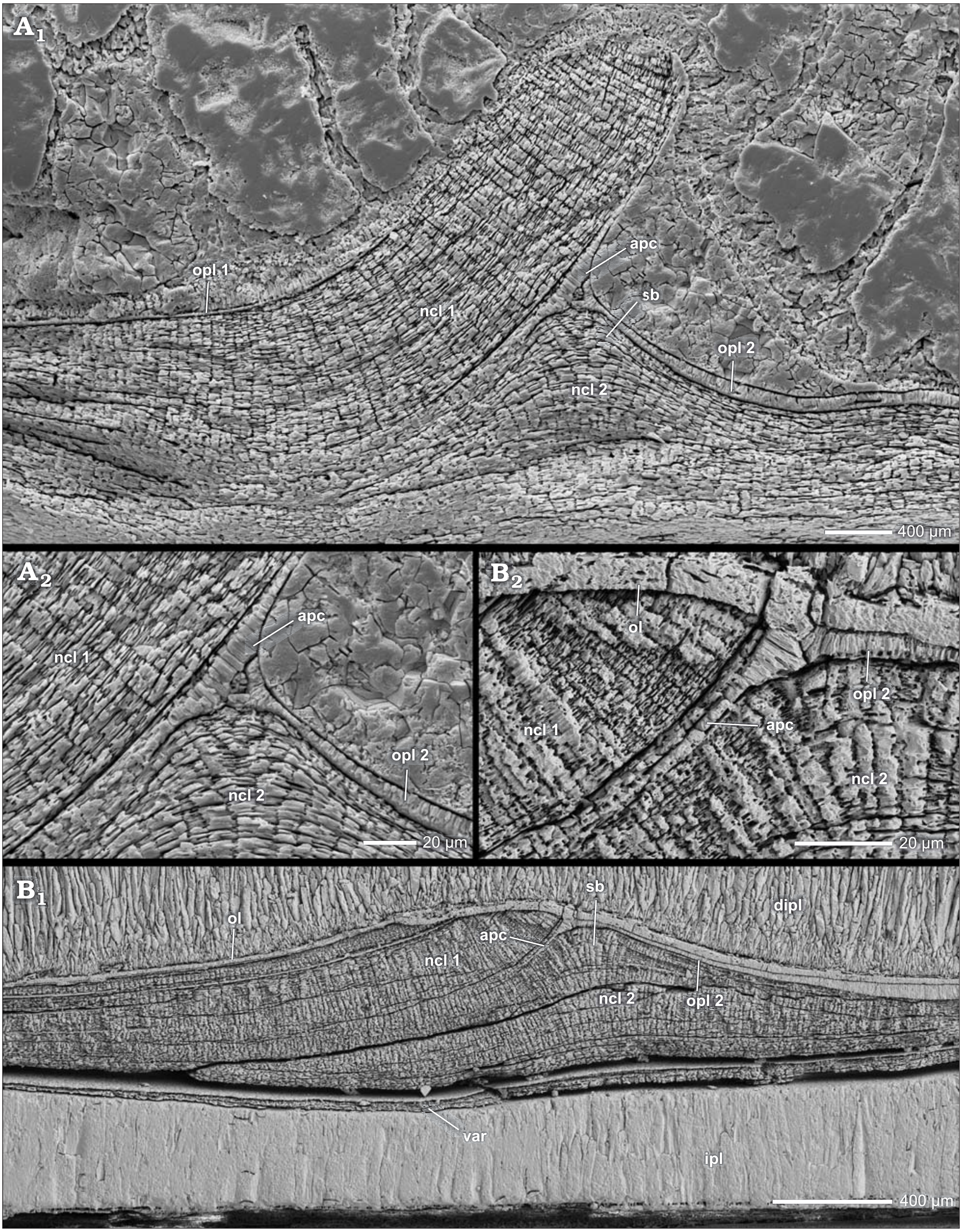
Modification of the flares.—The majority of examined flares was removed or modified (Figs. 3A$_1$, B$_1$, 4A). The question is which processes took place during their alteration. In rare cases, removed flares show irregularly broken surfaces (Fig. 4E). For those we assume a breakage due to mechanical stress. It seems likely that those structures represent accidents (e.g., collision, attacks). However, the majority of flares was presumably removed due to the resorption activity of mantle tissue on two occasions, namely during the formation of the actual whorl and again during overgrowth by the following whorl 360° later. Our interpretation is based on the following observations.

(i) Most of the flares show a more or less regular and recurring pattern of modification (rounded stumps of and/or horizontally cut flares) indicating a controlled process (e.g., resorption; Figs. 3A$_1$, B$_1$, 4A). Accordingly, we reject diagenesis or erosion that would produce irregular patterns. Broken flares as mentioned above are probably unaffected (irregular edge) because these are (already) short enough, making subsequent biologically controlled removal unnecessary.

(ii) All flares reduced in height show that all constituting shell layers (opl 1, ncl 1, apc) are affected (Figs. 3A$_1$, B, 4A, B). In particular, thereby, the remaining cut base of *Argonauticeras*' flares and the associated bulge together form a rib-like ridge ventrally. The relief of the shell is significantly reduced at these positions. Similar phenomena were reported for Recent gastropods during resorption activities of their mantle tissue on the inner shell surface (e.g., Kohn et al. 1979).

(iii) One specimen of *Argonauticeras* preserved a rounded stump of a flare (Fig. 3A$_1$) at the lower shell flank (whereas it is ventrally covered by the following whorl and is horizontally cut, i.e. rib-like ridges; Fig. 3B$_1$). We assume that this lateral portion was out of reach of the mantle of the following whorl. Therefore, the mantle of the actual whorl resorbed the major part of the flare prior to the beginning of a new shell formation cycle, probably during withdrawal (Fig. 5A–C). The distal part of the flare was probably shed through destabilization (resorption) of its base and the resulting breaking surface was smoothed directly afterwards

Fig. 3. Internal structure of flares (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. **A**. BSPG MAo-1705a. A$_1$. Partially resorbed flare, the primary shell bends outwards and ends in a round stump; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. A$_2$. Close-up of A$_1$, contact of the primary shell and secondary shell, the apertural prismatic coating of the primary shell and the outer prismatic layer of the secondary shell are in direct →



contact. **B**. BSPG MAo-1772. B_1. Resorbed flare, the primary shell bends outwards and is cut off horizontally to the shell surface; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare and a varix beneath. B_2. Close up of B_1, the flare is cut independently of the shell layers; condition of apertural prismatic coating and new outer prismatic layer as in A_2. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; ol, organic layer; sb, shell bulge; var, varix.

