



Aptychi microstructure in Late Cretaceous Ancyloceratina (Ammonoidea)

ISABELLE KRUTA, ISABELLE ROUGET, NEIL H. LANDMAN, KAZUSHIGE TANABE AND FABRIZIO CECCA

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The microstructure of aptychi (bivalved calcareous coverings on lower jaws) of three genera of Late Cretaceous Ancyloceratina, *Baculites*, *Polyptychoceras* and *Jeletzkytes* is described for the first time on the basis of well-preserved and in situ material from the Western Interior of the USA and Hokkaido, Japan. Optical and scanning electron microscope observations of aptychi on polished median and cross-sections reveal some variation in their relative size, shape and microstructure among the three genera. The aptychus of *Baculites* is composed of two calcitic layers: one with tilted lamellae and the other one with horizontal lamellae, whereas those of *Polyptychoceras* and *Jeletzkytes* consist of a thin layer with horizontal lamellae. Comparison with aptychi (e.g. *Laevaptychus*) of Jurassic Ammonitina shows that the aptychi of Ancyloceratina differ from those of Jurassic Ammonitina in the smaller number of layers and the absence of a sponge-like structure. We propose for the first time growth models for a sponge-like aptychus of Jurassic Ammonitina and the lamellar aptychus of Cretaceous Ancyloceratina. The remarkable microstructural variation of aptychi observed in Mesozoic Ammonoidea is probably related to the diversity of their modes of feeding and the secondary function of the lower jaws as opercula. □ *Ammonite, aptychi, microstructure, Ancyloceratina, Cretaceous.*

Isabelle Kruta [kruta@mnhn.fr], Muséum National d'Histoire Naturelle (MNHN), Centre de recherche sur la Paéodiversité et les Paléoenvironnements CNRS UMR 7207, UPMC, Case 104 – 4 Place Jussieu, 75252 Paris Cedex 05, France; Isabelle Rouget [isabelle.rouget@upmc.fr] and Fabrizio Cecca [fabrizio.cecca@upmc.fr], Université Pierre et Marie Curie, Centre de recherche sur la Paéodiversité et les Paléoenvironnements CNRS UMR 7207, Case 104 – 4 Place Jussieu, 75252 Paris Cedex 05, France; Neil H. Landman [landman@amnh.org], Division of Paleontology (Invertebrates), American Museum of Natural History, New York, New York 10024, USA; Kazushige Tanabe [tanabe@eps.s.u-tokyo.ac.jp], Department of Earth and Planetary Science, University of Tokyo, Tokyo 113-0033, Japan; manuscript received on 18 April 2008; manuscript accepted on 19 August 2008.

Aptychi are pairs of calcareous plates that occur individually, and/or within the body chambers of ammonites, in Jurassic and Cretaceous marine carbonate rocks (Schindewolf 1958). Meek & Hayden (1865) first described the co-occurrence of the aptychus and upper jaw in the body chamber of a Late Cretaceous scaphitid ammonite from the Western Interior Province, USA, and interpreted the aptychus as the lower jaw element. Subsequent workers, however, have regarded the aptychi as ammonite opercula on the basis of their occasional occurrence just closing an ammonite shell aperture (Trauth 1927–1936; Arkell 1957; Schindewolf 1958; Keupp 2007). More recently, aptychus-bearing larger lower jaws and smaller upper jaws have been discovered together within the body chambers of Mesozoic Ammonoidea belonging to the Ammonitina and Ancyloceratina, some of which also accompanied a radula (Lehmann 1967, 1972, 1979, 1980, 1981; Tanabe *et al.* 1980; Kulicki *et al.* 1988; Tanabe & Landman 2002; Kennedy *et al.* 2002; Landman *et al.* 2007). In such well-preserved

material, an aptychus covers the ventral side of the outer chitinous layer of the lower jaw, indicating that the aptychus represents an outer calcareous covering of the lower jaws of Ammonitina and Ancyloceratina (Lehmann 1980; Morton 1981; Tanabe & Fukuda 1999). In view of the unusually large size and the presence of a median 'hinge' line, aptychi-bearing lower jaws of some Jurassic ammonites have been interpreted to have an opercula-like secondary function by tilting upwards to seal the shell aperture (Lehmann & Kulicki 1990; Seilacher 1993; Engeser & Keupp 2002). Previous authors (e.g. Tanabe & Landman 2002) have suggested that the study of jaw features is particularly relevant to improve our knowledge about the palaeobiology of ammonites, since the relative size, shape and the degree of development of an outer calcareous covering of the lower jaws exhibit remarkable taxonomic variation.

Several analyses regarding the microstructure have been carried out on Jurassic aptychi (Pozzi 1965; Farinacci *et al.* 1976; Turculet 1982; Hewitt *et al.*

1993; Michalik 1996; Kozlova & Arkadieff 2003). Although the study of Landman *et al.* (2006) showed the calcitic nature of placenticeratid jaws, Cretaceous aptychi are instead still poorly known and their microstructure and mineralogy are virtually unknown to date. Because of the strong relationship with ammonoid palaeobiology, the function of aptychi is still heavily debated and makes the study of their microanatomy necessary. The improved knowledge of the organization of aptychi internal features is the only way to understand their construction process and provide clues for the understanding of their function.

The aim of this paper is to describe the internal microstructure of aptychi of three Late Cretaceous genera of the suborder *Ancyloceratina* Wiedmann, 1960. In order to evaluate the aptychi structural diversity, the microstructure is compared with the well-known Jurassic *Laevaptychus*.

Material and methods

This study is mainly based on Late Cretaceous aptychi and aptychi-bearing lower jaw specimens of *Ancyloceratina* from the USA and from Japan. They are housed in the Yale Peabody Museum (YPM), Black Hills Museum of Natural History (BHI), Muséum National d'Histoire Naturelle Paris (MNHN), and University Museum, University of Tokyo (UMUT).

