

Jurassic ammonite aptychi: functions and evolutionary implications

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Abstract Nine proposals of aptychus (*sensu stricto*) function have been published (in historical order): operculum, micromorphic males, lower mandible, protection of gonades, ballast for lowering of aperture, flushing of benthic prey, filtering microfauna, pump for jet propulsion, and active stabilizer against rocking produced by the pulsating jet during forward foraging and backward swimming. Some ammonites bear thick, laevaptychus- and lamellaptychus-type aptychi (aspidoceratids and haploceratoids) that may have improved lowering of the aperture as part of a mobile cephalic complex, enabling many of these functions. Aptychi were multifunctional, most commonly combining feeding (jaw, flushing, filtering) with protection (operculum), and/or with propulsion (ballast, pump, diving and stabilizing plane). Multifunctionality would have been a strong constraint in ontogeny and evolution as shown by the limited diversity of aptychi with respect to the wide variety of shell morphologies known in the Mesozoic Ammonitina. Calcification of aptychi in the Jurassic Ammonitina is known from the Early Toarcian *Hildoceras* which is also the first ammonite with males bearing well-formed lateral peristomatic projections or lappets. Calcification allowed aptychi to be involved in functions, which would have improved, in different degrees and combinations, feeding, propulsion and protection. It is herein suggested that multifunctional calcareous aptychi allowed the gradual development of a wide variety of new life-styles.

These new life-styles would have led to the origin and early evolution of haploceratids and stephanoceratids producing the wide diversification of the Ammonitina observed from the Early Aalenian.

Keywords Ammonitina · Aptychus multifunctionality · Protection · Feeding · Locomotion · Aalenian diversification

Introduction

Aptychi (*sensu stricto*) are calcitic, bivalved plates commonly found singly or in pairs, isolated or associated with ammonites where they usually occur in the body-chamber. Aptychi are universally accepted as integral parts of the ammonite organism and there is wide consensus that aptychi were part of the buccal mass (e.g. Dzik 1981; Dagys et al. 1989; Lehmann and Kulicki 1990; Nixon 1996). They are paired outer calcareous plates of the lower jaw, typically wing-shaped, showing a range of morphotypes. Aptychus morphologies commonly differ distinctly among Ammonitina families and occur in both sexual dimorphs (see Arkell 1957: L437–L440; Lehmann 1981; Dagys et al. 1989; Morton and Nixon 1987; Dzik 1981; Schweigert 2009; Parent et al. 2011, 2014 and references therein). The types of Jurassic aptychi are illustrated and briefly described in Fig. 1, based on Arkell (1957), Lehmann (1976), Schweigert (2000), Parent et al. (2014) and references therein.

In a previous paper, we have demonstrated with experiments that ammonites with thick aptychus were potentially able to swim forwardly at moderate velocities (Parent et al. 2014), likely enhancing propulsion and feeding from the aptychus acting as a ballast. This framework provided strong support to the hypothesis of multifunctionality:

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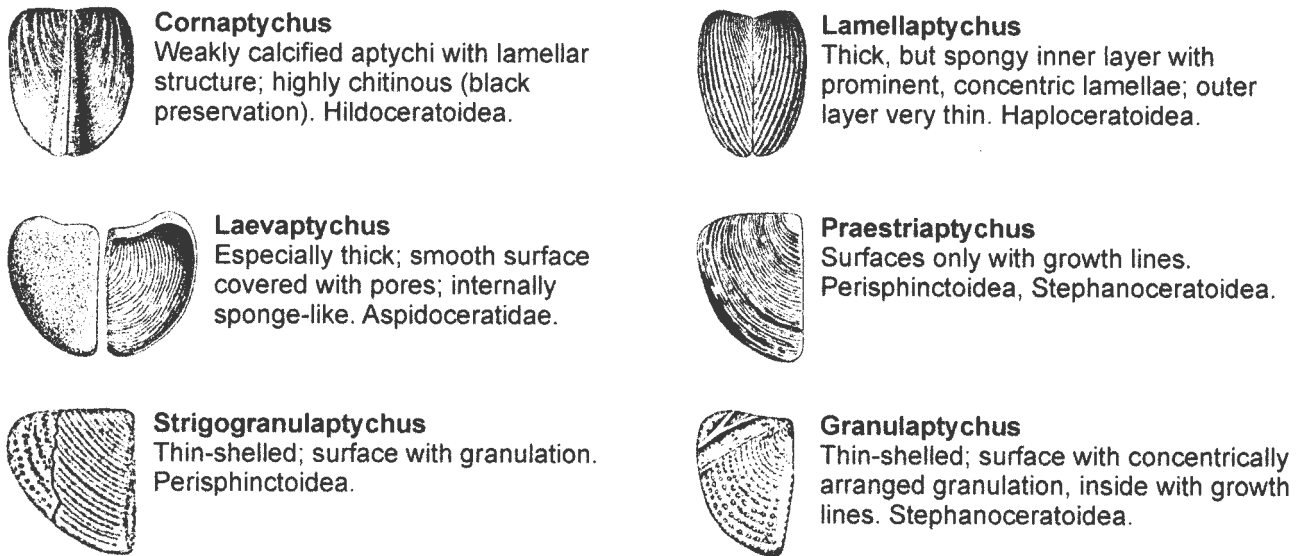


Fig. 1 Aptychus types characterized by main features. Illustrations not to scale, modified from Trauth (1937) and Lehmann (1976)

Aptychi commonly served more than one function and functional combinations differed among higher taxa.