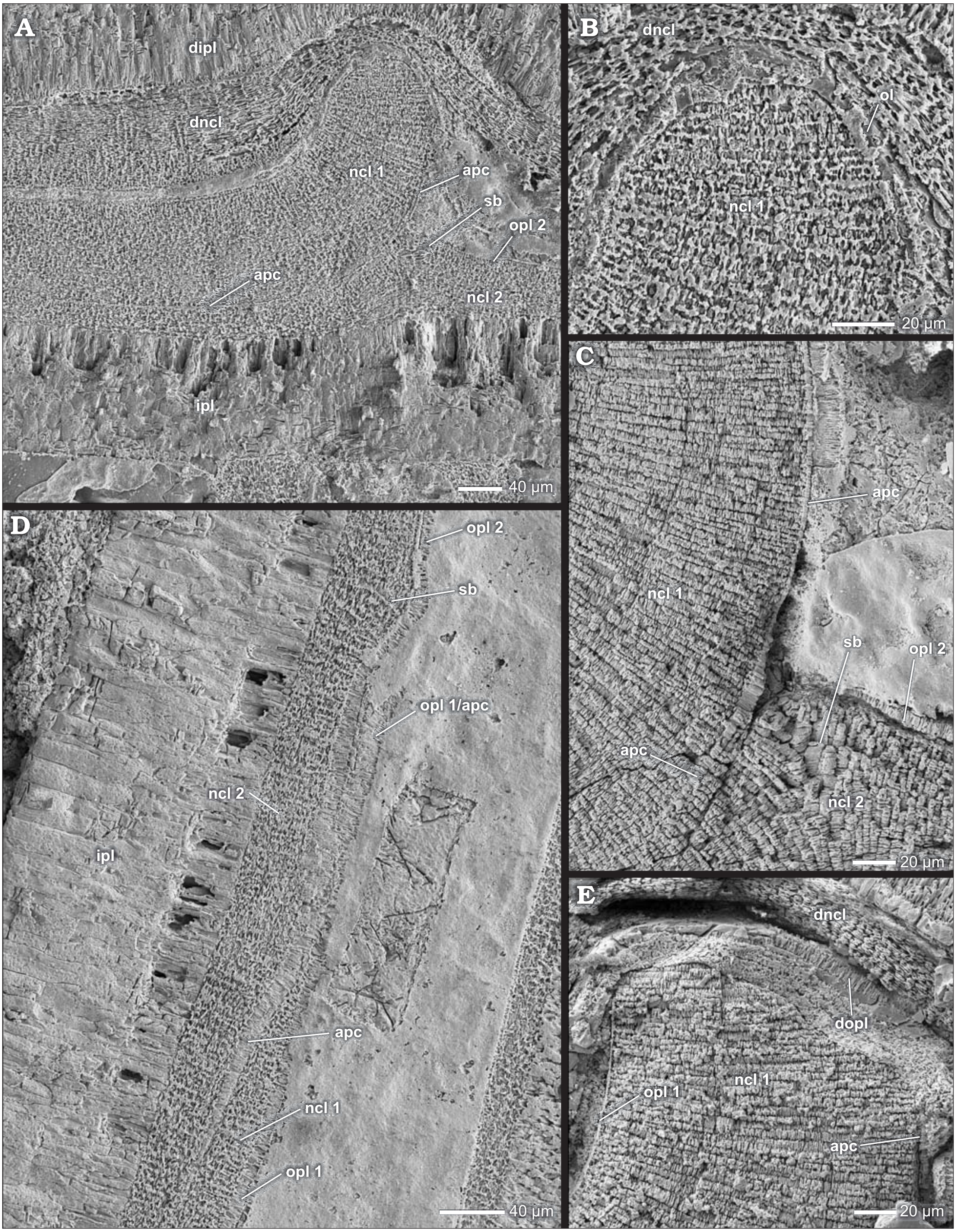


Fig. 4. Internal structure of flares (median section, growth direction right) in *Protetragonites fraasi* (Daqué, 1910) (BSPG MAn-4734) from Sakaraha, Morondava Basin, SW Madagascar; Upper Oxfordian, Jurassic. **A**. Partially resorbed flare, the primary shell bends outwards and ends in a round stump; secondary shell material is attached from beneath and forms a prominent bulge in front of the flare. **B**. Close-up of A, the flare's end is rounded through resorption. **C**. Contact of the primary shell with the secondary shell; the apertural prismatic coating is in contact with the outer prismatic layer of the secondary shell. **D**. Dorso-lateral equivalent of a flare, only a short shell extension is formed by the outer prismatic layer. **E**. Overgrown and broken flare, the →

by the mantle; Seilacher and Gunji (1993: 255) show corresponding, isolated “apertural rings” in the *Posidonia* Shale basin of Germany. We expect that this applies generally for removed flares with rounded stumps.

(iv) In several lytoceratid taxa, the resorption of flares is restricted to the contact area of the subsequent whorl; the frills are preserved at the whorl flanks. At the position of the subsequent whorl the flare has a cutting hole that matches with the perimeter of the subsequent whorl (e.g., Drushits et al. 1978; Doguzhaeva et al. 2010), indicating activity of the mantle of the following whorl. This is similar to the observations in *Argonauticeras* mentioned above; horizontally cut flare-bases are restricted to the ventral shell portions (Fig. 3B$_1$) whereas lateral, rounded stumps of the flares prevail (Fig. 3A$_1$). In *Argonauticeras*, each ventral, cut flare represents a cutting hole caused by the mantle of the following whorl. The horizontal cutting edge ends at the same height as the adoral bulge of the second shell generation. The bulge acts as a template for height (Fig. 5F, H, I). It is rather unlikely that the actual mantle could anticipate the needed height of the rib-like ridges or cut off the flare frill horizontally.

However, observations of an organic-rich dorsal coating layer covering the complete conch of *Gaudryceras* (Drushits et al. 1978; Birkelund 1980) may indicate a significantly larger potential extension of the mantle. It provides an explanation how flares of older, preceding whorls could be resorbed ventrally and laterally by the mantle of the following whorl (Fig. 5A, G–I). If this is true, the amount of resorption of the flare seems to be dependent on the position in the whorl, ventral (cut flare-bases) or lateral (rounded flare stumps), at least in *Argonauticeras*.

We prefer the possibility that the mantle removed and smoothed portions of the flares on two occasions, namely during formation of the actual aperture and during overgrowth by the following whorl (after 360°). Still, we cannot exclude the possibility that ventral and lateral portions of the flares were removed and smoothed by the mantle tissue on only one occasion—overgrowth by the following whorl.

According to our interpretation, ammonoid mantle tissue removes flares that are about 100 μm thick. Thus, the resorption ability in ammonoids resembles that of recent *Nautilus*, which is able to resorb outer shell portions of up to 150–200 μm thickness during overgrowth (Signor 1985; Ward 1987). It has to be noted that the removal of flares has a potential for misinterpretation. The varices associated with the rib-like ridges of *Argonauticeras* indicate the presence of flares but were handled as common ribs or varices in other works (e.g., Arkell et al. 1957; Hoffmann 2010). In this study we report on flares in *Argonauticeras* for the first time.

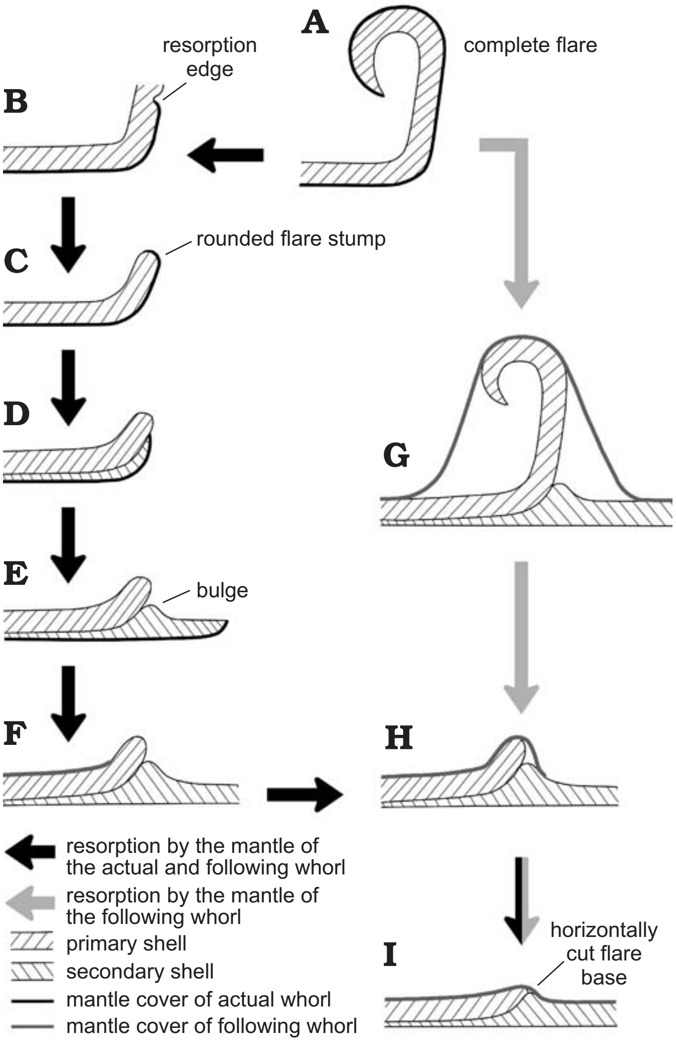


Fig. 5. Resorption process in flares of Lytoceratoidea. **A**. A complete flare with mantle cover. **B**. The retracting mantle begins resorption of shell material at the base of the flare. **C**. The mantle tissue rounds the flare stump through resorption. **D**. The retracted mantle begins secretion of secondary shell material. **E**. The mantle continues secreting the secondary shell. **F**. The mantle of the subsequent whorl begins to overgrow the flare stump of the preceding whorl. **G**. The mantle of the subsequent whorl overgrows the complete flare of the preceding whorl and begins its resorption. **H**. The mantle of the subsequent whorl resorbs the flare stump of the preceding whorl. **I**. The mantle of the subsequent whorl has smoothed the shell surface of the preceding whorl.