The microstructure of the following specimens (Table 1) has been analysed:

1. Eleven aptychi valves, found isolated in the sediment, attributed to *Baculites* sp. (smooth to weak flank ribs), from the lower Campanian Mooreville Chalk, Alabama.
2. A single aptychus-bearing lower jaw of *Polyptychoceras pseudogaultinum* Yokoyama, 1890 found *in situ* (i.e. inside the body chamber of the shell), from the Campanian Osoushinai Formation, Wakkawebetsu Creek, Nakagawa Town, northern Hokkaido.
3. A single aptychus-bearing lower jaw (both valves) of *Jeletzkytes nebrascensis* (Owen 1852) found *in situ* within the body chamber, from the lower Maastrichtian Fox Hills Formation, Ziebach County, South Dakota.

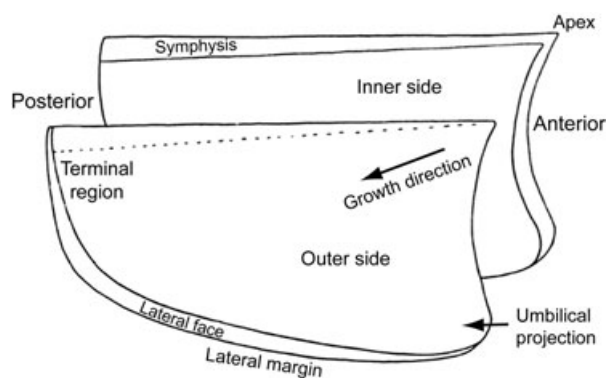


Fig. 1. Schematic drawing of an aptychus (modified from Arkell 1957).

In addition, three valves of *Laevaptychus* from the upper Kimmeridgian of Cap de la Hève, France (MNHN), were used for comparison of microstructure with Cretaceous aptychi. These occur as loose specimens and are attributed to the *Aspidoceratidae* (either *Aspidoceras* or *Hybonotoceras*, or *Physodoceras*) of the *Ammonitina* (Arkell 1957; Schindewolf 1958). The terminology used to describe the external morphology (Fig. 1) is the one proposed by Trauth (1927–1931) and Arkell (1957). We employ the terms inner side, outer side, anterior and posterior to refer to the jaws as they were oriented in life.

The different forms of aptychi have been treated as parataxa with generic names and binomial nomenclatures. However, we do not support parataxonomical nomenclature and, in agreement with Engeser & Keupp (2002), the terms proposed by Trauth for aptychi of *Baculites* (*Rugaptychus*), *Scaphitidae* (*Synaptychus*) and *Aspidoceratidae* (*Laevaptychus*) are only used in an informal way and will therefore not appear in italics.

In the description of the microstructure we use the term lamella for the calcitic sheets deposited and the term layer as a sum of lamellae having the same orientation and nature.

For microstructural observation, all aptychi specimens were cut in parallel or perpendicular to the median hinge line and polished with a graded series of carborundum and cerium oxide.

The sectioned surface was etched with 5% acetic acid solution for 10–30 s (depending on the specimen), and the wall microstructure was observed by a tabletop Hitachi TM 1000 scanning electron microscope

Table 1. Repositories and numbers of the sectioned specimens under study

Taxon	Repository	Number of specimen
<i>Jeletzkytes nebrascensis</i>	Peabody Museum of Natural History, Yale	YPM 23223
<i>Baculites</i> sp.	Black Hills Museum of Natural History	BHI 5801-5811
<i>Polyptychoceras pseudogaultinum</i>	University Museum, University of Tokyo	UMUT MM 29548
<i>Aspidoceras</i> , <i>Hybonotoceras</i> , <i>Physodoceras</i>	Muséum National d'Histoire Naturelle	MNHN A27275-A27277

(SEM) at the Laboratoire de Micropaléontologie (University Paris VI, CNRS UMR 7207) without coating. Also, the amounts of major and trace elements (Ca, Fe, Sr, Zn, S, P, Al, Si, Mn, Mg) in the aptychi and surrounding sediments were determined by electron probe micro-X ray analysis (EPMA) to investigate potential differences of the chemical compositions of the layers, but also to evaluate the degree of diagenetic alteration.

The shells of Cretaceous ammonites (*Polyptychoceras* and *Jeletzkytes*) with preserved aptychi still bear a nacreous layer. The preservation of the co-occurring aptychi is also good and allowed examination of their microstructure. The aptychi of *Baculites* sp. were found isolated in chalky sediment, but the comparison with the *in situ* aptychi clearly indicates their assignment to *Baculites* sp. (smooth and weak flank ribs) (Landman et al. 2007).

Mineralogy and microstructure

Aptychi of Baculites sp.

External morphology. – The two valves of this aptychus have a semilunate shape with sharp ribs (called rugae) on the external side (Fig. 2A). The ribs follow the lateral margin of the aptychus and bend to the symphysis forming a right angle. The symphysis is bordered by a thin flange. As in all forms of aptychi, the inner side of the valve shows co-marginal lirae