In this paper, after a brief account of the functions attributed to aptychi and probable combinations of multifunctionality proposed in Parent et al. (2014), we review the ammonite-aptychi associations under the current systematics of the Jurassic Ammonitina. Then, multifunctionality and the consistent associations founded are discussed focusing on: (1) the low diversity of aptychi with respect to the large variety of Jurassic ammonite morphologies, and (2) the broad increase of ammonite diversity from the Early Aalenian after a very low diversity originated in the generalized extinction of lineages during the Late Pliensbachian–Early Toarcian.

Functions attributed to aptychi

The following is a brief summary of the functions attributed to aptychi documented in detail in Parent et al. (2014). Most of the listed functions are represented in Fig. 2 from the reconstruction of an ammonoid (based on Dzik 1981) with thick aptychus having various functions.

1. *Operculum* (Rüppell 1829) The almost perfect fit of many aptychi to the terminal body-chambers of the shells in which they are found strongly suggests that such aptychi functioned as an operculum to close off the body chamber and protect the soft body. An operculum needed to cover only the major parts of the whorl section to protect the soft body from predator attacks. The spaces commonly left open are in the umbilical whorl overlaps, presumably for continuous
2. *Micromorphic males* (Braun in Siebold 1848, p. 372). It was suggested that aptychi were micromorphic males probably allocated into the body chamber of the females (macroconchs). Interestingly it is one of the oldest indications of sexual dimorphism in ammonites.
3. *Lower jaw element* (Meek and Hayden 1864) The aptychus represents the bivalved calcitic plates that covers the outer surface of the chitinous lower jaw lamella (Lehmann 1976). This function probably derived from ammonoid ancestors, and should be regarded as the primary function of ammonite aptychi (Lehmann 1971, 1976; Dzik 1981). The mandibles or jaws were part of the buccal mass (Nixon 1996), which also contained the radula between lower and upper jaws (e.g. Lehmann 1967, 1979; Doguzhaeva and Mutvei 1992; Klug and Jerjen 2012).
4. *Protecting the nidamentary glands and/or gonads of females* (Keferstein 1866) This idea was immediately cast into serious doubt (e.g. Gray 1873).
5. *Ballast for lowering the aperture* (Gasirowski 1960) The thick and relatively heavy Laevaptychus of the Aspidoceratidae and Lamellaptychus of the Haploceratoidea, when projected from the aperture with the cephalic mass, would have depressed the aperture of these brevi-/mesodomes during foraging and feeding episodes (Fig. 2b, c). This hypothesis was tested with experiments by Parent et al. (2014).
6. *Flushing benthic prey* (Lehmann 1976) In some ammonites, the aptychus (or anaptychus) may have

water circulation required for the gills and at mid-venter, probably for the hyponome (Lehmann 1990). Trauth (1927) developed this hypothesis in the terms it is now considered by modern authors.

