

Patterns of the evolution of aptychi of Middle Jurassic to Early Cretaceous Boreal ammonites

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Abstract Here we are providing a review of aptychi records in ammonites of Boreal origin or that inhabited Boreal/Subboreal basins during the Bathonian–Albian with special focus on new records and the relationship between the evolution of ammonite conch and aptychi. For the first time we figure aptychi that belong to Aulacostephanidae, Virgatitidae, Deshayesitidae, Craspeditinae and Laugeitinae. A strong difference between aptychi of micro- and macroconchs of co-occurring Aspidoceratidae is shown, which, along with their shell morphologies suggests niche divergence of these dimorphs. Aptychi of Aptian *Sinzovia* (Aconeceratidae) should be tentatively ascribed to *Didayilamellaptychus*, while their previous assignment to rynchaptychi was caused by misidentification. Aptychi of Middle Jurassic–Early Cretaceous Boreal and Subboreal ammonites are characterized by a very thin calcareous non-porous outer layer lacking distinct ribs and tubercles (only radial striae sometimes occur), and mainly should be assigned to *Praestriaptychus*. Some ammonoid groups (i.e. Ancylocerina and Desmoceratoidea) are characterized by the presence of different aptychi types irrespective of their shell shape. This fact could indicate that bivalved praestriaptychi could have easily transformed into single-valved “anaptychi” and vice versa. Size and form of aptychi in relation to those of the aperture of ammonite conchs vary within different lineages and at least some

Stephanoceratoidea and Perisphinctoidea have aptychi significantly smaller than the aperture diameter.

Keywords Aptychi · Jurassic · Cretaceous · Ammonites · Evolution

Introduction

Aptychi are organic (in some cases with calcite layers of variable thickness) and usually bivalved plates, associated with ammonites and considered as parts of the lower jaws albeit other functions are also widely discussed (Parent et al. 2014). During the nearly 200-year history of aptychi research, a great number of formal species and genera have been described. However, only uncommon records of aptychi were mentioned from the Boreal Middle Jurassic to Early Cretaceous (e.g. Blake 1875; Weerth 1884), and aptychi of many ammonite groups (especially of those with Boreal and Subboreal affinities) remain unknown until now. Significant progress in the study of Boreal aptychi has been achieved over the last decades in which numerous aptychi (including in situ findings in ammonoid body chambers) were described and/or figured (cf. Etches and Clarke 1999; Engeser and Keupp 2002; Rogov and Gulyaev 2003; Rogov 2004a, b; Mitta and Keupp 2004; Keupp and Mitta 2013; Mironenko 2014). Aptychi–ammonite conch associations sometimes are used for reconstructing ammonite evolution (Trauth 1927; Engeser and Keupp 2002). However, aptychi records are still significantly incomplete, and the ammonite phylogenetic tree based on aptychi distribution contradicts some aspects of phylogenies based on other features, especially the sutural development (Rogov 2004a, b).

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Material

In this study, we focus on little-known aptychi from Boreal and Subboreal areas (Fig. 1). Most of the studied specimens have been collected by the authors, and some specimens or photos of aptychi were transferred to us by colleagues. Studied aptychi were discovered within the body chambers of ammonites or ascribed to particular ammonite groups due to their co-occurrences. As ammonite diversity is relatively low in many stratigraphic levels of the Boreal Jurassic (in many cases 1–2 genera belonging to 1–2 families), such co-occurrences could help significantly even when aptychi are found separately from the conchs of the corresponding ammonite. In some cases (for example, in suspected Middle Volgian virgatitid aptychi), a cross sections of ammonites versus aptychi relative length was also used to infer ammonite–aptychi relationships. In addition to newly collected material, we are also reviewing some recent records of aptychi in Boreal and Subboreal ammonites.

Systematics of higher ammonite taxa used herein is based on Besnosov and Michailova (1991) with some additions from Kvantaliani et al. (1999) and Shevyrev (2006). As aptychi usually occurred outside the host conchs and their relation to ammonoid taxa are unclear, generic and species names used for aptychi are separate from those of ammonoid shells and treated as parataxa (Engeser and Keupp 2002). A brief description of major aptychi types is given by Engeser and Keupp (2002).

For the stages around the Jurassic/Cretaceous boundary, we are using the Volgian and Ryazanian as preferred names, because these stages could be easily used for all Boreal regions (cf. Rogov and Zakharov 2009), while their

correlation with international Tithonian and Berriasian stages remains unclear.