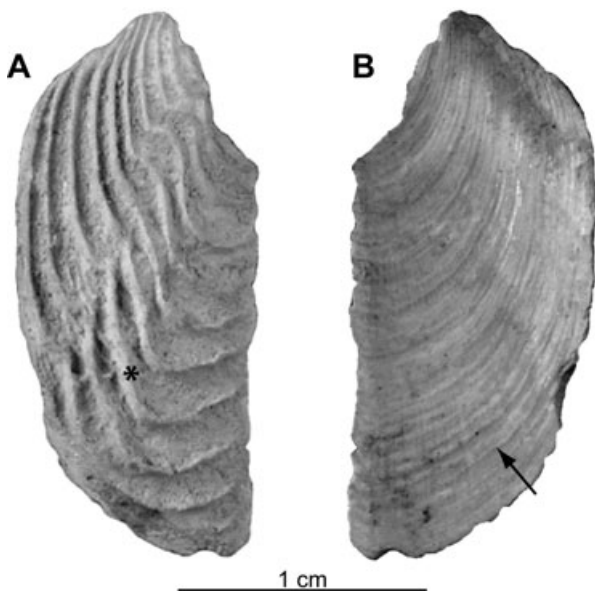


Fig. 2. Pictures of an aptychus of *Baculites* sp. (smooth and weak flank ribs). A. The outer side. B. The inner side. Specimen (BHI 5153) from Mooreville Chalk, Dallas and Green counties, Alabama. Symbols: (*) rugae; arrow, lirae.

traditionally interpreted as growth lines (Fig. 2B). The average length of those aptychi is around 27 mm and the average width is around 12 mm. The thickness of the aptychus in cross-section ranges from 600 μm between the rugae to 1 mm on the top of a ruga.

Microstructure and chemical composition. – This aptychus is mainly made of two layers of calcite in cross-section (Fig. 3A). The thicker inner layer (R1) is formed by several calcitic lamellae that are inclined at approximately 30 degrees towards the inner side of the aptychus (Fig. 3A, C). The thinner second layer, here described as an outer layer (R2), forms the rugae. The R1 layer forms 80% of the total thickness of the aptychus. The lamellae that form this layer are visible on the inner side of the aptychus and form the growth lines (Fig. 3B). This layer is made of overlapping calcitic lamellae that are 10 μm thick. The R2 layer is made of thin (around 3 μm) calcitic lamellae that are arranged parallel to the outer side of the valve. This layer is discontinuous and disappears on the top of the rugae (Fig. 3D).

The result of EPMA (Table 2) shows that all the aptychi specimens conserved components (Sr and Mg) linked to the biomineralization process (Crick et al. 1987; Mann 1992). The Sr is scarce in the sediment compared to the aptychus. The R1 layer differs from the R2 layer by smaller amounts of SrO, SO₂ and MgO.

Aptychus of Jeletzkytes nebrascensis

The aptychus of *Jeletzkytes nebrascensis* is morphologically identified as *Synaptychus* Fischer, 1882 (= *Striaptychus* Trauth 1927), a noun that gathers all aptychi found in the body chamber of Scaphitidae (Fig. 4A). The external morphology of the studied specimen was described by Landman & Waage (1993).

External morphology. – Although this type of lower jaws occurs abundantly in the US Western Interior outcrops (e.g. north central South Dakota), only the inner chitinous layer is usually preserved. The reasons why the calcitic layer is usually absent (Landman & Waage 1993) is still unclear; Landman et al. (2006) suggest that the microenvironment created within the buccal mass, and the thickness of the aptychus (thinner than the ammonite's aragonitic shell) could be factors able to promote local dissolution. The rarity of preservation of the calcitic part is the reason why the examination of the microstructure of the aptychus has only been done on one specimen of Scaphitidae, *Jeletzkytes nebrascensis* (Owen 1852). Only the outer side of the two valves in connection is visible. Weak rounded ribs can be observed on the outer side of the aptychus.