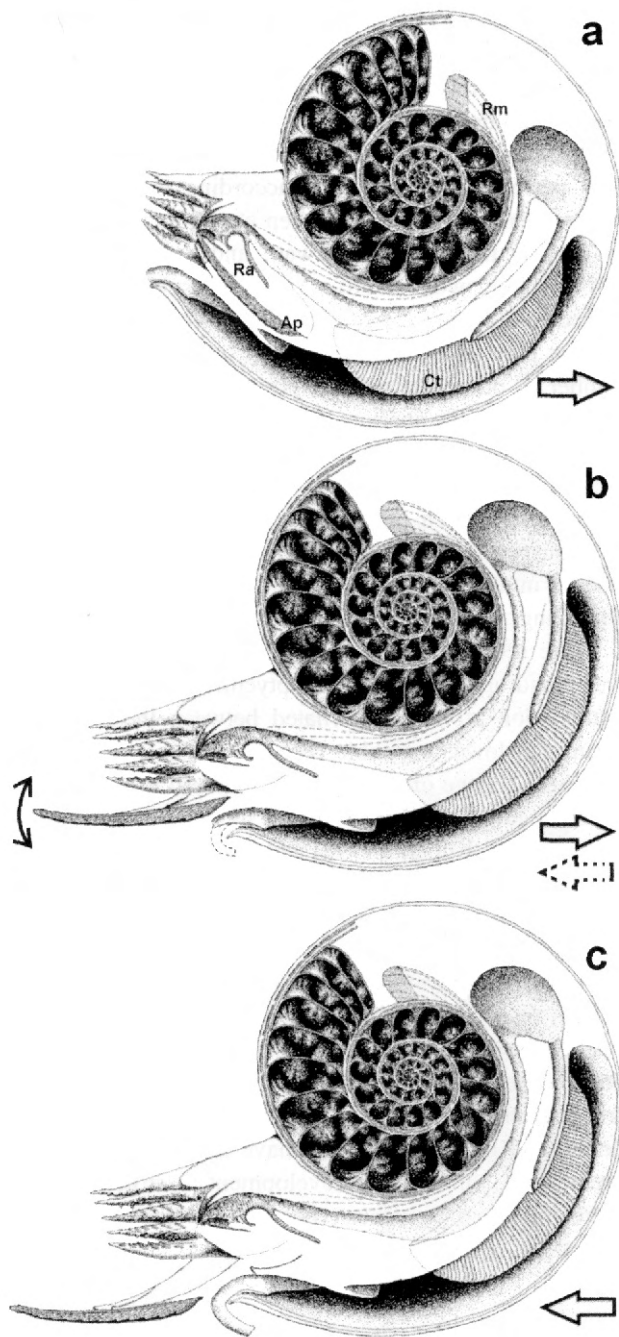


Fig. 2 Reconstruction of an ammonite with thick aptychus (Ap) having various functions. Sagittal section based on modifications from Parent et al. (2014, based on Dzik 1981, Fig. 9a). **a** Partially retracted cephalic complex for resting and backwards swimming. **b** Projected cephalic complex with independently moving aptychus functioning as stabilizer by flapping in harmony with the jet pulse to prevent rocking, simultaneously acting as ballast and diving plane during forward and backward swimming. **c** Projected cephalic complex with independent aptychus flushing demersal prey, as well as acting as ballast and diving plane during forward swimming. Ct ctenidia, Rm paired retractor muscles, Ra radula. White arrows indicate direction of swimming

functioned as a hydroplane allowing to keep the forward swimming ammonite just above the seafloor, where it produced currents that flushed mainly demersal microfauna into the basal water column, thus enabling to capture them (Fig. 2c). The static conditions associated with this function were discussed in Parent et al. (2014).

7. *Filtering of microfauna* (Morton and Nixon 1987) The aptychus was a stiffening device creating a fine slit between the narrowly separated jaws for filtering microfauna (Fig. 2b).
8. *Pump for jet propulsion* (Westermann 1990) The aptychus may have acted as a pump to produce the jet, i.e. as a reciprocating folding board or hinged fan, without moving the entire cephalic complex as in *Nautilus*.
9. *Stabilizer against pitching* (Parent et al. 2014) Some aptychi functioned as active horizontal stabilizers against pitching ('rocking') caused by the pulsing jet mainly during forward swimming.

Multifunctionality of aptychi

The seven functions 1, 3, 5–9 can be grouped in three main categories of vital requirements: (a) *protection*: operculum, (b) *feeding*: lower mandible, flushing demersal microfauna, filtering, and (c) *propulsion*: pump for jetting, ballast for lowering the aperture, stabilizer against pitching.

Functional morphologists have argued for and against attributing single or multiple functions to aptychi (Schindewolf 1958; Farinacci et al. 1976; Lehmann 1981; Lehmann and Kulicki 1990; Morton 1981; Seilacher 1993; Trauth 1927–1938). Parent et al. (2014) formulated the hypothesis of multifunctionality: aptychi commonly served more than one function and functional combinations differed among higher taxa (Fig. 3).

While backward swimming has been by far the most commonly assumed form of ammonite locomotion, some ammonoids with conventional soft-body anatomy and propelled by a coleoid-type hyponome might have had the potential to swim forward as well as backward (Parent et al. 2014). The low angle of the ventral peristome needed in ammonites for the hyponome to bend beneath the shell to produce a horizontal jet stream would have been achieved by moving the cephalic complex (without aptychus) forward and half-way out of the aperture.

The propulsion system required by ammonoids is unknown; no remains of hyponome or pumping organs have been found. Possible pumping systems include a

Types of aptychus	Lower mandible	Operculum	Ballast	Flushing	Filtering	Pump	Stabilizer
Cornaptychus In hildoceratoids	●	○			○	○	
Lamellaptychus In haploceratoids	●	●	●	○	○		●
Laevaptychus In aspidoceratids	●	●	●	○	●		●
Praestriaptychus In perisphinctoids and stephanoceratoids	●	●	○	○	●	○	○
Strigogranulaptychus In perisphinctoids	●	●	○	○		○	○
Granulaptychus In stephanoceratoids	●	●	○			○	

Fig. 3 Aptychus types, taxonomic association and proposed functions as explained in the text. Our assessment of the likelihood that aptychi performed the functions are as follows: probable (*black circle*), possible (*white circle*). Illustrations not to scale (see Fig. 1). Modified from Parent et al. (2014)

coleoid-like muscular mantle (Jacobs and Landman 1993), and the aptychus function listed above (pumping for propulsion). The arms and tentacles of coleoids are sometimes preserved due to their high muscular content (e.g. Fuchs et al. 2013). In contrast, the appendages of ammonites have never been found yet, suggesting they were different from those of coleoids and very likely contained little musculature, thus unable to act as effective steering devices (cf. Seilacher 1993).