Studied specimens are stored in the Moscow State University Museum (MSU) and Vernadsky State Geological Museum of the Russian Academy of Sciences (SGM), both in Moscow, Russia, with exception of those specimens which are available as photos thanks to the help of our colleagues; the latter specimens are kept in the University of Oslo (PMO, Norway), Cambridge Arctic Shelf Programme (CASP, Cambridge, UK) and Museum of Jurassic Marine Life (K, Kimmeridge, UK).

Review and description of new aptychi records

Stephanoceratoidea

Cardioceratidae

Both in situ records of cardioceratid aptychi and their isolated occurrences are only known from the Lower Callovian of the European part of Russia (Mitta and Keupp 2004), while Late Callovian aptychi, which belong to *Quenstedtoceras*, are also known from northern Poland (Lehmann 1972; Dzik 1986). Surprisingly, mass occurrences of cardioceratids, which sometimes crowded the bedding planes in the Upper Oxfordian or Upper Kimmeridgian black shales are lacking cardioceratid aptychi, albeit the Upper Oxfordian shales of the Kostroma region yielded perisphinctid aptychi. Taking reported uncalcified cephalopod jaws into account, which co-occur with numerous cardioceratids described by Dzik (1986) from the Upper Callovian of Poland and the absence of a calcitic

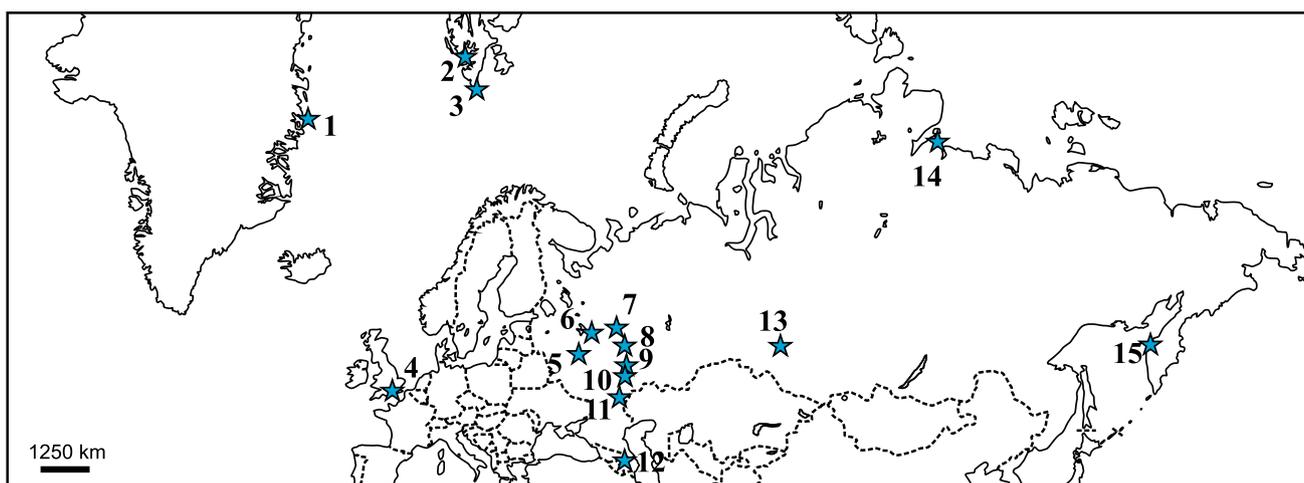


Fig. 1 Map showing aptychi-bearing sites, specimens from which are figured or discussed. 1 Kuhn Island, 2 Janusfjellet Mt, Vasstak Elva, Cape Festningen, 3 Sorkapland, 4 Kimmeridge Bay, 5 Eganovo, Rybaki, 6 Ivanovskoe, Glebovo, 7 Mikhalenino, 8 Hvadukassy, 9

Gorodischi, Ulianovsk, 10 Kashpir, Marievka, 11 Shirokij buerak, 12 Kelevudagh Mt, 13 Veselovskaya 5 well, 14 Nordvik, 15 Cape Hajryuzova

layer in the Early Callovian ones, cardioceratid aptychi could have been fully organic and their absence might be primarily taphonomic in the Upper Jurassic. The shape of cardioceratid aptychi allows them to be described as *Praestriptychus* Trauth, 1927.