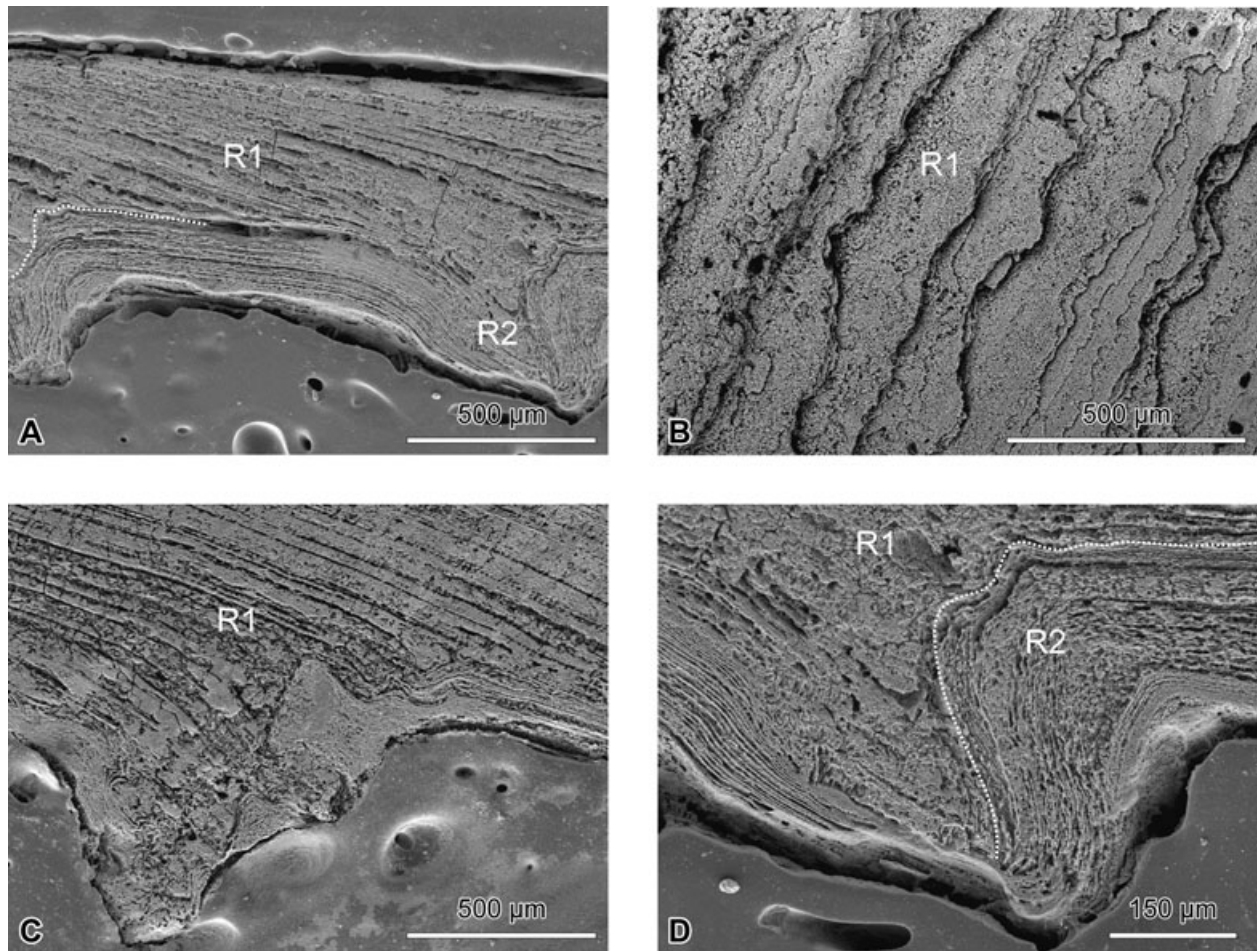


Fig. 3. Scanning electron microscope pictures. A. Overview of the cross-section of a *Baculites* sp. (smooth and weak flank ribs) aptychus showing the main lamellar layer (R1) and the outer layer (R2). The dotted line underlines the border of the two layers. B. View of the inner side of the aptychus showing the calcitic increments of the main lamellar layer. C. Cross-section showing the inclination of the lamellae forming the main lamellar layer. D. Close up of the cross-section of a ruga showing the upper lamellar layer (R2). The dotted line indicates the border of the two layers.

Table 2. Averages of compound concentrations obtained by an electron probe micro-X ray analysis

	Number of measures	MgO	MnO	SiO ₂	P ₂ O ₅	SO ₂	ZnO	CaO	FeO	SrO	Al ₂ O ₃
<i>Polyptychoceras</i> aptychus	2	0.643	0.202	0.062	14.376	0.335	0.069	50.828	0.509	0.14	–
<i>Polyptychoceras</i> sediment	2	0.052	0.056	0.51	7.551	0.026	0	12.519	0.251	0.063	–
<i>Baculites</i> aptychus outer layer (R2)	5	0.342	0.027	0.011	0.045	0.056	0.034	57.576	0.326	0.108	0
<i>Baculites</i> aptychus inner layer (R1)	4	0.727	0.023	0.018	0.118	0.211	0.039	59.678	0.116	0.291	0.013
<i>Baculites</i> sediment	1	0.733	0.009	21.066	0.408	0.052	0.007	23.565	1.734	0.071	7.983
<i>Jeletzkytes</i> Black Layer	2	2.007	2.612	0.734	0.44	0.364	0	40.85	1.458	0.097	0.044
<i>Jeletzkytes</i> aptychus	2	0.423	0.075	0.035	0.145	0.207	0	58.949	0.055	0.201	0.028
<i>Jeletzkytes</i> sediment	2	3.337	1.456	44.356	0.231	0.394	0.038	4.95	4.205	0	19.6

In cross-section (Fig. 4B), the thickness of the aptychus seems to be quite constant all along the symphysis (around 500 μ m) and then increases gradually towards the lateral faces (around 1 mm) and finally becomes thinner on the lateral margin (Fig. 4C). The symphysis is bordered by a flange. A black layer found on the inner side of the valve was described by Landman & Waage (1993) as a chitinous

layer attached to the aptychus. This black layer bends back towards the lateral margins of the aptychus (Fig. 4D). It seems therefore that a part of the chitin forming the lower jaw originally covered the lateral margins of the aptychi.

Microstructure. – The calcitic layer forming the aptychus is readily observable under the stereomicroscope