Flushing of epifaunal microfauna from the seafloor into the water above the substrate surface provides for the capture in the basal water column of prey by filtration of the water. This activity should be greatly improved by forward swimming at moderate velocities. Ostracods and foraminifers in the crop content of some ammonites (Lehmann 1975) indicate that this kind of activity may have been possible in at least some ammonites. Other ammonites seem to have been capable of feeding also on macrofauna, by biting with the aptychus acting as lower mandible (see above). This function is supported by crop contents that include fragments of ammonite shells (e.g. Lehmann 1973, p. 11,

Fig. 5). Michael (1894) has described the crop contents of a *Neochetoceras* with shell fragments and small aptychi (possibly from males) of similar or even conspecific ammonites.

Operculum and lower-mandible functions could have been performed alternatively, according to the changing requirements for protection when at rest and for foraging, by moving the aptychus forward and backward past the arms (Schindewolf 1958). At least aspidoceratids and haploceratoids may have improved lowering of the aperture as part of a mobile cephalic complex, enabling a number of other feeding and propulsion functions. When projected from the aperture, the aptychus could at the same time have provided vertical steering when the ammonite foraged just above the seafloor (function of flushing benthic prey, above). Such an aptychus may have had the same functions in backward swimming. This would be another case of multifunction of aptychi: ballasting, steering and stabilizing.

There seems to be no barrier against double, triple or even quadruple functions of aptychi. The most frequent combination probably alternated between those of operculum and lower mandible (Fig. 3). Possible ways of the positional change of the aptychus required to serve one or the other function were discussed by Schindewolf (1958), Lehmann and Kulicki (1990) and Seilacher (1993). Possible additional functions of the same aptychus would be steering and stabilizing, as discussed above.

Most likely, only some of the total range of aptychi functions were developed in a single ammonoid species or perhaps even family. The phylogenetic changes from one function or set of functions to another in different ammonite lineages must have involved modifications of shape, structure and microstructure of the different aptychi. Furthermore, Kruta et al. (2009) have stressed that the differentiation in the development, structure and microstructure of aptychus types likely indicate differences in mode of life and feeding habits.

Associations between aptychus type and ammonite taxa

The association of types of aptychus with the corresponding ammonites has been studied profusely by Trauth (1927–1938). After the detailed compilation of Arkell (1957), there have been several papers dealing with new records of associations, summarized in Engeser and Keupp (2002), Parent et al. (2014), Tanabe et al. (2015), and references therein. The most consistent set of associations is presented in the following under a phylogenetic context (Fig. 4). The phylogeny adopted is based on Donovan et al. (1981) and Howarth (2013), keeping the subfamily

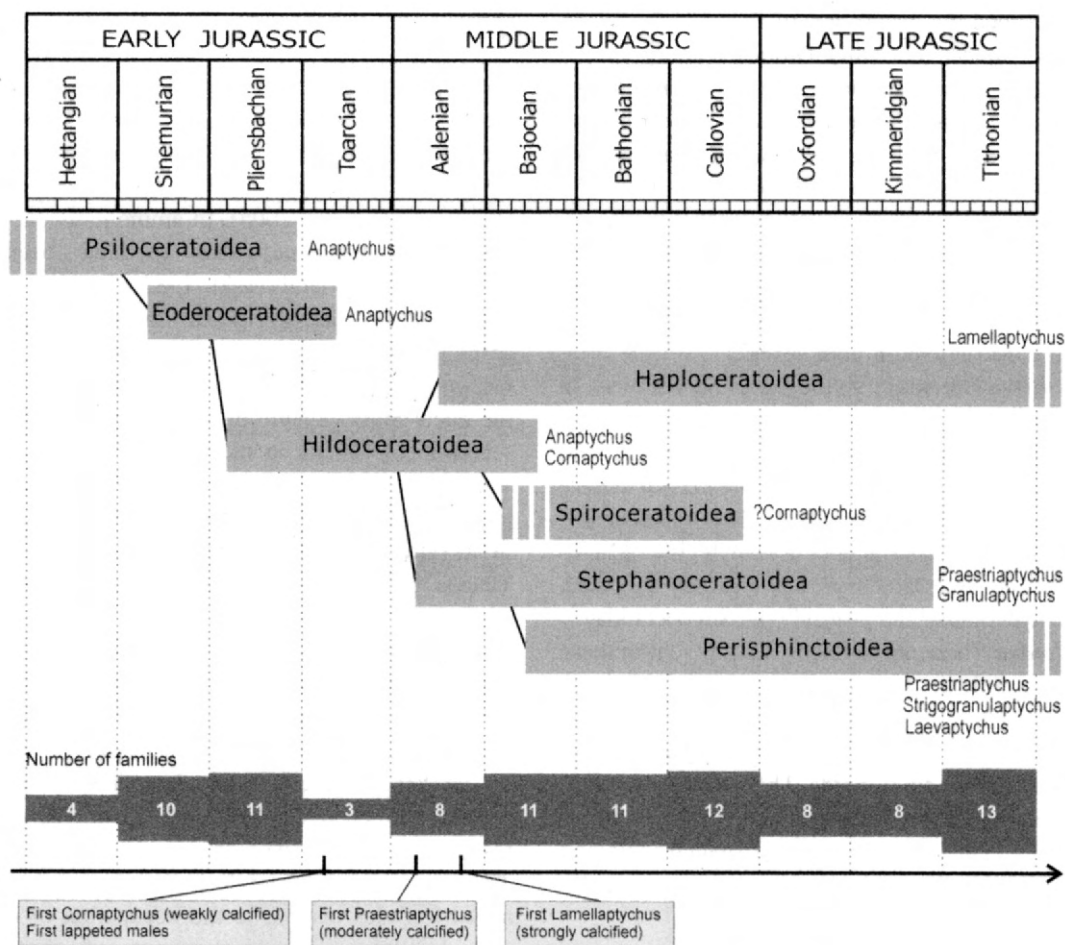


Fig. 4 Stratigraphic ranges, phyletic relationships, aptychus types, and number of families in the Jurassic Ammonitina. Aptychi main evolutionary changes and occurrence of first lappeted microconchs (*Hildoceras*) indicated as explained in text. Phylogeny based on