Kosmoceratidae

Numerous occurrences of kosmoceratid aptychi have become known since recently. Schweigert (2000) described an in situ record of *Kosmogranulaptychus* Rogov, 2004a (originally referred by Schweigert to *Granulaptychus* Trauth, 1927) within the body chamber of Late Callovian *Kosmoceras*. A few years later, the suggested kosmoceratid aptychi, which were assigned to this family by co-occurrence of conchs with corresponding aptychi, were described from the Upper Bathonian (Mitta 2009) and Middle Callovian (Rogov 2004a, b) of the Russian Platform. Finally, Keupp and Mitta (2013) described and illustrated both isolated and well-preserved in situ aptychi of Early Callovian kosmoceratids. It should be noted that generic classification of kosmoceratid aptychi still remains unclear, as in some cases, they are represented by internal moulds without any traces of a calcitic layer, thus they could be assigned either to *Kosmogranulaptychus* or to *Praestriptychus*. However, at least some Early Callovian kosmoceratids bear praestriptychi (Keupp and Mitta 2013, Figs. 13–14), which can be distinguished from kosmogranulaptychi by a smooth outer calcitic layer. It stands to reason that the early kosmoceratids which bore praestriptychi could have transformed into kosmogranulaptychi with outer surfaces covered by granules (Keupp and Mitta 2013). Additional records of kosmoceratid aptychi, which are assigned to this ammonite family due to their occurrence in concretions crowded with *Kepplerites*, were found recently by the authors in the Upper Bathonian of Moravia. It should be noted that aptychi, which were recovered from the body chambers of Lower Callovian kosmoceratid macroconchs (Keupp and Mitta 2013, Figs. 12, 15) are characterized by a significantly smaller size compared to the corresponding ammonite conchs.

Perisphinctoidea

Perisphinctidae and Ataxioceratidae

During the last decade, findings of aptychi, which belong to the Proplanulinae, were discovered in the Lower Callovian of European Russia (Rogov and Gulyaev 2003; Keupp and Mitta 2013). In situ records of praestriptychi are only known from microconchs of these ammonites (Rogov and Gulyaev 2003, Fig. 2), while large-sized aptychi, assigned to perisphinctid macroconchs were found apart from their