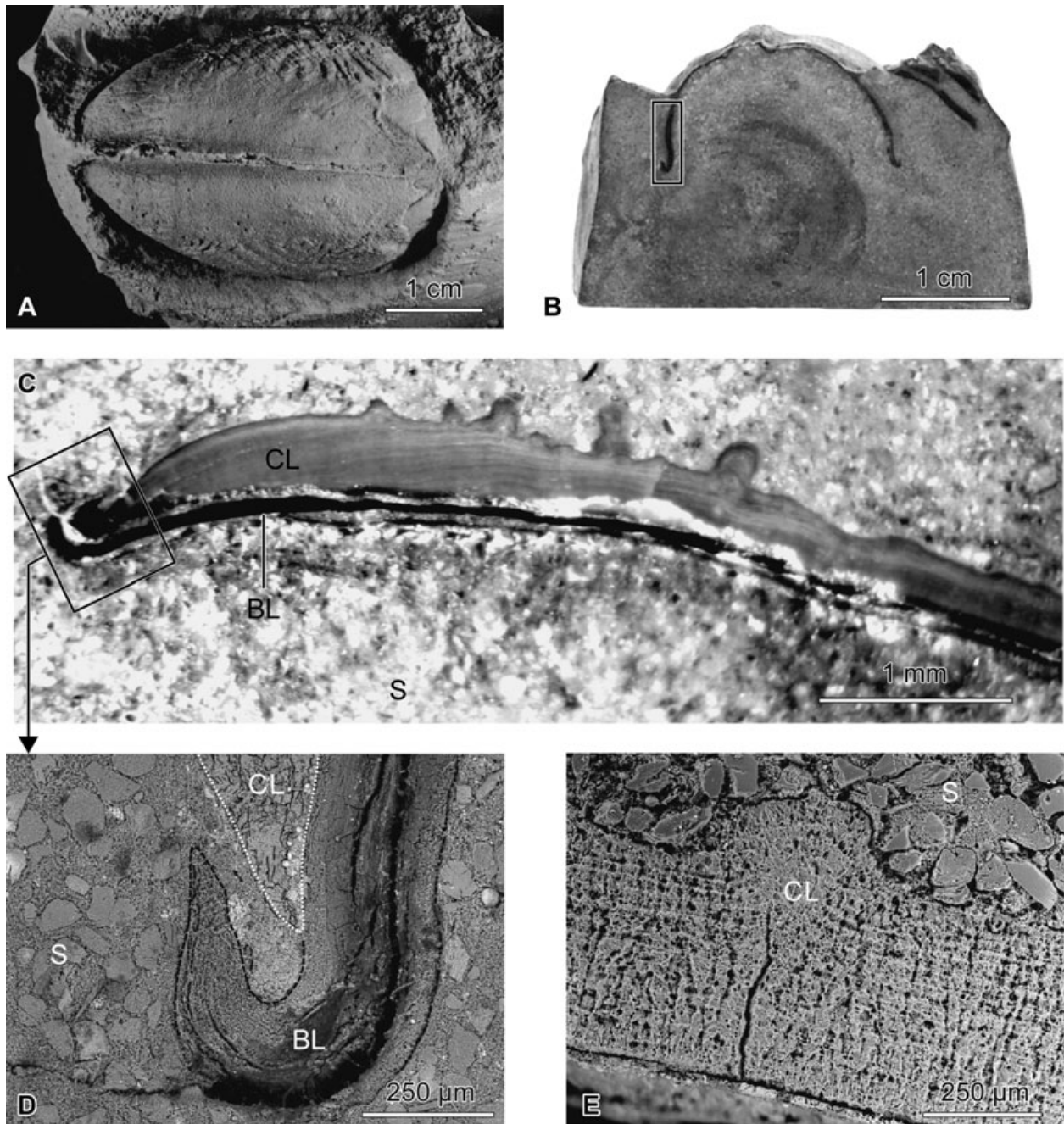


Fig. 4. A. View of the outer surface of the lower jaw of the related scaphitid ammonite *Jeletzkytes spedeni* (YPM 23220), modified from Landman & Waage 1993. B. Cross-section of the specimen (YPM 23223) showing the two valves of the aptychus. C. Cross-section of the rectangular area in Figure 4B showing the calcite layer (CL) forming the aptychus and the black layer (BL). The specimen is surrounded by the sediment (S). D. Scanning electron microscope picture, close up of the squared area in Figure 4C. The black layer (BL) forms a hook that contains the margins of the calcitic layer of the aptychus (CL). The specimen is surrounded by sediment (S). E. Cross-section of the calcitic layer (CL). The section of a rounded rib is visible; the lamellae are parallel to the inner side of the aptychus. The top of the image coincides with the top (outer side) of the aptychus. The outer side is covered with sediment (S).

but is very difficult to observe under the SEM. This is probably due to diagenetic problems and to the etching. The layer is made of overlapping calcitic lamellae. The lamellae are parallel to the outer side of the aptychus and follow the bending of the lateral margin (Fig. 4E). The lamellae are

approximately 7 μm thick. Differentiations in several layers were not observed. The ribs of the aptychus show an irregular shape in cross-section. Those ribs are formed by the overlapping of calcitic lamellae parallel to the outer side of the aptychus (Fig. 4E).

Aptychus of *Polyptychoceras pseudogaultinum*

The aptychus of *Polyptychoceras* was first described by Nagao (1931a,b) as an operculum, and no parataxonomic name has been yet proposed for it. The structure was re-examined by Tanabe & Landman (2002) and interpreted as the outer calcareous covering of the lower jaw, because the black chitinous lamella of the lower jaw is covered by the aptychus, and furthermore, it was found together with the upper jaw within the body chamber.

External morphology. – Only one of the two valves (right valve) of the *in situ* specimen (Fig. 5A) is preserved in the present specimen, so that only the inner mould and the inner side of the valve could be studied (Fig. 5B, C). The growth lines present on the internal mould are imprints of the inner side of the aptychus (Fig. 5C). The aptychus is small; 10.29 mm long and 8.40 mm wide. The valve of the aptychus is curved, and horseshoe-shaped in cross-section. The convexity of this aptychus is twice that in the other aptychi observed. The symphysis could not be observed.

Microstructure. – The aptychus consists of a single thin calcite layer, ca. 30 μm in maximum thickness (Fig. 5D). It is made of very thin calcitic lamellae, 1 μm thick. The lamellae are overlapping and are parallel to the inner side of the valve. Longitudinal sections show the increasing thickness of the aptychus from the anterior part of the aptychus (apex) to the posterior part (lateral margins). Near the apex, during the initial stage of growth, the thickness of the aptychus is 9 μm , then 15 μm , 18 μm , and finally 30 μm in proximity of the lateral margin. The variation of thickness exactly follows the growth of the aptychus. The morphology of the layers suggests a lack of ornamentation on the outer side of the aptychus.

The *Polyptychoceras pseudogaultinum* aptychus shows a significant amount of P_2O_5 , probably linked to diagenesis.

