



## Aptychi and their significance for taxonomy of Lower Cretaceous ammonites

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**ABSTRACT.** Scarce data on the occurrence of anaptychi and aptychi in shells of Lower Cretaceous ammonites were summarized and compared with the current classification of ammonites. It is suggested that the Haploceratoidea did not survive the Hauterivian and supported the view that the Desmoceratoidea originated from the Phylloceratina.

**KEY-WORDS.** Anaptychi, aptychi, Neoammonoidea, taxonomy, Lower Cretaceous.

### INTRODUCTION

In living chambers of Lower Cretaceous ammonites, fossilized elements are rarely found, which are usually regarded as masticatory apparatuses of ammonites, although a number of other explanations were proposed. These elements are classified according to the principles of artificial systematics. If indeed remains of ammonite bodies, their classification should correspond with the natural system of Lower Cretaceous ammonites. I tried to test this assumption in the present paper.

### RESULTS AND DISCUSSION

Taking Wright et al.'s (1996) classification as a standard, the order Ammonoidea Zittel is divided into the following four suborders: Phylloceratina Arkell, 1950, Lytoceratina Hyatt, 1889, Ammonitina Hyatt, 1889 and Ancyloceratina Wiedmann, 1966. Subsequently, modifications of this schema were proposed by Kvataliani et al. (1999), Kakabadze et al. (2005), Klein (2005), Fischer & Gauthier (2006), Vermeulen (2006) and Mihajlova & Baraboskin (2009).

Engeser & Keupp (2002) discussed the classification of Jurassic and Cretaceous ammonites (Neoammonoidea) from the point of view of the rather rare occurrences of the elements of aptychi preserved in living chambers of ammonites. They analyzed function and calcification of aptychi and distinguished uni- or single-valved horny anaptychi and calcified rhynchaptychi and aptychi with distinct two valves (thin-walled synaptychi and thick-walled diaptychi). Independently, Tanabe & Landman (2002) analyzed the mor-

phological diversity of jaws of Cretaceous (however especially Upper Cretaceous) ammonites.

Engeser & Keupp (2002) included the aptychi-possessing Neoammonoidea into a new major taxonomic unit named Aptychophora.

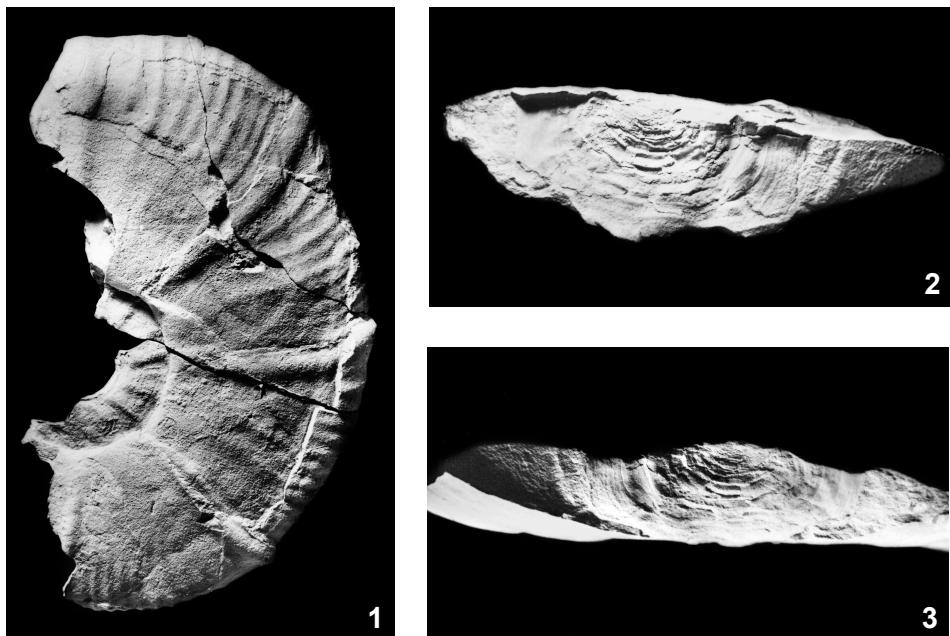
Wright et al. (1996) and Klein et al. (2009) divided the superfamily Haploceratoidea into the families Haploceratidae Zittel, 1884, Oppeliidae H. Douvillé, 1890 (with sub-families Streblitinae Spath, 1925 and Aconeratinae Spath, 1923) and Binneyitidae Reeside, 1927. Haploceratidae are characterised by the presence of well-calcified valves of aptychi in their living chambers.