Donovan et al. (1981). Distribution of types of aptychus (Fig. 1) after Arkell (1957), Lehmann (1976), Schweigert (2000), Parent et al. (2014) and discussed in text. Minor subdivisions of each stage correspond to the zonal subdivision of Cariou and Hantzpergue 1997

Hammatoceratinae within the Phymatoceratidae. Ammonites of the Psiloceratoidea and Eoderoceratoidea had Anaptychus.

Hildoceratoidea This superfamily, derived from the Eoderoceratoidea early in the Pliensbachian, typically includes ammonoids with Anaptychus but also some few with the first aptychus s.s., in the form of Cornaptychus. This latter occurs for first time in the Early Toarcian genus *Hildoceras* (Howarth 2013) which, furthermore, includes the first ammonites whose microconchs (males) bear well-developed lateral peristomatic projections or lappets.

Haploceratoidea Jurassic haploceratoids derived from the Phymatoceratidae (Hildoceratoidea), and most of them have Lamellaptychus. The microconchs have peristomic lappets. An exception could be the family Strigoceratidae (recently reviewed by Schweigert et al. 2007). According to Schweigert (pers. comm. 2015) there seems to be not a single record of aptychus associated with strigoceratid

ammonites, although they could have been very thin and thus not preserved. The shells of the body chambers are very thin and very rarely preserved by which the aptychus could have been lost prior to burial of the shell.

Stephanoceratoidea These ammonoids, derived from the Hammatoceratinae (Phymatoceratidae) early in the Aalenian, include ammonoids with Praestriaptychus, others with Granulaptychus, and some with no aptychus and no lappets. The Otoitidae (e.g. Westermann 1954), Stephanoceratidae (e.g. Trauth 1930) and Cardioceratidae (Lehmann 1972; Mitta and Keupp 2004) bear Praestriaptychus, whereas the Kosmocerotidae bear Granulaptychus (e.g. Schweigert 2000).

The Sphaeroceratidae is a large group in which, currently, no members are known to bear aptychus (Sandoval pers. comm. 2015; Alberti pers. comm. 2015; Fernández-López pers. comm. 2015). The records cited by Engeser and Keupp (2002) seem to be misinterpretations of Trauth

(1930) who recorded the occurrence of *Praestriptychus* in “*Sphaeroceras*” *sauzei* (currently *Otoites*, Family Otoitidae) and “*Sphaeroceras*” *bullatum* (currently *Bullatimorphites*, Family Tutilidae, Perisphinctoidea). According to Donovan et al. (1981, p. 147), the Sphaeroceratidae differentiate gradually during the Early Bajocian from the Otoitidae (typically with lappeted microconchs) via *Frodgenites* and *Labyrinthoceras*. The most significant changes are the loss of lappets in the microconchs, the reduction of the sexual size dimorphism, and the development of deep terminal constrictions in both sexes.

Perisphinctoidea Derived from the Stephanoceratoidea in the early Bajocian, the Perisphinctoidea mostly include ammonites with *Praestriptychus*. Some genera of the subfamily Lithacoceratinae (Ataxioceratidae) are known to have *Strigogranulaptychus* (Schweigert 2000). The Aspidoceratidae bear the large and conspicuous *Laevaptychus*. Microconchs of Jurassic perisphinctoids are typically lappeted, except the Pachyceratidae and probably the Simoceratidae.

Spiroceratoidea There are no records of aptychi in these ammonoids (G. Dietl pers. comm. 2015), except for a single recent case in Tanabe et al. (2015). G. Dietl suspects that the lack of record would be due to the weak or non-calcification of the aptychus of these ammonoids. This possibility seems to be confirmed by the Callovian specimen of *Spiroceras* figured by Tanabe et al. (2015, Fig. 10.6.d), which contains a very thin aptychus into the bodychamber.

Evolutionary implications

Aptychus diversity is low in comparison to the large variety of Mesozoic ammonite morphotypes, and, as reviewed above (see Figs. 3, 4), there is a consistent association between aptychus type and ammonite taxon (cf. Engeser and Keupp 2002, pp 86–90; Tanabe et al. 2015). This important pattern should be a consequence of the several functions aptychi must have been involved in—like most organs or organic structures. And it is herein interpreted as that multifunctionality imposes evolutionary constraints. The more functions an organ is involved in, the more likely it is that a change in morphology and/or function would produce perturbations on others. Consequently it is expected that evolution of a multifunctional organ or structure would proceed at lower rates, by being strongly constrained. This would be the case of the ammonite aptychi involved in several vital functions of feeding, protection and propulsion.