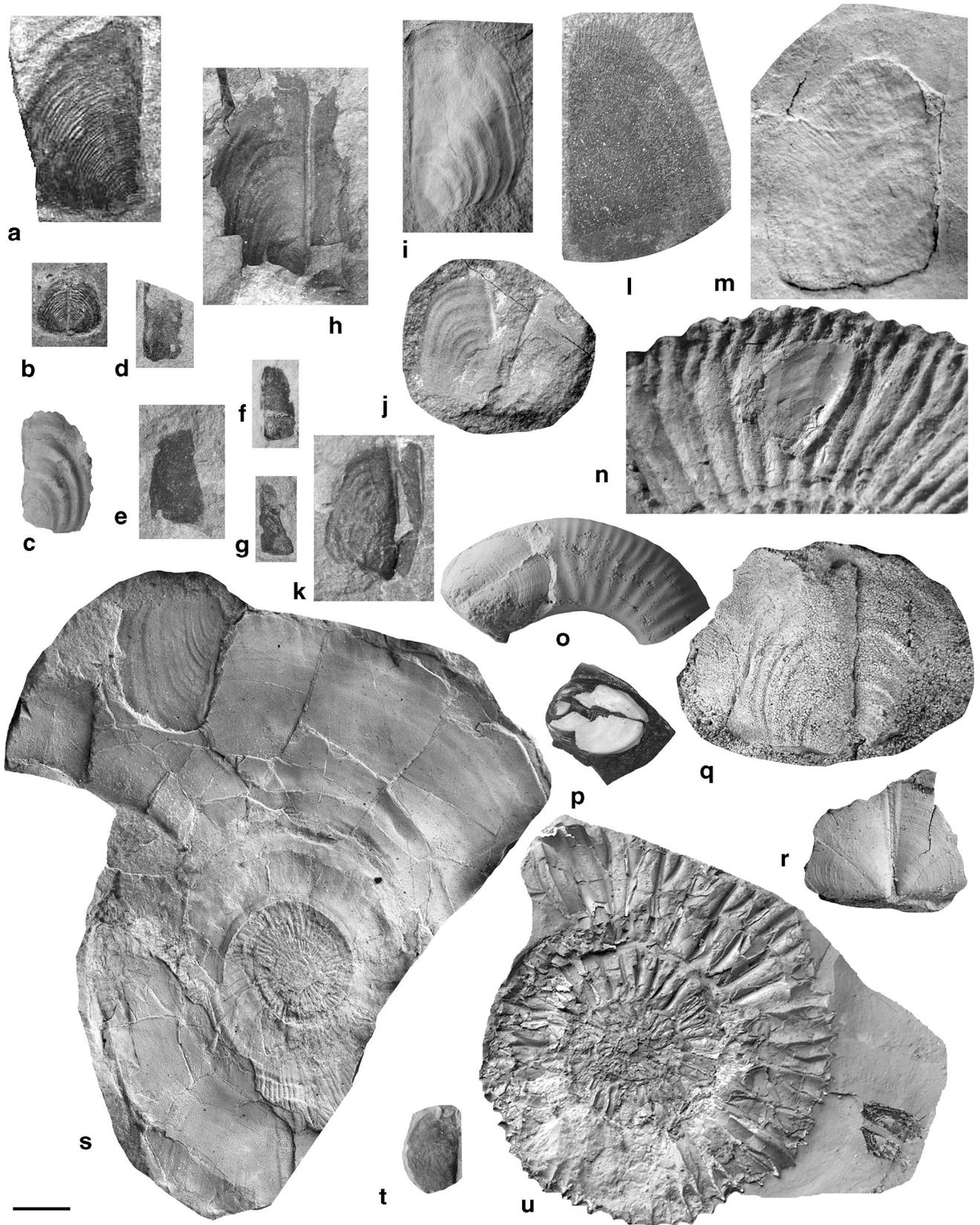
conch (Keupp and Mitta 2013, Fig. 13e). Similar aptychi were also found within the body chamber of the Late Bathonian *Homoeoplanulites* from NE Iran (Seyed-Emami and Schairer 2011, Fig. 3B). A poorly preserved *Praestriptychus* was also discovered associated with *Elatmites* (Grossouvriinae, Keupp and Mitta 2013, Fig. 21). Upper Oxfordian clays and black shales, intensively studied in the Kostroma region of European Russia during the last decade (Glowniak et al. 2010; Tesakova et al. 2012), are also known as a source of the suspected perisphinctid aptychi. *Praestriptychus* was usually found in black shales as isolated plates (Fig. 3f), but in situ findings are also known. The in situ occurrence of relatively small-sized *Praestriptychus* within the body chamber of *Dichotomosphinctes* from the Upper Oxfordian Serratum Zone of Mikhalenino (Kostroma region, Fig. 2n) is the most interesting among these records. Ataxioceratid ammonites were mainly typical for Sub-mediterranean areas, except their short-lived Subboreal offshoot, separated as the subfamily Gravesiinae by Zeiss (in Fischer and Zeiss 1987). Aptychi were recorded in Early Volgian *Gravesia gigas* from Northern France (Boulogne-sur-Mer, see Hahn 1963, pl. 13, Fig. 1), and isolated aptychi co-occurred with *Gravesia gravesiana* in Swabia (Scherzinger et al. 2006). These aptychi should be referred to as *Praestriptychus*.

Aulacostephanidae

Aptychi of aulacostephanid ammonites were not known previously (Ziegler 1962). During the field work in Sorkapland (Svalbard), our colleagues from the Polar Marine Geological Expedition (Lomonosov, Russia) collected some Kimmeridgian ammonites. In one of the specimens ascribed to as *Rasenia cymodoce* (d'Orb.) [M], there is a relatively large-sized imprint of *Praestriptychus*, characterized by well-visible wide ribs on the opposite side of the slab (Fig. 2i). Our suggestion that these aptychi are belonging to *Rasenia cymodoce* is based on both its size and shape, while other ammonites, known from the Lower Kimmeridgian *cymodoce* horizon of Svalbard are characterized by a much smaller conch size compared to those of *Rasenia* (Rogov 2014a).