Měchová et al. (2010) developed a new classification of Early Cretaceous aptychi, as a substitute for earlier classifications by Trauth (1927, 1935, 1938) and Gąsiorowski (1962). They recognized the following genera of Lower Cretaceous aptychi: *Lamellaptychus* Trauth, 1927, *Beyrichilamellaptychus* Turculet, 1994, *Thorolamellaptychus* Turculet, 1994, *Didayilamellaptychus* Turculet, 1994 and a new genus *Mortilletlamellaptychus* (collectively called lamellaptychi), and *Punctaptychus* Trauth, 1927 and another new genus *Cinctpunctaptychus* (collectively called punctaptychi). They did not recognize the genus *Laevilamellaptychus* Trauth, 1930 from the Lower Cretaceous.

The last confirmed records of calcareous aptychi (lamellaptychi) are from the Upper Hauterivian, (e.g. Vašíček & Michalík 1995) but they were sporadically reported even from the lowermost Barremian (e.g. Renz 1983). Moreover, Gräf & Turculet (1988) suggested, on the basis of joint occurrence with ammonites, that lamellaptychi existed in the Upper Barremian. However, the aptychi described by these authors were not found in living chambers of ammonites (described as *Lamellaptychus minimus* and *L. zizinensis*), represent thin-walled, simply ribbed and very small-sized (5-7 mm in diameter) forms and were always preserved with both valves joined together, so that they do not belong to lamellaptychi. They might represent a new genus of thin-walled, slightly calcified aptychi close to the genus *Striaptychus* Trauth, 1927 or belong in the latter genus. Neither a sudden return of the primitive type of ribbing of the valves, nor substantial reduction in calcification are probable toward the end of the existence of lamellaptychi in the Hauterivian.

These data indicate that post-Hauterivian ammonites do not belong to haploceratids, i.e. to the superfamily Haploceratoidea. Engeser & Keupp (2002) have already come to a similar conclusion, because they observed that rhynchaptychi and not lamellaptychi occur in the living chambers of the Aptian *Aconeras trautscholdi* (Sinzow, 1870) according to Doguzhaeva & Mutvei (1991, 1992).

In the suborder Phylloceratina, anaptychi occur in living chambers (see e.g. Lehmann 1990, Keupp & Veit 1996, Tanabe & Landman 2002). On the other hand, Bachmayer (1963) described and illustrated two shells of phylloceratid *Ptychophylloceras ptychoicum* (Quenstedt, 1845) with living chambers from the locality of Štramberk, Czech Republic, with aptychi named *Lamellaptychus beyrichi* var. *ptychoicum* Bachmayer. According to Engeser & Keupp (2002) the position of the mentioned aptychi in living chambers indicates that they are valves redeposited into the living chambers of the ammonites; I agree with this.



Figs. 1-3. *Pseudohaploceras matheroni* (d'Orbigny). 1 – Lateral view of a shell ( $\times \frac{2}{3}$ ); 2 – Rhynchaptynchus in the living chamber ( $\times 1$ ); 3 – An imprint of the same anaptychus at a slightly different angle ( $\times 1$ ). The material was whitened with ammonium chloride before taking the photos. Photos: K. Mezihoráková (Ostrava).

Aptychi were not yet recorded in situ from the Lower Cretaceous ammonites of the suborder Lytoceratina. Only anaptychi and rhynchaptynchi are known from the Lower Jurassic (Arkell et al. 1957, Lehmann 1970) and Upper Cretaceous (Tanabe et al. 1980, Kanie 1982) lytoceratids.

A complex situation is in the suborder Ancyloceratina. Wright et al. (1996: 216) stated that praestriaptychi occur in the Lower Cretaceous genus *Ancyloceras* d'Orbigny, 1842 (from the family Ancyloceratidae Gill, 1871). Lukeneder & Tanabe (2002) recorded aptychi in situ in the Lower Barremian *Karsteniceras ternbergense* Lukeneder et Tanabe, 2002. In small shells of the latter species, slightly calcified tiny valves, arranged in pairs, were found, belonging in the genera *Praestriaptychus* Trauth 1927 and *Striaptychus*.