The Anaptychus was a rather conservative structure, little changing in the Early Jurassic Psiloceratoidea and Eoderoceratoidea. It appears evident that earliest *Hildoceras* derived its weakly calcified Cornaptychus from an Anaptychus-type lower jaw by developing an incipient

capacity for calcification. The ammonite shell is aragonitic whereas the aptychi are calcitic. Precipitation of both polymorphs of Calcium carbonate in different locations of a same organism is well known in several molluscs, e.g. in many bivalves including oysters (Stenzel 1971) or in gastropods the operculum of *Neritopsis* (Kaim and Sztajner 2005). In ammonoids, the lower jaws, except the aptychus, seem to have been aragonitic (Kulicki and Wierzbowski 1983; Tanabe et al. 2015). Rare calcified anaptychi are known in some Triassic ammonoids (Dagys and Weitschat 1988; Engeser and Keupp 2002), indicating they already possessed tissues in the bucal mass capable of locally secreting Calcite. Thus, secretion of Calcite in the late Early Jurassic *Hildoceras* should not be an evolutionary novelty (sensu Dommergues 1987) but the reactivation of the secretory function in specific locations where the aptychus was formed (see Tanabe et al. 2015 for possible anatomical organization of the buccal mass).

Considering the associations of types of aptychus in haploceratoids, stephanoceratoids and, latter, perisphinctoids in their phylogenetic context, it is apparent that they increased the secretory function leading to the production of thicker calcareous aptychi. These thicker aptychi enabled the several additional functions possible with respect to those of the Cornaptychus of the hildoceratids. These new functions might have induced the evolution of new life-styles leading to the occupation of new biotopes and habitats and development of new ecological relationships.

It is well known that Toarcian ammonite diversity is very low respect to the Pliensbachian for several lineages became extinct during the Late Pliensbachian and earliest Toarcian (Hallam 1987; Page 1993). Eleven families are known from the Pliensbachian but most of them became soon extinct, and only three are known from the Toarcian: Dactylioceratidae, Hildoceratidae and Phymatoceratidae (Fig. 4). In the early Aalenian eight families originated from the Phymatoceratidae, producing a notorious increment of morphologic diversity within the Suborder Ammonitina. This post-Toarcian diversification has been studied by several authors and from different points of view, but mainly focussed in the regional scope of the changes in diversity (see Macchioni and Cecca 2002 and Cecca and Macchioni 2004 and references therein).

In the context of the hypothesis of multifunctionality of calcareous aptychi, it can be argued that their development during the Early Aalenian must have played a crucial role in the evolution of the post-Toarcian Ammonitina. The varied feeding and propulsion potential behaviours proposed above for ammonites with these aptychi (multifunctionality above) could have allowed them to develop new life-styles and so to colonize different new biotopes

adopting new ecological niches perhaps already from the earliest Aalenian. The palaeogeographic and palaeobiogeographic changes, which probably induced the Toarcian extinctions and evolution of the phymatoceratids into new lineages by adaptation, cannot be considered herein. However, they are widely discussed in, e.g. Hallam (1987), Macchioni and Cecca (2002), and Cecca and Macchioni (2004) and references therein.

Conclusion

We suggest that ammonite aptychi were commonly multifunctional, i.e. involved in several vital requirements of feeding, propulsion and protection. Multifunctionality must have constrained the ontogeny and evolution as reflected in (1) the conservative morphology of aptychi, with (2) a very consistent association of aptychus type with specific ammonite lineages, in accord with the proposed differences in functions and their combinations. These properties give aptychi a high value for ammonoid systematics—important to reconstruct the ammonoid phylogeny as pointed out by Landman and Grebneff (2006, p. 128).

Development of thick calcitic aptychi enabled the last-associated functions in Jurassic haploceratoids, stephanoceratoids and perisphinctoids, likely improving swimming abilities and prey-capture, as well as protection from predators.

Calcification of aptychi, the essential process for multifunctionality, is herein proposed to have been a key evolutionary process that must have triggered the wide post-Toarcian diversification of the Ammonitina.

This post-Toarcian diversification includes the establishment of a conspicuous sexual dimorphism in which most of the species have lappeted males. An interesting issue to be studied in order to better understanding the functions of aptychus is the function of lappets in male shells (see Klug et al. 2015 for a hypothesis) and their relationships, since both structures arose simultaneously in the Early Toarcian *Hildoceras*.