Secondary flares.—Secondary flares occur on the outer whorls as a sequence of 4–12 regularly spaced, weak rib-like ridges preceding the formation of a fully developed flare in *Argonauticeras* (Fig. 6) but they had smaller dimensions. Similar to the primary flares, secondary flares mark the junction of two shell generations; ventrally, they appear like primary flares with a horizontally cut base (opl 1 and ncl 1 in Fig. 6). In contrast to the primary flare the participating nacreous layer is significantly thinner (ncl 1 in Fig. 6). In front of the cut secondary flare a bulge is present contributing to its rib-like appearance (sb in Fig. 6). The relief of the

---

primary shell ends in an irregular breaking edge. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; ol, organic layer; sb, shell bulge.

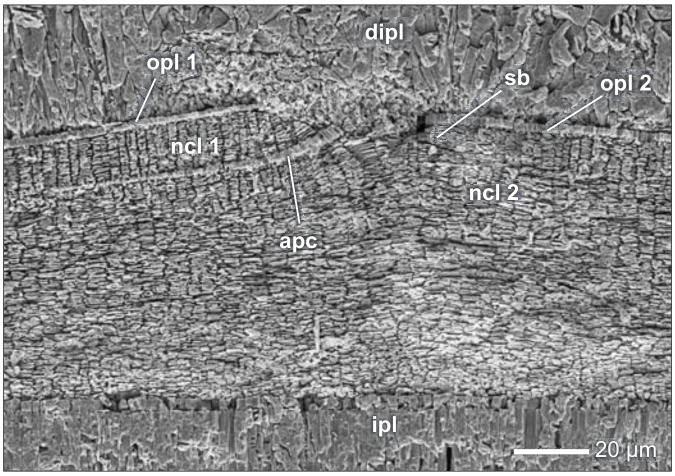


Fig. 6. Internal structure of a secondary flare (median section, growth direction right) in *Argonauticeras besairiei* Collignon, 1949 (BSPG MAo-1802) from Ambatolafia, Mahajanga Basin, NW Madagascar; Lower Albian, Cretaceous. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; sb, shell bulge.

bulges can form a corresponding internal furrow, i.e., an undulation of the shell wall that the ipl smoothes out. It is likely that secondary flares developed like primary flares but were probably smaller marking a shorter interruption of growth.

Parabolae.—*Choffatia* developed a regularly spaced number of parabolae, up to nine per whorl. None of the observed parabolae is completely preserved. Structurally, parabolae resemble flares in several aspects in particular showing the junction of two shell generations, the primary and secondary shell. In median cross section, the primary shell appears to be cut perpendicular or sub-perpendicular to the shell surface (ncl 1 in Fig. 7A, B), at the position of parabolae. It changes the relative orientation to the shell surface depending on its position in the shell whorl. At the ventral saddle, the primary shell has a horizontal orientation, parallel to the shell surface. At shell portions adjected to the notches, the shell bends slightly outwards (Fig. 7D) and at the notches, the cutting edge remains clearly elevated (80 µm) above the shell surface (Fig. 7C). In transversal cross section, the primary shell forms characteristic slots at the parabolic notches (Fig. 8); the primary shell ends abruptly (ncl 1 in Fig. 8B–E), being similar to the observation in median section. The primary shell seems to be simply constructed; only the involvement of a thin ncl 1 (16–20 µm) was usually observed. Although the opl 1 is not preserved, we assume its presence. This is because Sprey (2002: pl. 4: 7) shows that parabolae of juvenile *Binatisphinctes* are exclusively composed of the opl 1. Similar to the flares, parabolae form an apc but only at the position of the notches as part of the outward bending shell edge (apc in Fig. 7C). The apc thickens distally but vanishes nearly completely towards the parabola-base.

As in flares the shell wall is locally doubled at the position of parabolae through the formation of the secondary shell from beneath (ncl 2 in Figs. 7, 8). It is this new generation that forms the parabolic nodes by undulation within the parabolic notches (Fig. 7D). The secondary shell seems to consist only of an ncl 2. A thin prismatic layer, or in most cases a void, separates the two shell generations (Fig. 7A, B). The ncl 1 and ncl 2 merge at varying distances aboral of the cutting edge (up to a half length of a septal chamber); therefore the beginning of the ncl 2 cannot be determined. Only at the notches, the secondary shell forms a prominent prismatic thickening (pt in Fig. 7C). In cross section, the pt has a symmetric triangular outline and has the same height as the outward bending cutting edge in front of which it is formed. The outer prisms habitus is much fainter than at the broad pt-base. The aboral margin of the pt wedges out underneath the free cutting edge and in the adoral direction. The pt and the apc of the free edge are separated by a discontinuity. Interestingly, Doguzhaeva (2012) describes prismatic “lens-like inclusions” at the same position (parabolic notches) in *Indosphinctes* (Perisphinctoidea). Each parabola is underpinned by a continuous inner prismatic layer (Fig. 8B–D).

Formation of parabolae.—As in flares, the junction of two shell generations in parabolae indicates the end of a secretion cycle, which is accompanied by the formation of a (not preserved) temporary aperture (halt in growth), and the subsequent withdrawal of the mantle for secretion of a new shell segment of the conch tube (continuing growth). The temporary aperture of parabolae was probably covered with mantle tissue as in flares (apc): it is likely that the apc of both is equivalent, but was perhaps diagenetically altered here (change in thickness). However, the temporary aperture was modified afterwards (cutting-edge, see below).

After formation of the aperture, the mantle retracted into the living chamber to begin secretion of the new shell segment in front of it (shell duplication). The withdrawal of the mantle edge was probably very extensive, as is indicated by the wide aboral extension of the prismatic separation layer of the shell generations. This layer could be the opl 2 (usually secreted by the adoral mantle edge). However, we prefer the possibility that the separation is accomplished by the apc and that the opl 2 begins near the cutting-edge, which is more in accordance with the observations in flares (begining at the base). Also in shell injuries, the opl 2 of the replacement shell begins immediately beneath the breaking-edge (e.g., Keupp 1998, 2012; GR personal observations). Similar to flares, there is evidence suggesting compression of the mantle tissue during formation of the parabolic nodes of the secondary shell (undulation). The soft tissue is probably compressed during withdrawal of the mantle and thus pressed outwards in reaction (compare Teisseyre 1883, 1889).