Engeser & Keupp (2002) illustrated longitudinally striated anaptychi in two representatives of the family Crioceratitidae (in their sense), namely *Aegocrioceras* cf. *compressum* Rawson, 1975 and *Crioceratites* cf. *nolani* Kilian, 1910. According to Klein et al. (2007), *Aegocrioceras* Spath 1924 belongs to the family Aegocrioceratidae Vermeulen, 2006 (superfamily Protancyloceratoidea Breistroffer, 1947) and not to the Crioceratitidae, whereas *Crioceratites* Léveillé, 1837 belongs to the family Crioceratitidae Gill, 1871 (superfamily Ancyloceratoidea Gill, 1871 in Klein et al. 2007). According to these data, true ancyloceratids bear thin-walled aptychi (synaptychi) in their living chambers, where-

as aegocrioceratids and crioceratitids bear anaptychi. Thus, according to anaptychi, the last-mentioned should be transferred from the suborder Ancyloceratina to the suborder Protancyloceratina (sensu Vermeulen 2006).

Engeser & Keupp (2002) recorded *praestriaptychi* from some Lower Cretaceous Perisphinctoidea, which diversified around the Jurassic/Cretaceous boundary. The families Craspeditidae Spath, 1924, Olcostephanitidae Haug, 1910, Berriasellidae Spath, 1922 and Oosterellidae Breistroffer, 1940 should belong here.

The Desmoceratoidea belong either in the suborder Phylloceratina (Arkell et al. 1957) or Hoplitoidea (e.g. House 1988, Wiedmann & Kullmann 1996, Page 1996). In-situ finds of apptychi are sporadic. Tanabe (1983) recorded anaptychi in two Upper Cretaceous desmoceratids in Japan.

Below I describe a previously unreported anaptychus from the shell of the Lower Cretaceous desmoceratid *Pseudohaploceras matheroni* (d'Orbigny, 1841), which I collected in spring 1970 at the Barremian stratotype near Angles, France (deposited in the Collections of the Institute of Geological Engineering, VŠB – Technical University of Ostrava, inv. number Angles/1970/21). The incomplete shell was deformed onto the bedding plane in the debris of Upper Barremian deposits. Its maximum diameter was ca. 115 mm. The preserved part of the shell begins with the end of the phragmocone; the whole remaining part belongs to the living chamber (Fig. 1). After a random knock by hammer, an rhynchaptychus appeared in the living chamber between the first and the third main rib (Figs. 2-3). It has a preserved thin calcite layer, through which a black organic layer shines. The slightly vaulted rhynchaptychus has rather rough concentrical ribs. Morphologically, it is close to the anaptychus illustrated in Tanabe & Landman 2002, text-fig. 3/2) under the name *Menuites* (Desmocerataceae). On the best preserved parts on the rhynchaptychus circumference, the calcite layer bears fine and dense growth lines. In the black organic layer, polygonal cellular structure strongly resembling the structure of calcareous valves of punctaptychi and lamellaptychi can be seen in places. The maximum width of the rhynchaptychus is 37 mm, its preserved height is 16 mm. This record supports the opinion that at least part of the Desmoceratoidea (see Engeser & Keupp 2002: 93) split from the Phylloceratina, not from the Hoplitoidea, because only slightly calcified apptychi were recorded from the latter superfamily.

## CONCLUSIONS

Engeser & Keupp (2002) presented a phylogenetic tree of the Ammonoidea, which is consistent with the distribution of the different apptychi types. However, the data on Lower Cretaceous apptychi indicate that the Haploceratoidea did not survive the Hauterivian. Consequently, I cannot agree with the conclusions of House (1988) and Wiedmann & Kullmann (1996) that the stock Desmocerataceae/Hoplitaceae/ Acanthocerataceae is a descendant of the Haplocerataceae.

The record of anaptychus in the living chamber of *Pseudohaploceras matheroni* described above supports Engeser & Keupp's (2002) opinion that Desmoceratoidea originated from the Phylloceratina.

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