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References

- Arkell, W. J. (1957). Aptychi. In W. J. Arkell, B. Kummel, C. W. Wright, & R. C. Moore (Eds.), *Treatise on invertebrate paleontology, (L) mollusca 4* (p. 22+490). Kansas/New York: University of Kansas Press and Geological Society of America.
- Cariou, E. & Hantzpergue, P. (1997). Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. *Bulletin du Centre de Recherche Elf-Exploration et Production*, 17, 79–86.
- Cecca, F., & Macchioni, F. (2004). The two Early Toarcian (Early Jurassic) extinction events in ammonoids. *Lethaia*, 37, 35–56.
- Dagys, A. S., & Weitschat, W. (1988). Ammonoid jaws from the boreal triassic realm (Svalbard and Siberia). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 67, 53–71.
- Dagys, A. S., Lehmann, U., Bandel, K., Tanabe, K., & Weitschat, W. (1989). The jaw apparatus of ectocochleate cephalopods. *Paläontologische Zeitschrift*, 63, 41–53.
- Doguzhaeva, L. A., & Mutvei, H. (1992). Radula of the early cretaceous ammonite *Aconeceras* (Mollusca: Cephalopoda). *Palaeontographica*, A223, 167–177.
- Domergues, J.-L. (1987). L'évolution chez les Ammonitina du Lias Moyen (Carixien, Domerien basal) en Europe occidentale. *Documents des Laboratoires de géologie Lyon*, 98, 1–272.
- Donovan, D. T., Callomon, J. H., & Howarth, M. K. (1981). Classification of the Jurassic ammonitina. In J. R. Senior (Ed.), *The ammonoidea. Systematics association special volume* (Vol. 18, pp. 101–155). London: Academic Press.
- Dzik, J. (1981). Origin of the Cephalopoda. *Acta Palaeontologica Polonica*, 26, 161–191.
- Engeser, T., & Keupp, H. (2002). Phylogeny of the aptychi-possessing Neoammonoidea (*Aptychophora* nov., Cephalopoda). *Lethaia*, 35, 79–96.
- Farinacci, A., Mariotti, N., Matteucci, R., Nicosia, U., & Pallini, G. (1976). Structural features of some Jurassic and early Cretaceous Aptychi. *Bolletino della Società Paleontologica Italiana*, 15, 111–143.
- Fuchs, D., Keupp, H., & Schweigert, G. (2013). First record of a complete arm crown of the early Jurassic coleoid *Loligosepia* (Cephalopod). *Paläontologische Zeitschrift*, 87, 431–435.
- Gasiorowski, S. M. (1960). Remarques sur les Laevaptychi. *Annales de la Société Géologique de Pologne*, 30, 59–97.
- Gray, J. E. (1873). Observations on M. Favré's paper on a new classification of ammonites. *The Annals and Magazine of Natural History*, 11, 451–454.
- Hallam, A. (1987). Radiations and extinctions in relation to environmental change in the marine Jurassic of north west Europe. *Paleobiology*, 1, 152–168.
- Howarth, M. K. (2013). Part L, revised, Volume 3B, Chapter 4: Psiloceratoidea, Eodoceratoidea, Hildoceratoidea. *Treatise Online*, 57, 1–139.
- Jacobs, D. K., & Landman, N. H. (1993). *Nautilus*: a poor model for the function and behaviour of ammonoids? *Lethaia*, 26, 101–111.
- Kaim, A., & Sztajner, P. (2005). The opercula of neritopsid gastropods and their phylogenetic importance. *Journal of Molluscan Studies*, 71(3), 211–219.
- Keferstein, W. (1866). Cephalopoden. *Bronn's Klassen und Ordnungen der Weichthiere*, 3(2), 1337–1406.
- Klug, C., & Jerjen, I. (2012). The buccal apparatus with radula of a ceratitic ammonoid from the German Middle Triassic. *Geobios*, 45, 57–65.
- Klug, C., Zátón, M., Parent, H., Hostettler, B., & Tajika, A. (2015). Mature modifications and sexual dimorphism. In R. H. Mapes