It is very likely that the prismatic “lens-like inclusions” described by Doguzhaeva (2012) and our pt are equivalent structures indicating a general feature for parabolae, probably of biological origin. This pt could originate in the opl 2. However, we cannot exclude a diagenetic formation. The gradual fainting of its prisms from the inside to the out-

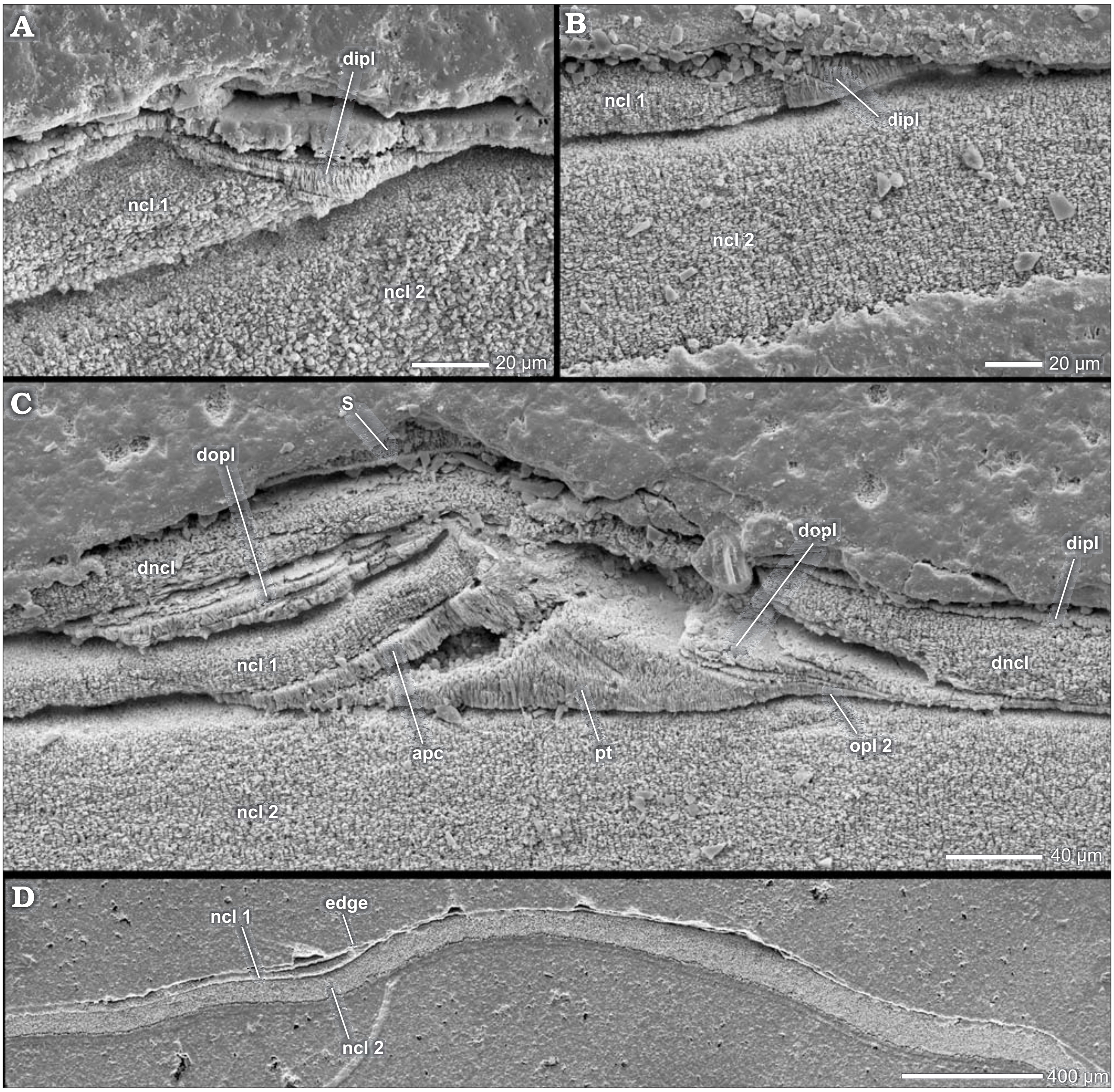


Fig. 7. Internal structure of parabolae (median section, growth direction right) in *Choffatia* sp. (BSPG MAn-4520) from Dubki near Saratov, SW Russia; Upper Callovian, Jurassic. **A**, **B**. Discontinuity of the parabola, the primary nacreous layer ends abruptly. A secondary nacreous layer is attached from beneath. The relief is compensated by the dorsal inner prismatic layer. **C**. Discontinuity of parabolae at the position of the notches. The primary shell bends outwards and has an apertural prismatic coating. The secondary shell is attached from beneath. In front of the free edge of the primary shell a symmetric, prismatic thickening is formed. The dorsal shell compensates the relief. **D**. Lateral parts of the notches show the typical outward undulation of the new shell of the parabolic node. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; dncl, dorsal nacreous layer; dopl, dorsal outer prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell; opl 1/2, outer prismatic layer of the primary/secondary shell; pt, prismatic thickening; S, septum.

side indicates an outward-tending growth independent of the mantle tissue. This could be the product of diagenetic epitaxy or remote shell biomineralization, e.g., it mineralized out of a plug of extrapalial fluid with the opl 2 as the nucleolus for mineralization without direct control by the mantle tissue (Chinzei and Seilacher 1993; Seilacher and Chinzei 1993).

Finally, with continuing shell growth, the apical mantle portions secrete the inner prismatic layer (e.g., Kulicki 1979, 1996; Birkelund 1980), covering (and smoothing) the inner surface of the whorl.

Modification of parabolae.—A complete temporary aperture is not preserved; the primary shell is cut off. It is rather unlikely that the changing orientation of the primary shell and its cutting edges at the ventral saddle and the parabolic notches was caused by resorption (actual or subsequent whorl). Furthermore, the expected smoothing