Dorsoplanitidae

First reports on the aptychi which belong to dorsoplanitid ammonites were published by Blake (1875) who mentioned an “*Aptychus*” from his Bed 38 of the Kimmeridge Clay of the Kimmeridge area in Dorset (Lower Volgian Elegans Zone, see Cope 1967) as well as a co-occurrence of *Aptychus biplex* (nomen dubium) with a conch of *Ammonites biplex* auct. non Sow. (species used for most Late Kimmeridgian [sensu *anglico* = Early Volgian and earliest



◀ **Fig. 2** Selected Upper Jurassic–Lower Cretaceous aptychi. Specimens figured at **c, i, m, o, q–s** are coated with ammonium chloride. **a–n, q, s–u** *Praestriptychus* spp., **a** K952b, Kimmeridge Bay, Middle Volgian, Pallasiodes Zone; **b** K477, Kimmeridge Bay, Lower Volgian, Pectinatus Zone; **c** PMO225.170, Janusfjellet Mt, Upper Volgian, Okensis Zone, Originalis Subzone (refigured from Hryniewicz et al. 2015, Fig. 9D); **d, f, g** Marievka, Upper Volgian: **d** MSU 121/41, Catenulatum Zone, *catenulatum* horizon, bed M15, **f** MSU 121/35, Fulgens Zone, *involutum* horizon, bed M14, **g** MSU 121/42, Fulgens Zone, *tenuicostatum* horizon (?), beds 10–12; **e** MSU 121/12, Kashpur, Upper Volgian, Fulgens Zone, bed 23, *subfulgens* horizon: **h** MSU 121/43, Nordvik, Middle–Upper Volgian boundary beds: **i** MSU 121/44, Sorkapland, Lower Kimmeridgian, Cymodoce Zone, *cymodoce* horizon, section 4, bed 5; **j, k** Kuhn Island, Middle Volgian, Groenlandicus Zone, *lambecki* horizon, **j** CASP K16185, **k** CASP K16154; **l** MSU 121/20, Veselovskaya 5 well, Middle–Upper Volgian boundary beds: **m** SGM 1355/89, in situ record within the body chamber of *Dorsoplanites* sp., Vasstak Elva, Middle Volgian; **n** specimen in private collection of A. Stupachenko, in situ record within the body chamber of *Dichotomoceras* sp., Mikhalenino, Upper Oxfordian, Serratum Zone; **q** MSU 121/27, Glebovo, Middle Volgian, Nikitini Zone; **s** SGM 1355/57, in situ record within the body chamber of *Laugeites lambecki* (Ilov.), Festningen, Middle Volgian, Groenlandicus Zone, *lambecki* horizon, bed 131; **t** MSU 121/19, Kelevudagh Mt, Lower Hauterivian, bed 177; **u** SGM VH17/39, Gorodischi, Upper Kimmeridgian, Autissiodorensis Zone, Subborealis Subzone, *subborealis* horizon, bed 9/24; **o, p** *Laevilamellaptychus* sp., Rybaki, Upper Oxfordian, Serratum Zone, **o** MSU 121/1, imprint of the inner surface, **p** MSU 121/2; **r** imprint of the inner surface of *Laevaptychus* sp., MSU2549, Hvadukassy, Upper Kimmeridgian, Mutabilis Zone

Middle Volgian] British ammonites prior to 1913, cf. Cope 1967, p. 5) found in bituminous shales near Fulleby (Lincolnshire). These historical records were not figured or described, but their assignment to dorsoplanitid ammonites is based on the absence of other ammonite groups within the discussed strata. Typical praestriptychi, which belong to *Pavlovia* were figured by Oates (1974, pl. 10, Fig. 3) from the Hartwell Clay of Buckinghamshire and additional records were made by Etches (Etches and Clarke 1999; refigured herein, Fig. 2a) while aptychi of older dorsoplanitids (Pectinatitinae: *Pectinatites* or *Paravirgatites*) were discovered by Etches at Dorset (Etches and Clarke 1999; refigured herein, Fig. 2b). In both these cases, the aptychi assignment to the conchs of particular ammonite genera was based on their co-occurrences with ammonites. Few in situ aptychi of later dorsoplanitids were found in Svalbard. The *Praestriptychus*, which was found in the body chamber of *Dorsoplanites* sp., shows thin radial striae (Fig. 2m), whereas more typical *Praestriptychus* was found in the body chamber of *Laugeites lambecki* (Ilov.) from the latest Middle Volgian (Fig. 2s). The aptychi, very similar to those from the body chamber of Svalbard *Laugeites*, were also found together with *L. parvus* Donovan of the same age in the Kuhn Island (East Greenland) by the CASP expedition (Fig. 2j, k). Very similar isolated aptychi, which could be assigned either to Laugeitinae or to