Comparison with the aptychi microstructure of Jurassic ammonites

The Late Jurassic aptychi of the Aspidoceratidae (*Laevaptychus* of Trauth 1931) used for comparison, (60 mm length to 40 mm width, and 8 mm thick), are smooth on the outer side, with numerous small punctuations (Fig. 6A), while concentric growth lines are present on the inner side (Fig. 6A). The shape presents an umbilical projection. All of the aptychi

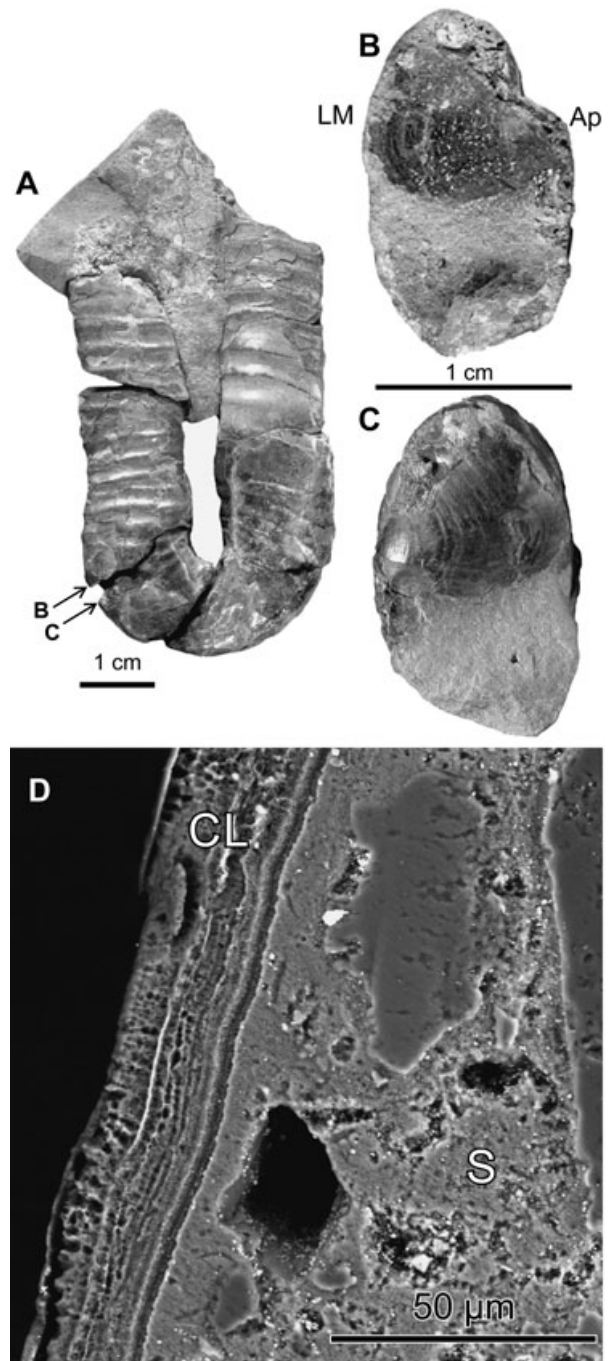


Fig. 5. A. Overview of the shell of *Polyptychoceras pseudogaultinum*. The aptychus is indicated by the arrow. B. The arrow C points to the inner mould. B. Cross-section of the shell showing the aptychus (dark area). C. Cross-section of the shell showing the inner mould. The co-marginal lirae are present on the dark area. D. Cross-section of the calcitic layer (CL) of the aptychus. The inner side is on the left and the outer side is on the right, covered by the sediment (S). (LM) is the lateral margin, (Ap) is the apex.

consist of two layers with different microstructure, i.e. a basal lamellar layer (L1) and an upper 'honeycomb like' tubular layer (L2) (Fig. 6B, C). The basal layer, approximately 100 μm thick, is observable on

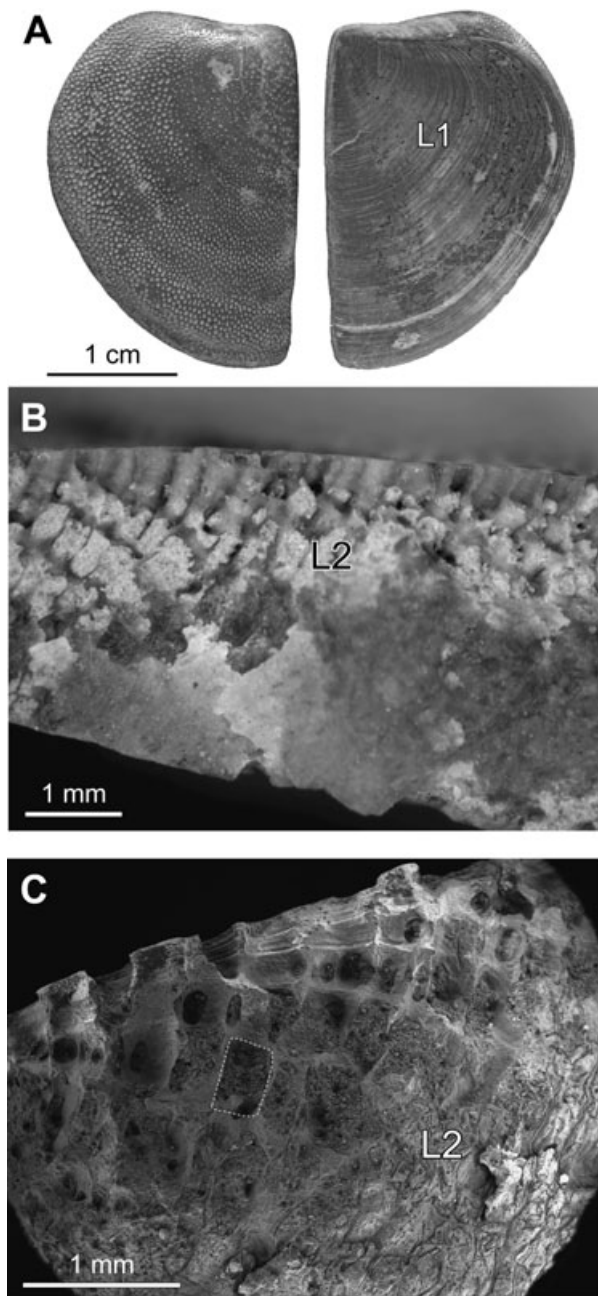


Fig. 6. A. Picture of the outer side (left) and the inner side (right) of a *Laevaptychus* (MNHN A27278). The calcitic layer observable on the inner side is the basal layer (L1). B. Cross-section of *Laevaptychus* showing the tubular layer L2 (MNHN A27278). C. Overview of the *Laevaptychus* (MNHN A27278) cross-section. The tubes are sectioned. The dotted rectangle indicates a section of tube between two growth lines.