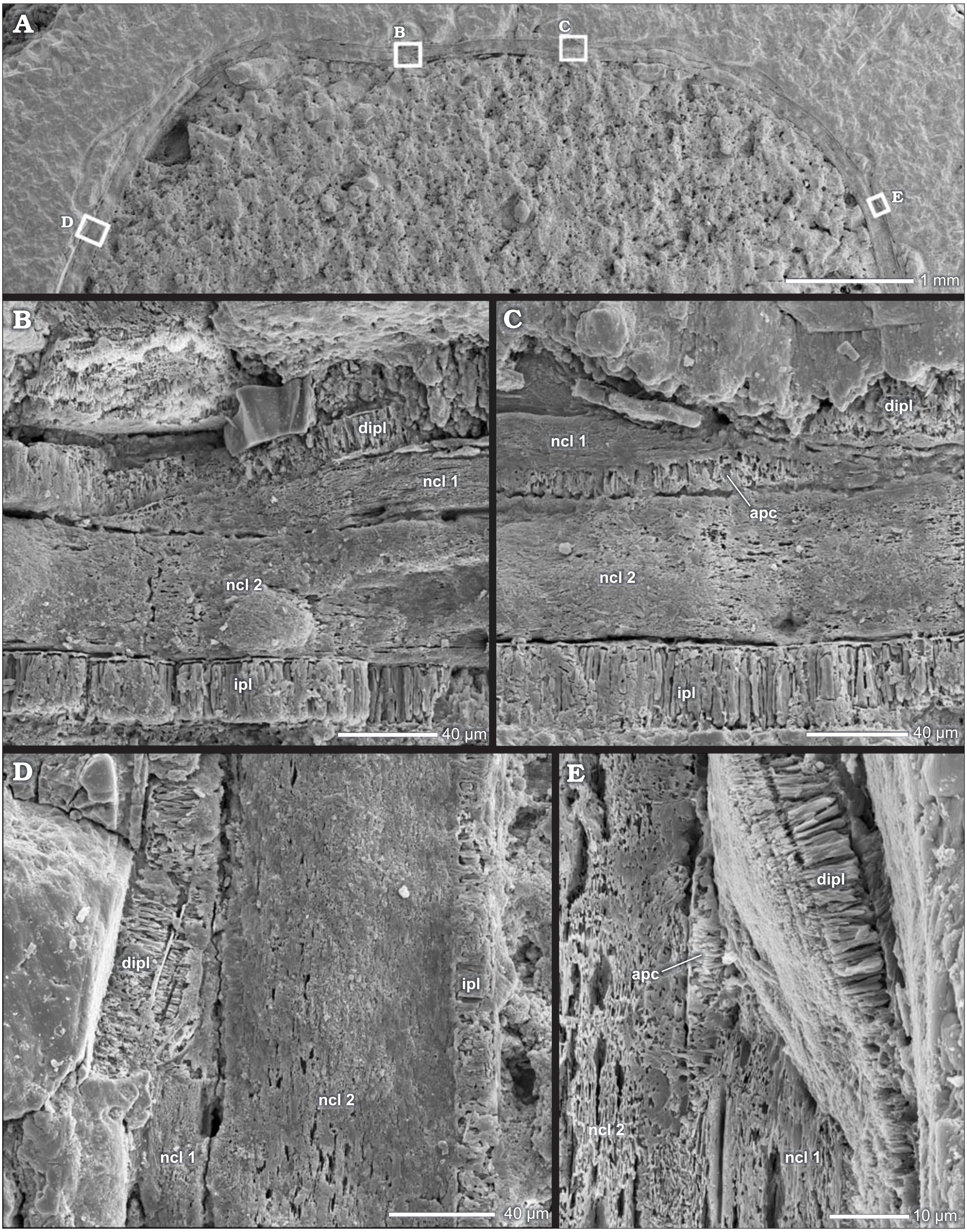


Fig. 8. Internal structure of parabolae (transversal section) in *Choffatia* sp. (BSPG MAn-4519) from Dubki near Saratov, SW Russia; Upper Callovian, Jurassic. **A**. Parabola with notches. **B**–**E**. Discontinuity of the parabolae, the primary shell forms slots at the position of the notches. A secondary shell is attached from beneath. The relief is compensated by the dorsal inner prismatic layer. Abbreviations: apc, apertural prismatic coating; dipl, dorsal inner prismatic layer; ipl, inner prismatic layer; ncl 1/2, nacreous layer of the primary/secondary shell.

or rounding of the shell is absent (e.g., Kohn et al. 1979). However, observed cutting edges are similar to reported breaking-edges of injuries (e.g., Keupp 1998, 2012; GR personal observations). Hence, we propose that the removal of the former aperture results from breakage, probably caused by the overgrowth of the subsequent whorl. Due to the more or less fragile character of the primary shell, shell portions would easily break off.

Primary shape of parabolae.—The ultrastructural data allow some substantiated assumptions about the original morphology of parabolae. Our observations contradict the model of resorbed, temporary apophyses (Teisseyre 1883, 1889; Siemiradzki 1898–1899; Brinkmann 1929; Hiltermann 1939). According to this model the ventro-lateral sinus of the parabolic notch is equivalent to the sinus of the apophyse. Both are supposed to be formed by the same processes, which for the apophyse are a local decrease in shell growth rates, i.e., it is not affected by resorption (or other kind of shell removal). In the apophyse model, resorption takes place only laterally (shortening of the apophyse) and ventrally at the aperture. Contrary to that, the removal (breakage or resorption) takes place along the complete length of parabolae. Furthermore, the original aperture of parabolae was enlarged at the position of the notches, an observation more or less unknown from the sinus of the apophyse, and the shell relief is rather smooth. The notch results from a folding of the aperture (see below). Several macroscopic aspects give further support, i.e., parabolae are affected by sculptural compensation in reaction to injuries; their position in the shell is not determined in contrast to that of apophyses which are always unaffected, even by previous injuries (Keupp 1973, 2000, 2012; Keupp and Dietze 1987), indicating a different formation process. The difference is also reflected in dimorphism, whereas parabolae occur in micro- and macroconchs of the same species. Namely, only adult microconchs develop apophyses, and smooth apertures are typical for adult macroconchs. The formation of the terminal aperture seems to be decoupled from the development of parabolae. It is rather unlikely that juvenile parabolae are ontogenetically connected to adult apophyses.

The enlargement of the parabolic aperture at the notches points to at least two possible primary shapes prior to removal.

(i) It was presumed that a parabolic notch could be a relic of a spine (Stieler 1922; Wendt 1968; Bucher and Guex 1990). In fact, Checa and Martin-Ramos (1989) highlighted the similarity of spines of *Aspidoceras* to those of parabolae in other Aspidoceratinae and assumed a morphogenetic connection. The outward bending cutting-edge of each notch would represent the aboral base of a former spine and parts of its flank. These spines have to be adorally open, as indicated by the apc (Fig. 1B: right expression), which corresponds to the assumptions of Stieler (1922) and Wendt (1968). Similar spines are known from some Recent gastropods, e.g., *Murex*.

(ii) Why, however, is the breaking edge not restricted to parabolic notches but continues at the flank? The observations match with Michalski's (1908) assumption that parabolic lines are the remains of a flare-like extended aperture, i.e., a frill. A parabolic notch represents a local folding of the frill. Michalski (1908) based his interpretation on the morphological transition of parabolae into flares in the Early Jurassic lytoceratid Pleuroacanthitinae (compare Wähner 1894). Recently Hoffmann and Keupp (2010) examined the phylogenetic relationship between parabolae and flares in well-preserved specimens of early Liassic *Analytoceras* from Timor and confirmed that flares represent morphological derivates of parabolae (Fig. 9). Hence, parabolae and flares are not only similar in internal structure (Table 2) but are alike in appearance (Fig. 1B: middle expression).

Table 2. Shell wall components of shell generations of flares and parabolae.

Shell	Primary	Secondary
Outer prismatic layer	opl 1	opl 2
Nacreous layer	ncl 1	ncl 2
Apertural prismatic coating	apc	
Inner prismatic layer		ipl

In large specimens of *Analytoceras* the folds of parabolae are morphologically similar to adorally open, semi-closed spines (e.g., Bucher 1997; Hoffmann and Keupp 2010). This observation is in line with the assumed formation process of aspidoceratid spines (Checa and Martin-Ramos 1989). Therefore, we regard parabolae as frilled, temporary apertures with local folding at the future notches that can form spine-like extensions. The parabolae and their parabolic spines probably formed a rather small enlargement of the aperture. In our parabolae, the thin shell lamellae of the ncl 1, in comparison to the thick ncl 2 (Figs. 7B, 8B–D), indicate an early mineralization state near the former apertural edge, or rather secretion area. Therefore, the frills (and spines) were probably not much larger than the preserved outward bending cutting edges at the notches, probably slightly higher than the observed 80 μm.

A frill-like enlargement probably does not prevail for the whole parabola. For example, the ventral saddle of parabolae in *Analytoceras* forms a ridge-like undulation and end parallel to the shell surface (Fig. 9A). This could also explain the horizontal orientation of the primary shell at the ventral saddle in our parabolae; ventrally the apertural edge could be horizontally orientated (Fig. 1B: middle and right expression) as in other ammonoids (e.g., Mutvei 2014). Alternatively, the frill could break off at its base. In some Perisphinctoidea, like *Orthosphinctes*, the lateral parabolae form a rib-like undulation of the aperture; the shell bends outwards and then returns to the height of the normal shell surface, no frill is formed.

Secondary effects of frilled parabolae.—The frill-like aperture assumption for parabolae results in several implications: analogously to flares we assumed that some parabolic ribs represent shortened or stumps of frills which are reinforced by the secondary shell.

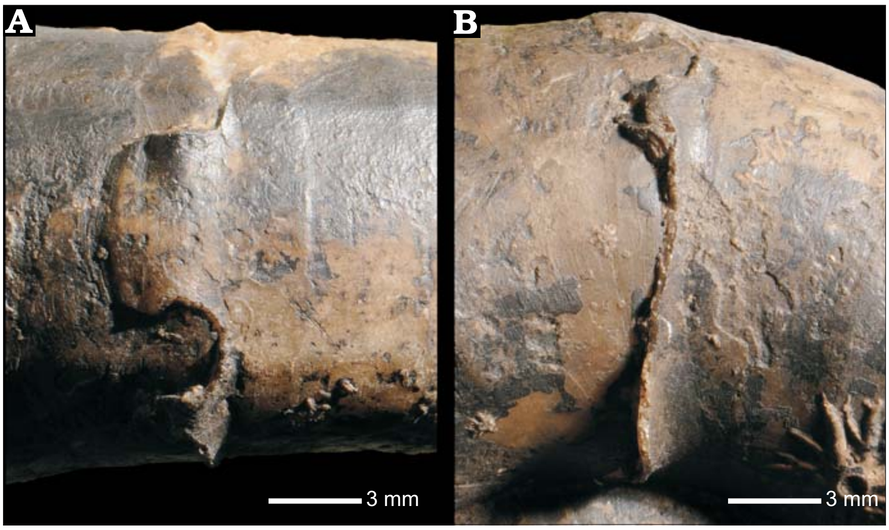


Fig. 9. Transition of parabolae and flares in *Analytoceras hermanni* (Gümbel, 1868) (BSPG Man-x) from Bihati river valley south of Baun, SW Timor, Hettangian, Jurassic (compare Hoffmann and Keupp 2010); in ventral (**A**) and lateral (**B**) views.