- (Ed.), *Ammonoid paleobiology: From anatomy to ecology: Topics in geobiology*. Netherlands: Springer.
- Kruta, I., Rouget, I., Landman, N., Tanabe, K., & Cecca, F. (2009). Aptychi microstructure in late Cretaceous Ancyloceratina (Ammonoidea). *Lethaia*, 42, 312–321.
- Landman, N. H., & Grebneff, A. (2006). Jaws of Triassic ammonoids from New Zealand. *New Zealand Journal of Geology and Geophysics*, 49, 121–129.
- Kulicki, C., & Wierzbowski, A. (1983). The Jurassic juvenile ammonites of the Jagua formation, Cuba. *Acta Palaeontologica Polonica*, 28, 369–384.
- Lehmann, U. (1967). Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. *Paläontologische Zeitschrift*, 41, 38–45.
- Lehmann, U. (1971). Jaws, radula, and crop of *Amioceras* (Ammonoidea). *Palaeontology*, 14, 338–341.
- Lehmann, U. (1972). Aptychen als Kieferelemente der Ammoniten. *Paläontologische Zeitschrift*, 46, 34–48.
- Lehmann, U. (1973). Zur Anatomie und Ökologie von Ammoniten: Funde von Kropf und Kiemen. *Paläontologische Zeitschrift*, 47, 69–76.
- Lehmann, U. (1975). Über Nahrung und Ernährungsweise von Ammoniten. *Paläontologische Zeitschrift*, 49, 187–195.
- Lehmann, U. (1976). *Ammoniten, ihr Leben und ihre Umwelt* (p. 171). Stuttgart: Enke-Verlag.
- Lehmann, U. (1979). The jaws and radula of the Jurassic ammonite *Dactylioceras*. *Palaeontology*, 22, 265–271.
- Lehmann, U. (1981). Ammonite jaw apparatus and soft parts. In J. R. Senior (Ed.), *The ammonoidea. systematics association special volume* (Vol. 18, pp. 275–287). London: Academic Press.
- Lehmann, U. (1990). *Ammonoideen. Haeckel Bücherei Volume 2*. Stuttgart: Ferdinand Enke Verlag.
- Lehmann, U., & Kulicki, C. (1990). Double function of aptychus (Ammonoidea) as jaw elements and opercula. *Lethaia*, 23, 325–331.
- Macchioni, F., & Cecca, F. (2002). Biodiversity and biogeography of middle-late ammonoids: Implications for the early Toarcian mass extinction. *Geobios*, MS, 24, 165–175.
- Meek, F. B., & Hayden, F. V. (1864). Paleontology of the upper Missouri. *Smithsonian Contributions to Knowledge*, 14, 1–135.
- Michael, R. (1894). Über ammoniten-Brut mit Aptychen in der Wohnkammer von *Oppelia steraspis*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 46, 697–702.
- Mitta, V. V., & Keupp, H. (2004). Ammoniten-Kiefer aus dem Callovium Russlands. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 88, 125–134.
- Morton, N. (1981). Aptychi: The myth of the ammonite operculum. *Lethaia*, 14, 57–61.
- Morton, N., & Nixon, M. (1987). Size and function of ammonite aptychi in comparison with buccal masses of modern cephalopods. *Lethaia*, 20, 231–238.
- Nixon, M. (1996). Morphology of the jaws and radula in ammonoids. In N. H. Landman (Ed.), *Ammonoid palaeobiology. Topics in geobiology* (Vol. 13, pp. 23–42). Netherlands: Springer.
- Page, K. N. (1993). Mollusca: Cephalopoda (Ammonoidea: Phylloceratina, Lytoceratina, Ammonitina and Ancyloceratina). In M. J. Benton (Ed.), *The fossil record* (Vol. 2, pp. 213–227). London: Chapman & Hall.
- Parent, H., Garrido, A. C., Schweigert, G., & Scherzinger, A. (2011). The Tithonian ammonite fauna and stratigraphy of Picún Leufú, southern Neuquén Basin, Argentina. *Révue de Paléobiologie*, 30, 45–104.
- Parent, H., Westermann, G. E. G., & Chamberlain, J. A. (2014). Ammonite aptychi: Functions and role in propulsion. *Geobios*, 47, 45–55.
- Rüppell, E. (1829). Abbildungen und Beschreibung einiger neuer oder wenig gabeckannten Versteinerungen aus der Kalkschiefer-Formation von Solnhofen. Frankfurt a.M., p. 12.
- Schindewolf, O. H. (1958). Über Aptychen (Ammonoidea). *Palaeontographica*, A111, 1–46.
- Schweigert, G. (2000). Über den Aptychus der mittelljurassischen Ammonitengattung *Kosmoceras*. *Neues Jahrbuch für Geologie und Paläontologie Mh.*, 2000(11), 698–704.
- Schweigert, G. (2009). First three-dimensionally preserved in situ record of an aptychophoran ammonite jaw apparatus in the Jurassic and discussion of the function of aptychi. *Berliner paläobiologische Abhandlungen*, 10, 321–330.
- Schweigert, G., Dietze, V., Chandler, R. B., & Mitta, V. V. (2007). Revision of the Middle Jurassic dimorphic ammonite genera *Strigoceras*/*Cadomoceras* (Strigoceratidae) and related forms. *Stuttgarter Beiträge zur Naturkunde*, B373, 1–74.
- Seilacher, A. (1993). Ammonite aptychi: how to transform a jaw into an operculum. *American Journal of Science*, 293, 20–32.
- Siebold, C. T. (1848). *Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere* (p. 679). Berlin: Verlag von Veit & Comp.
- Stenzel, H. B. (1971). Oysters. In C. Teichert (Ed.), *Bivalvia. Treatise on invertebrate paleontology, part N (volume 3), Mollusca* (Vol. 1–4, pp. 953–1224). Kansas & New York: University of Kansas and Geological Society of America.
- Tanabe, K., Kruta, I., & Landman, N. H. (2015). Ammonoid buccal mass and jaw apparatus. In C. Klug (Ed.), *Ammonoid paleobiology: From anatomy to macroevolution. Topics in geobiology* (p. 44). Netherlands: Springer.
- Trauth, F. (1927–1938). Aptychenstudien. I–VIII. *Annalen des Naturhistorischen Museums in Wien*, 41, 171–260, 42, 121–193, 44, 329–411, 45, 17–136, 47, 127–145.
- Westermann, G. E. G. (1954). Monographie der Otoitidae (Ammonoidea), *Otoites*, *Trilobitoceras*, *Itinsaites*, *Epalxites*, *Germanites*, *Masckeites*, *Normannites*. Beihefte zum Geologischen Jahrbuch, 15, 1–364.
- Westermann, G. E. G. (1990). New developments in ecology of Jurassic-Cretaceous ammonoids. In F. Pallini, F. Cecca, S. Cresta, & M. Santantonio (Eds.), *Proceedings Second Pergola symposium (1987)* (pp. 459–478). Evoluzione, Ambiente: Fossili.