Craspeditinae were found in the Middle–Upper Volgian of the Veselovskaya 5 well (Western Siberia, Fig. 2l) and the Nordvik section (Northern Siberia, Fig. 2h). Isolated *Praestriptychus* (Fig. 2q) from the Middle Volgian Nikitini Zone of the Yaroslavl region should be also assigned to Dorsoplanitidae, as other ammonites are unknown from these strata. The latter record possibly belongs to either *Epivirgatites*, *Laugeites* or *Lomonossovella*. This aptychus, as well as a specimen from the body chamber of *Dorsoplanites* from Svalbard shows not only concentric ribs, but also thin radial striae (they are visible near the transition from the lateral to frontal margin), which became common in some Cretaceous praestriptychi.

Virgatitidae

Virgatitids are short-lived (latest Kimmeridgian–Middle Volgian) Subboreal ammonites with a narrow geographic distribution (one endemic species is described from Subpolar Urals, while other taxa are restricted to the European part of Russia and Poland). Several relatively narrow praestriptychi were found together with an early member of this family, the Late Kimmeridgian *Sarmatisphinctes* (Fig. 2u), however, some uncertainties concerning the aptychi assignment remain as they were found close to—but outside of the body chambers of ammonites. It should be noted, however, that such praestriptychi were also found in the Autissiodorensis Zone of the Peri-Caspian depression, where ammonite assemblages consist of *Sarmatisphinctes* and lamellaptychi-bearing oppeliids. Middle Volgian praestriptychi (*P. volgensis* Rogov), which are characterized by even more narrow valves, were primarily assigned to either *Pavlovia* or *Zaraiskites* (Rogov 2004a). They were collected outside of ammonites, but their comparison with true aptychi of *Pavlovia* and other dorsoplanitids gave ground to the assumption that they should be ascribed to *Zaraiskites*. Very similar narrow-valved praestriptychi, which probably belong to virgatitid ammonites, were also found in the uppermost part of the Lower Volgian (Fig. 3h).

Craspeditidae

Craspeditid aptychi have been discovered only recently in the Upper Volgian of the Middle Volga region (Rogov and Mikhailova 2006). Intensive studies of the Upper Volgian succession in the Moscow region lead to numerous records of aptychi (*Praestriptychus fulgens* Mironenko) and upper jaws in *Kachpurites* (Mironenko 2014). Additional occurrences of aptychi, which belong to Garniericeratinae are also known, providing possibilities to compare evolutionary changes of shell versus aptychi shape. This subfamily consists of the two genera