The sculptural discontinuity is a morphogenetic effect of frill formation, its subsequent removal and the reattachment of the shell-secreting mantle tissue. After withdrawal, the mantle edge attaches to the curved base of the parabolae (note that in flares the base is usually straight and therefore paralleling the growth lines) and bridges the slots of the notches. The sculpture of the secondary shell was formed parallel to the attachment line of the mantle edge and is therefore independent of the aboral sculpture of the primary shell that is to be cut off. Furthermore, it is likely that the aboral sculpture continues at the frill, probably influenced by the folding. The parabolic notches represent a lack of shell material (frill-folds/spines), instead of a cut through the adoral sculpture, increasing the impression of different sculptural orientation of the primary and secondary shell. Formation of the frill-folds/spines was presumably the reason for the often-observed local deceleration in growing near the parabolic notches and the accompanied compression of growth lines (Keupp 1973).

As previously indicated, the parabolic nodes are secondary infillings of the parabolic notches resulting from the reattachment of the mantle and secretion of new shell material while the mantle is pressed outwards. The mineralized shell copies the resulting outer relief of the mantle. Hence, the parabolic nodes are equivalent to the hollow floors in hollow spines of other ammonoids (e.g., *Pleuroceras*, *Kosmoceras*), which are subsequently added as shell growth continues (e.g., Erben 1972; Keupp 1973; Birkelund 1980).

Derivation of frill-model from superstructure-model for parabolae.—Doguzhaeva (2012) proposed the interesting hypothesis that parabolae represent a band-like superstructure of the musculature. According to her, the parabolic line represents the trace of a simultaneous internal and outer attachment of the musculature indicating a (semi-) internal shell. The interpretations of parabolae as temporary apertures were therefore dismissed by her. The hypothesis of Doguzhaeva (2012) is based on the following observations and interpretations: (i) Impressions of parabolic notches preserved as nodes (knobs) at the internal mould represent pits of the shell wall which reflect sites of muscle attachment at the position of the notches. (ii) The dorsal shell portions bear parabolic nodes as well, which represent dorsal muscle attachment. (iii) The ventral saddle and lateral areas adjoining the parabolic notches have a characteristic striation representing a part of the band superstructure. (iv) Instead of an interruption in shell growth, the parabolic notches are represented by prismatic lens-like embeddings in the nacreous layer. These are accompanied by small nacreous chips denoting compression pressure from muscular activity.

The interpretation of Doguzhaeva (2012) is in contradiction to observations reported in the sections above. However, her observations can be reinterpreted in favour of the frill-model. In this study the whole parabolic line as well as the notches are associated with a discontinuity in shell growth (junction of two shell generations, withdrawal of the mantle). (i) Instead of representing muscular attachment pits, the parabolic nodes are formed as secondary infillings of an undulated secondary shell within the parabolic notches (Fig. 7D), caused by reattachment accompanied by compression of the mantle. The internal relief of the node is preserved as a knob-like mark on the internal mould (Fig. 7D) as Doguzhaeva (2012) observed. (ii) A dorsal equivalent of parabolae could not be recognized in median or transversal cross section but the dorsal shell of the succeeding whorl compensates the relief. Accordingly, dorsal parabolic nodes merely represent the cast of the former whorl in the dorsal shell (Fig. 7C). (iii) The striations of the ventral saddle and of the adjected areas of the notches are probably equal to common growth increments, which were interrupted due to the loss of the parabolic folds/spines (notches). (iv) The pt associated with the frill-fold/spines (Fig. 7C) is probably equivalent to the prismatic embeddings found by Doguzhaeva (2012). Doguzhaeva (2012) cut this pt in transversal cross sections, simulating an embedding in the nacreous layer, but representing the ncl 1 and the ncl 2 separated by the pt. Only the embedded nacreous chips were not recognized by us but they could be a product of diagenetic disruption of the shell.

Homology.—Based on the identical internal structure (opl 1, ncl 2, apc; Table 2) and formation process, the similar primary shape and transitional structures in Pleuroacanthitinae, we propose a general homology for flares and parabolae. Occurrences of parabolae in Phylloceratoidea—the stem group of Jurassic and Cretaceous Ammonitina—suggest that these were passed on to the Lytoceratoidea and Perisphinctoidea, probably as a facultative feature. Accordingly, their internal construction is identical. Parabolae seem to be the primary state whereas the simpler flares of Lytoceratoidea are the derived state (Michalski 1908; Hoffmann 2010; Hoffmann and Keupp 2010). It can be assumed that in the perisphinctids a second evolutionary trend can be recognized in addition to the flares in lytoceratids: the closed hollow spines of aspidoceratids are probably derived from the parabolae, i.e., the parabolic folding forms the spines (Checa and Martin-Ramos 1989). For the Late Devonian parabolae-bearing Clymeniida the relation to Jurassic and Cretaceous taxa is difficult to estimate but a similar structure and formation process of their parabolae is likely.

Megastriae.—Parabolae, flares and secondary flares are in accordance with the definition of megastriae proposed by Bucher and Guex (1990), i.e., radial linear elements associated with a discontinuity in shell growth comprising the outer prismatic (opl 1 × opl 2) and the nacreous (ncl 1 × ncl 2) layer (compare Bucher et al. 1996; Bucher 1997). It is questionable whether this strict definition can be always used for radial linear elements associated with an interruption in shell growth that are normally assigned to megastriae. For example, Drushits and Doguzhaeva (1981) and Sprey (2002) show flares and (juvenile) parabolae that are only formed by the opl 1. Strictly speaking, these sculptural elements cannot be taken as megastriae according to Bucher and Guex (1990). However, the observations of Sprey (2002) may indicate a structural change of parabolae during ontogeny. Parabolae of juveniles are composed of the opl 1 while parabolae of adults are composed of the opl 1 and the ncl 1. This is likely since Sprey's (2002) and our observations were made in closely related genera: *Binatisphinctes* and *Choffatia*. In our opinion, the differences in structure do not necessarily imply a different morphogenesis, i.e., the withdrawal of the mantle edge. Instead, they indicate earlier activity of additional shell-secreting mantle tissue prior to retraction, i.e., formation of the ncl 1. Variations in structure may just indicate a different timing of formation (prolonged or short periods of shell precipitation). Although structurally very similar, the primary and secondary flares represent a difference in time of formation, too, as indicated by their different scale. However, both would be handled equally as megastriae according to Bucher and Guex (1990). In our opinion the strict definition of megastriae excludes a number of related, radial linear sculptures or does not consider morphological or temporal differences. We recommend a broader definition of megastriae, i.e., radial linear elements associated with an observable interruption of shell growth in a single or multiple shell layers. For the distinction of megastriae subtypes, different time frames have to be taken into account. It is noteworthy that the identification of a megastriae (sensu Bucher and Guex 1990; Bucher et al. 1996 and as defined here) does not automatically imply the presence of an originally enlarged aperture, comparable to flares or parabolae.

Possible function of a frilled aperture.—Since the frill formation constituted a certain effort for the animal, it is likely that the frill was used for a special purpose and was not instantly replaced as proven by the apc of flares and parabolae which indicates a resting stage (permanent mantle attachment).