the convex side of the aptychus and forms the co-marginal lirae that are visible on the inner side of the aptychus and were interpreted as growth lines. This layer is described by Farinacci *et al.* (1976) as a succession of thin laminae inclined and overlapping each other. The tubular layer is the thickest (ca. 95% of the thickness), and as the name suggests, is composed of calcitic

tubes (Fig. 6B) in rounded section (each ~30 μm diameter) that are made by a succession of very thin layers of calcite. In cross section the bases of the tubes are inclined at 30° with the inside of the aptychus; toward the outside the tubes become straightened. The tubular layer is present in different forms of various aptychi of the Ammonitina (Farinacci *et al.* 1976).

Previous workers (Schindewolf 1958; Farinacci *et al.* 1976; Hewitt *et al.* 1993) reported that in addition to L1 and L2 layers, an upper lamellar layer is present in *Laevaptychi*, but this layer could not be confirmed in our specimens.

Growth models

In the literature the growth of aptychi is mostly unstudied or reduced to the counting of the lirae formed by the basal layer on the inner side of the aptychus (Hewitt *et al.* 1993). The complex microstructure, on the contrary, allows proposing growth models. The growth hypothetically occurs by the secretion of calcitic layers from an external tissue (Seilacher 1993; Tanabe & Fukuda 1999) located on the margin of the aptychus, as in the case of the outer calcareous covering on modern *Nautilus* jaws (Tanabe & Fukuda 1987). Meanwhile, as in the case of modern cephalopods, the main chitinous lower jaw lamella of ammonoids was formed from the inside by chitin-secreting cells (called the beccublasts by Dilley & Nixon 1976) that were connected with the jaw muscle with the buccal mass (Dilley & Nixon 1976; Tanabe & Fukuda 1987). The co-marginal lirae point to a growth direction running from the apex to the external margin of the aptychus.

Baculites sp. aptychus. – The growth of this aptychus seems to occur in three steps (Fig. 7). The first step is initiated by deposition of the main layer, R1 (Fig. 7A). The peculiar direction of the deposit (tilted lamellae) implies secretion over a broad surface area. The second step is the deposition of curved calcitic lamellae on the outer side of the aptychus (Fig. 7B). The configuration of the deposit is the only difference with the first step, indicating that this is part of the same main layer. The bending of the lamellae forms the beginning of the formation of the ruga. The last step of growth is ended by deposition of the upper layer (R2) (Fig. 7C).

There are two hypotheses for the production of the calcite at this stage of the growth: either two different tissues generate the two layers of calcite, or the same tissue creates the two layers (R1 and R2). In the first case the deposition of the upper layer would occur at the same time as that of the principal layer. In the

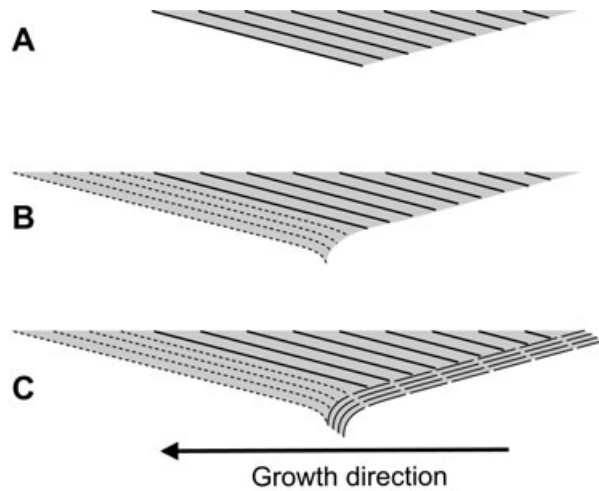


Fig. 7. Schematic growth of *Baculites* sp. aptychus. Cross-section, the inner side of the aptychus is on the top of the figure. A. Deposit of the tilted lamellae of the main layer (R1) from the apex (right) to the margins (left). B. The deposit of new lamellae of calcite (dotted line). The outer lamellae bend back forming the beginning of a ruga. C. Deposit of the lamellae forming the outer layer (R2) (dashed line).

second case we would have to imagine that the tissue, at the end of the second step would move forward in order to cover the calcitic lamellae of the main layer (R1) and to form the upper layer (R2).

Polyptychoceras pseudogaultinum and *Jeletzkytes nebrascensis aptychi*. – The growth of these aptychi occurs by the secretion of lamellae parallel to the inner side of the aptychus. Each calcitic increment is very elongate; therefore, the epithelium secreting those lamellae must have covered a broad area of the underlying outer chitinous lamella of the lower jaw.