Flares and parabolae extend the effective radius of the aperture. Similar apertural modifications are observed in some modern gastropods, such as Cassidae, Ranellidae, Personidae, and Muricidae (Wendt 1968; Linsley and Javidpour 1980; Seilacher and Gunji 1993; Vermeij 1993) and have a primary function of protection against predators. This kind of interpretation for flares and parabolae is supported by the fact that parabolae are predominantly restricted to juvenile ammonoid shells. Their small diameter made them vulnerable to attack. Development of some protective shell elements or strategies likely helped them to survive this critical period of their ontogeny. The ammonoid frill could impede attacks on the aperture. The larger radius probably complicates the grabbing of the whole aperture. We assume that flares and parabolae are very fragile structures that easily break off during an attack, allowing the ammonoid to escape or to withdraw the soft body into its living chamber, i.e., an easy-to-tear strategy (Checa 1994; see also Keupp 2012: 79). Additionally, it could serve as a certain deterrent of potential attackers, especially when armoured with spines. The permanent mantle cover (apc) possibly renders deterring colour patterns, as seen in modern molluscs (e.g., Vermeij 1993). Deterrence would be useful since flares and parabolae hinder fast movement in an escape. On the other hand, the extended surface of the aperture and its mantle cover could fulfil a sensory function. The frill could improve the perception of movements in the immediate vicinity and the chemical perception of predators, prey or mating partners.

In present day gastropods, e.g., *Murex*, similar temporary apertural frills are associated with an episodic growth mode (Wendt 1968; Vermeij 1993; Checa 1994; Bucher et al. 1996). The shell portion between frills represents a stage of fast growing periostracum whereas a frill represents a long lasting mineralization stage and pause in growth. The shell structure of ammonoid flares and parabolae reflects this situation, i.e., junction of two shell generations and pause in secretion. Hence, the apc indicates an episodic rhythm of growth in flares and parabolae. However, in *Argonauticeras*, two episodic patterns overlap each other: the pattern of the primary flares and that of secondary flares. The explicit formation of primary flares in contrast to secondary flares underlines its needed function.

Several authors have assumed that the repeated interruptions of growth represent a controlled reorientation of the shell aperture to compensate fabricational conflicts that disturb spiral growth (Seilacher and Gunji 1993; Bucher et al. 1996; Bucher 1997). Furthermore, these authors argue that the sculptural discontinuity seen in parabolae is directly related to the controlled reorientation of the aperture. Whereas a reorientation is within the realm of possibility, the sculptural discontinuity in parabolae is a morpho-fabricational secondary effect of frill formation and its removal, as mentioned above.

Conclusions

The internal structure of lytoceratid flares and perisphinctid parabolae indicate that both represent homologous constructions associated with episodic growth. Both structures represent the junction of two different shell generations, comprising the outer prismatic (opl 1 × opl 2) and nacreous (ncl 1 × ncl 2) layer. The second shell generation is formed after withdrawal and reattachment of the mantle tissue that causes the discontinuity of shell layers. Therefore, the term megastriae proposed by Bucher and Guex (1990) is applicable to both, flares and parabolae. During the final step of shell formation, the mantle tissue secretes the inner prismatic layer (ipl). Due to the internal structure of parabolae, an affiliation to a superstructure of the musculature system, hypothesized by Doguzhaeva (2012), can be dismissed.

Flares and parabolae are formed as episodic, temporary frill-like extensions of the aperture during pauses in growth. Their inner surface was covered by the mantle as indicated by an apertural prismatic coating (apc), which we report for the first time. The coating is probably homologous with the mantle adhesive layer of *Nautilus* (Erben et al. 1969; Doguzhaeva and Mutvei 1986; Mutvei and Doguzhaeva 1997; Mutvei 2014). The complete preserved flares of *Argonauticeras* show that these end in a backward reflection of the shell. A complete parabola was not observed. Their prominent parabolic notches represent traces of local foldings that can form open spines. The sculptural discontinuity usually associated with parabolae is not caused by resorption but is a morphogenetic effect that results from the withdrawal and reattachment of the mantle edge at the curved base of parabolae.

However, flares show evidence of resorption of the shell. Resorbed flares take the form of rounded stumps or were cut horizontally at their bases. Cut bases and the bulge (an undulation of the secondary shell in front of the flares) form weak rib-like ridges. These (false) ribs can be easily distinguished from common ribs (undulation) by the structural discontinuity but have the potential for macroscopic misinterpretation: for example, this study is a first report of flares for *Argonauticeras*, which have previously been described as ribs (Hoffmann 2010). We propose a removal of flares by the mantle tissue of the actual whorl and of the following whorl. The actual mantle tissue resorbed the distal parts of the flare prior to secretion of the secondary shell, forming rounded stumps as a result. The horizontally cut flares are the result of resorption of the ventral flare-stumps by the mantle of the following whorl during overgrowth. In contrast to resorption, breakage is assumed for the fragile parabolic frills of *Choffatia*.

The enlargement of the aperture of flares and parabolae probably had a certain defensive purpose against predatory attacks (e.g., expandable shell, deterrence). This effect could have been enhanced through coloured mantle tissue (warning or camouflage pattern) that might also have had a sensitive function.

Acknowledgements

We would like to thank Ulrich Kotthoff, Wolfgang Weitschat (both University of Hamburg, Germany) and Vasily V. Mitta (Russian Academy of Sciences, Moscow, Russia) for providing well-preserved material for this study. Furthermore, we would like to thank our reviewers, Kazushige Tanabe (University of Tokyo, Japan), Hugo Bucher (University of Zurich, Switzerland), Cyprian Kulicki (Institute of Paleobiology PAS, Warsaw, Poland) and Neil Landman (American Museum of Natural History, New York, USA), for constructive comments that helped us to improve the manuscript. And we thank our proofreaders, Anja Kühnel, Franziska Weißmann, and Giles Shephard (all Berlin, Germany) and Monika Bulang-Lörcher (Freie Universität Berlin, Germany) for making the drawings. This work was funded by the Berlin Universities Elsa Neumann Stipend.

References

Arkell, W.J., Kummel, B., Miller, A.K., Moore, R.C., Schindewolf, O.H., Sylvester-Bradley, P.C., and Wright, C.W. 1957. *Treatise on Invertebrate Paleontology, Part L Mollusca 4, Cephalopoda, Ammonoidea*, 1–490. The Geological Society of America and The University of Kansas Press, Lawrence.

Birkelund, T. 1980. Ammonoid shell structure. *In*: M.R. House and J.R. Senior (eds.), *The Ammonoidea*, 177–214. Academic Press, London.

Brinkmann, R. 1929. Statistisch-Biostratigraphische Untersuchungen an mittel-jurassichen Ammoniten über Artbegriff und Stammesentwicklung. *Abhandlungen der Gesellschaft der Wissenschaften in Göttingen, Mathematisch-Physikalische Klasse* 13: 1–249.

Bucher, H. 1997. Caractères périodiques et mode de croissance des ammonites: Comparaison avec les gastéropodes. *Geobios Mémoire Spécial* 20: 85–99.

Bucher, H. and Guex, J. 1990. Rythmes de crossance chez les ammonites triasique. *Bulletin de la Société Vaudoise des Sciences Naturelles* 80: 191–209.

Bucher, H., Landman, N.H., Klofak, S.M., and Guex, J. 1996. Mode and rate of growth in ammonoids. *In*: N.H. Landman, K. Tanabe, and R.A. Davis (eds.), Ammonoid Paleobiology. *Topics in Geobiology* 13: 407–461. Plenum Press, New York.

Checa, A. 1994. A model for the morphogenesis of ribs in ammonites inferred from associated microsculptures. *Palaeontology* 37: 863–888.

Checa, A. and Martin-Ramos, D. 1989. Growth and function of spines in the Jurassic ammonite *Aspidoceras*. *Palaeontology* 32: 645–655.

Chinzei, K. and Seilacher, A. 1993. Remote biomineralization I: Fill skeletons in vesicular oyster shells. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 190: 349–361.

Cochran, J.K. and Landman, N.H. 1984. Radiometric determination of the growth rate of *Nautilus* in nature. *Nature* 308: 725–727.

Cochran, J.K., Kallenberg, K., Landman, N.H., Harries, P.J., Weinreb, D. Turekian, K.K., Beck, A.J., and Cobban, W.A. 2010. Effect of diagenesis on the Sr, O, and C isotope composition of late Createceous mollusks from the Wesern Interior Seaway of North America. *American Journal of Science* 310: 69–88.

Doguzhaeva, L. 2012. Functional significance of parabolae, interpreted on the basis of shell morphology, ultrastructure and chemical analyses of the Callovian ammonite *Indosphinctes* (Ammonoidea: Perisphinctidae), Central Russia. *Revue* de *Paléobiologie* 11: 89–101.

Doguzhaeva, L. and Mutvei, H. 1986. Functional interpretation of inner shell layers in Triassic ceratid ammonids. *Lethaia* 19: 195–209.

Doguzhaeva, L., Bengtson, S., and Mutvei, H. 2010. Structural and morphological indicators of mode of life in the Aptian lytoceratid ammonoid *Eogaudryceras*. *In*: K. Tanabe, Y. Shigeta, T. Sasaki, and H. Hirano (eds.), *Cephalopods—Present and Past*, 123–130. Tokai University Press, Tokyo.

Drushits, V.V. and Doguzhaeva, L. 1981. *Ammonites in Electron Microscope*. 240 pp. Publishing House of Moscow State University, Moscow.

Drushits, V.V., Doguzhaeva, L., and Mikhailova, I.A. 1978. Unusual coating layers in ammonites. *Paleontological Journal* 12: 174–182.

Erben, H.K. 1972. Die Mikro- und Ultrastruktur abgedeckter Hohlelemente und die Conellen des Ammoniten Gehäuses. *Paläontologische Zeitschrift* 46: 6–19.

Erben, H.K., Flajs, G., and Siehl, A. 1969. Die frühontogenetische Entwicklung der Schalenstruktur ectocochleater Cephalopoden. *Palaeontographica A* 132: 1–54.

Guex, J. 1989. Note sur le genre *Franziceras* Buckman (Ammonoidea, Cephalopoda). *Bulletin de la Société Vaudoise des Sciences Naturelles* 79: 347–354.

Hiltermann, H. 1939. Stratigraphie und Palaeontologie der Sonninienschichten von Osnabrück und Bielefeld. 1. Teil: Stratigraphie und Ammonitenfauna. *Palaeontographica A* 90: 109–209.

Hoffmann, R. 2010. New insights on the phylogeny of the Lytoceratoidea (Ammonitina) from the septal lobe and its functional interpretation. *Revue de Paléobiologie* 29: 1–156.

Hoffmann, R. and Keupp, H. 2010. The myth of the Triassic lytoceratid ammonite *Trachyphyllites* Arthaber, 1927, in reality an Early Jurassic *Analytoceras hermanni* Gümbel, 1861. *Acta Geologica Polonica* 60: 219–229.

Keupp, H. 1973. Der Wert anomaler Perisphincten (Ammonoidea) für die Deutung der Parabelgenese. *Geologische Blätter für Nordost-Bayern und angrenzende Gebiete* 23: 20–35.

Keupp, H. 1998. Mundsaumverletzungen bei *Pleuroceras* (Ammonoidea). *Fossilien* 1998 (1): 37–42.

Keupp, H. 2000. *Ammoniten—Paläobiologische Erfolgsspiralen*. 165 pp. Thorbecke Verlag, Stuttgart.

Keupp, H. 2012. Atlas zur Paläopathologie der Cephalopoden. *Berliner Paläobiologische Abhandlungen* 12: 1–390.

Keupp, H. and Dietze, V. 1987. Analyse eines pathologischen Perisphinctiden. *Fossilien* 1987 (6): 274–277.

Kohn, A.J., Myers, E.R., and Meenakshi, V.R. 1979. Interior remodeling of the shell by a gastropod mollusc. *Proceedings of the National Academy of Sciences of the United States of America* 76: 3406–3410.

Kulicki, C. 1979. The ammonite shell: its structure, development and biological significance. *Acta Palaeontologica Polonica* 39: 97–142.

Kulicki, C. 1996. Ammonoid shell microstructure. *In*: N.H. Landman, K. Tanabe, and R.A. Davis (eds.), Ammonoid Paleobiology. *Topics in Geobiology* 13: 65–101. Plenum Press, New York.

Linsley, R.M. and Javidpour, M. 1980. Episodic growth in Gastropoda. *Malacologia* 20: 153–160.

Martin, A.W., Catala-Stucki, I., and Ward, P.D. 1978. The growth rate and reproductive behavior of *Nautilus macromphalus*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 156: 207–225.

Michalski, A. 1908. Schriften aus dem Nachlass von A. Michalski. Notizen über Ammoniten. II. *Mémoirs du Comite Geologique* 32: 100–125.

Mutvei, H. 2014. Shell wall structure and sharp-edged apertural shell margin in the Callovian *Quenstedtoceras* (Cephalopoda, Ammonoidea). *GFF* 136: 531–538.

Mutvei, H. and Doguzaheva, L.A. 1997. Shell ultrastructure and ontogenetic growth in *Nautilus pompilius* L. (Mollusca: Cephalopoda). *Palaeontographica A* 246: 33–52.

Neumayer, M. 1884. Über die Mundöffnungen von *Lytoceras immane* Opp.. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 3: 101–103.

Pompeckj, J.F. 1894. Über Ammonoideen mit „anormaler Wohnkammer“. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 50: 220–290.

Saunders, W.B. 1983. Natural rates of growth and longevity of *Nautilus belauensis*. *Paleobiology* 9: 280–288.

Seilacher, A. and Chinzei, K. 1993. Remote biomoneralization II: Fill skeletons controlling buoyancy in shelled cephalopods. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 190: 363–373.

Seilacher, A. and Gunji, P.Y. 1993. Morphogenetic countdowns in heteromorph shells. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 190: 237–265.

Siemiradzki, J. von 1898–1899. Monographische Beschreibung der Ammonitengattung *Perisphinctes*. *Palaeontographica 1846–1933* 45 (6): 69–352.

Signor, P.W. 1985. Surficial shell resorption in *Nautilis macromphalus* Sowerby, 1949. *Veliger* 28: 195–199.

Sprey, A.M. 2002. Early ontogeny of three Callovian ammonite genera (*Binatisphinctes*, *Kosmoceras* (*Spinikosmoceras*) and *Hecticoceras*) from Ryazan (Russia). *In*: H. Summesberger, K. Histon, and A. Daurer (eds.), Cephalopods—Present and Past. *Abhandlungen der Geologischen Bundesanstalt* 57: 225–255.

Stieler, L. 1922. Anomale Mündungen bei Inflaticeraten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band* 47: 295–346.

Teisseyre, L. 1883. Ein Beitrag zur Kenntnis der Cephalopodenfauna der Ornatenthone in Gouvernement Rjasan (Russland). *Sitzungsbericht der Kaislerlichen Akademie der Wissenschaften in Wien* 88: 608–624.

Teisseyre, L. 1889. Über die systematische Bedeutung der Schalenskulptur, zur Lebensentfaltung und zum Lebensbild der jüngeren skulpturtragenden Ammoniten (Meso- und Neoammonoidea). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band* 6: 570–643.

Vermeij, G.J. 1993. *A Natural History of Shells*. 207 pp. Princeton University Press, Princeton.

Wähner, F. 1894. Beiträge zur Kenntniss der tieferen Zonen des unteren Lias in den nordöstlichen Alpen. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 9: 1–54.

Ward, P.D. 1987. *The Natural History of* Nautilus. 267 pp. Allen & Unwin, Boston.

Wendt, J. 1968. *Discohelix* (Archaeogastropoda, Euomphlacea) as an index fossil in the Tethyan Jurassic. *Palaeontology* 11: 554–575.

Westermann, B., Beck-Schildwächter, I., Beuerlein, K., Kaleta, E.F., and Schipp, R. 2004. Shell growth and chamber formation of aquarium-reared *Nautilus pompilius* (Mollusca, Cephalopoda) by X-ray analysis. *Journal of Experimental Zoology* 301A: 930–937.