The growth of Laevaptychus. – Our observations point to a major difference with the results by Farinacci *et al.* (1976). These authors distinguished three layers, whereas we have observed only two layers. The growth model proposed hereby is based on the results of our observations. The growth increments are defined by the course of the growth lines (Figs 6C, 8). This aptychus grows in two directions: horizontal and vertical. In the horizontal plane both length and width of the aptychus valve were enlarged, thus increasing its surface. Growth occurs from the apex to the lateral margins, and results in the production of new calcitic tubes on the margins of the aptychus and in the new production of basal lamellae (Fig. 8). The vertical direction concerns the thickness of the aptychus. It results in the addition of new layers of calcite on the tubes that were formerly produced (Fig. 8B). The identification of a third layer by Farinacci *et al.* (1976) and others is probably due to this peculiar growth,

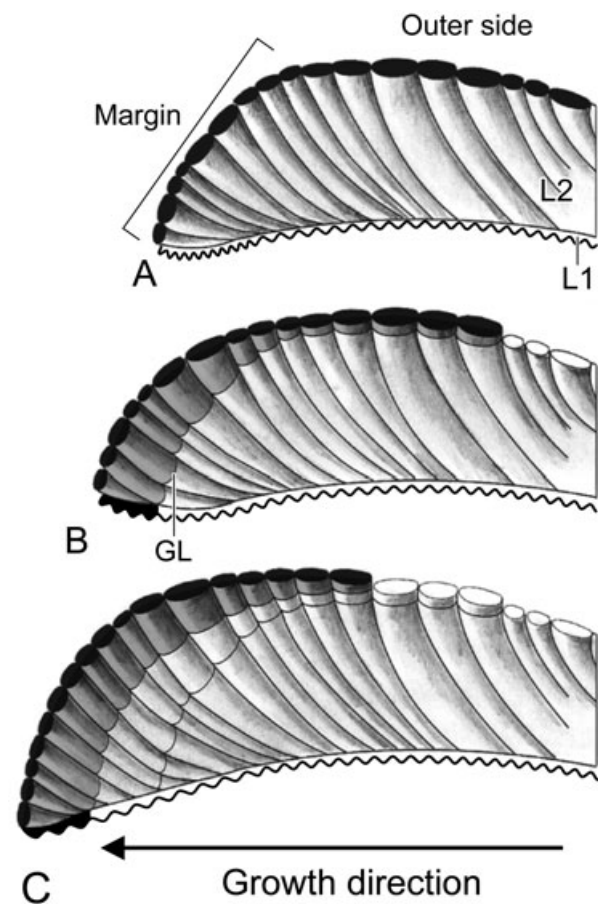


Fig. 8. Schematic cross-section through the posterior margin of a *Laevaptychus* showing the steps of growth. The steps of growth A, B, C have been based on the observation of the growth lines (GL). A. Cross-section, on the right the symphysis, on the left the lateral margins, on the top the outer side of the aptychus and on the bottom the inner side. The aptychus is made of a tubular layer (L2) and a lamellar layer (L1). B. When the aptychus grows new tubular layers (L2) are formed (dark-grey area). Also new lamellae of the lamellar layer (L1) are secreted. C. The accretion of the tubes is not homogenous; a reduced amount of calcite is deposited on the outer side of the aptychus than on the margins. This part is therefore thinner and forms what was interpreted by Farinacci *et al.* (1976) as the upper layer.

since the sections of the tubes added during the growth (vertical direction) are getting thinner towards the outer side of the aptychus (Fig. 8B, C).

Discussion

Most previous authors (Schindewolf 1958; Farinacci *et al.* 1976; Michalik 1996; Kozlova & Arkadiev 2003) recognized three layers in the aptychi of Jurassic and Cretaceous Ammonitina; i.e. a very thin inner layer, a thin prismatic layer and a lamellar outer layer. This organization of the microstructure is usually extended to all the different 'genera' of aptychi (Kozlova & Arkadiev 2003). On the contrary, we show that there

is an important variation in both the number of layers and the microstructure of calcite layers.

Our data demonstrate that there are differences between the aptychi of the Jurassic Ammonitina and the Cretaceous Ancyloceratina. These variations concern the thickness and the microstructure. The latter are thinner than the former, and do not develop a tubular layer, typically observed in Late Jurassic Laevaptychus, and instead only show lamellar deposition.

Taxonomic variation in the aptychi microstructure can also be observed among the Cretaceous Ancyloceratina. The aptychus of *Baculites* sp. is composed of several (two) layers while those of *Jeletzkytes* and *Polyptychoceras* consist only of one layer. The organization of the aptychi of the latter two genera is simpler than that in the Jurassic Ammonitina. Whether this feature reflects an evolutionary trend of Ancyloceratina towards the reduction of both thickness and microstructure complexity, or an adaptation for peculiar feeding habits remains an open question. As the variation in the microstructure is linked to a growth variation, three distinct growth models have been proposed.

The structure of aptychi is a direct product of the secretory activity of an epithelium which covered these hard skeletal elements of the ammonite buccal mass (Michalik 1996; Tanabe & Fukuda 1999). Therefore differences in the growth model also indicate a differentiation in the organization of the epithelium that secreted the aptychus. The differentiation in the development and the differences in the microstructure probably reflect important differences in mode of life, feeding and digesting habits between animals bearing different morphogenera of aptychi.

The complexity of these structures points to the need for further studies on aptychi. Deepening our knowledge on Jurassic Ammonitina and Cretaceous Ammonitina and Ancyloceratina could help us to understand better their radiation and their relationships. For example, on the basis of morphogenera, Farinacci *et al.* (1976) suggested that the sponge-like structure arises from lamellar aptychi in the Middle Jurassic and have an explosive development until the Early Cretaceous. Whether this explosion is associated to peculiar environmental parameters or is linked to feeding habits or phyletic radiation is still unknown. The use of aptychi in phylogeny has already been proposed by Engeser & Keupp (2002) but aptychi and taxa must be related without ambiguity. Therefore, phylogenetic studies must be done only on aptychi found inside the body chamber of the ammonite.

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