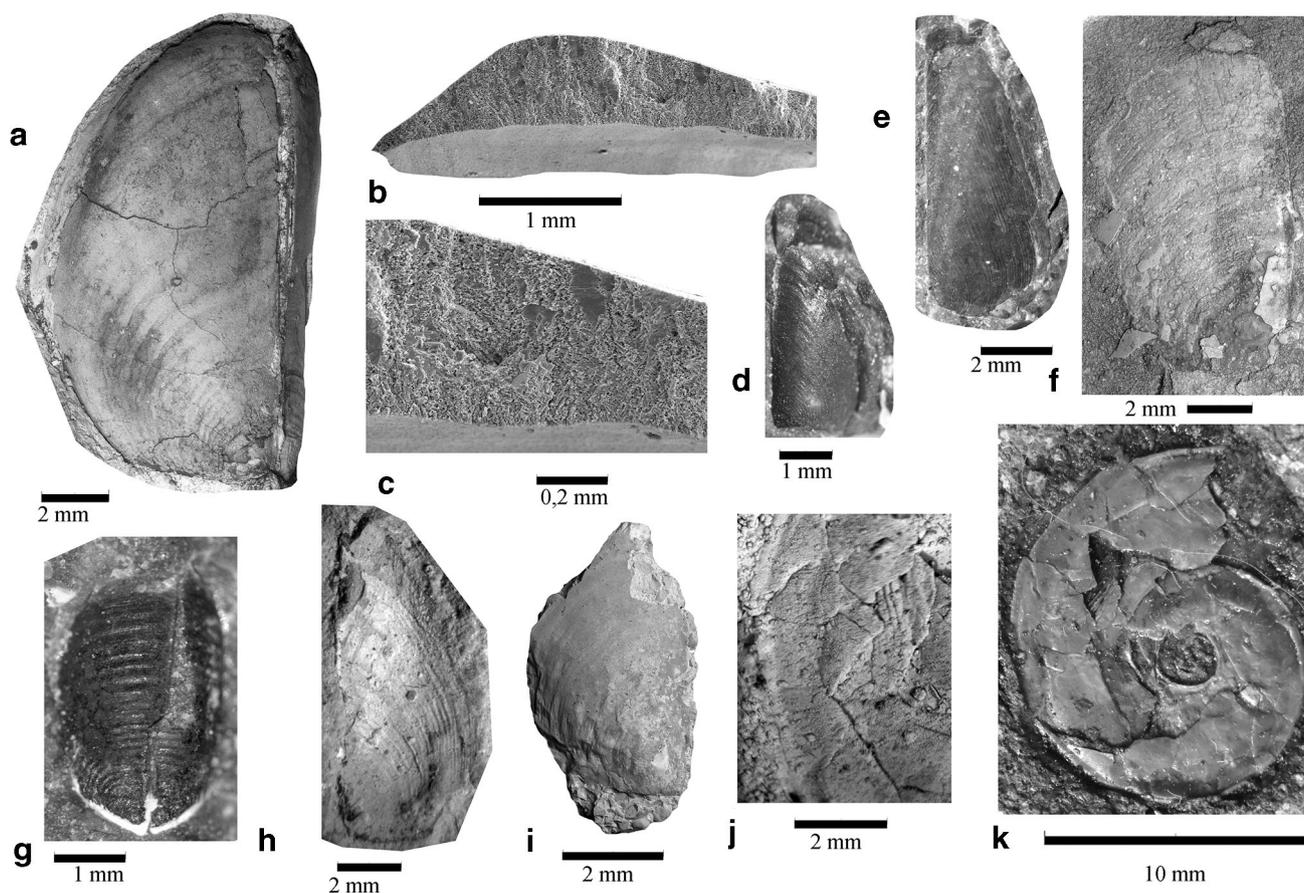


Fig. 3 VEGA/Tescan SEM (a–c, f, i) and microscopic (d, e, g, h, j, k) photographs of Upper Jurassic and Lower Cretaceous aptychi. Only j is coated with ammonium chloride. a–c *Laevilamellaptychus* sp., Rybaki, Upper Oxfordian, Serratum Zone, a specimen in private collection; b, c MSU 121/2, details of inner structure of aptychus; d, e, j, k *Didayilamellaptychus* (?) sp. Lower Aptian, Volgensis Zone,

d (MSU 121/3) e (MSU 121/4)—Ulianovsk, j, k in situ record within the body chamber of *Sinzovia*; f–i *Praestriptychus* sp., f MSU6070, Mikhailenino, Upper Oxfordian, Alternoides Zone, bed 8; g MSU 121/5, Ulianovsk, Lower Aptian, Volgensis Zone; h Gorodishi. MSUAP137, Lower Volgian, Puschi Zone, bed 1/6; i MSU 121/6, Kelevudagh Mt, Lower Hauterivian, bed 177

Kachpurites and *Garniericeras*, which show quick anagenetic evolutionary changes from nearly evolute well-sculptured early *Kachpurites* to keeled oxyconic *Garniericeras* (Rogov 2013, 2014b). Evolutionary changes in the shape of praestriptychi, associated with these ammonites (Fig. 2d–g), generally coincide with this trend, but aptychi evolution seems more gradual (Fig. 4). Some praestriptychi, collected from the lower part of the Upper Volgian from European Russia could belong to *Craspedites* (Craspeditinae), but to date only one record of *Praestriptychus* (Hryniewicz et al. 2015, Fig. 9D, refigured herein, Fig. 2c) from the upper part of the Upper Volgian Okensis Zone should be ascribed to this genus. Surprisingly, the intensive search for aptychi in the ammonite-rich sites of the earliest Cretaceous age (Ryazanian and Valanginian) did not provide any additional occurrences of craspeditid aptychi, although several ammonoid upper jaws were discovered in the Ryazanian of Northern Siberia (they will be described elsewhere).

Aspidoceratidae s.l.

Although aspidoceratids are not truly Boreal ammonites and they are typical for Tethyan areas, they sometimes invaded Boreal seas, in some cases reaching the Pechora region and Subpolar Urals. Two subfamilies, included in the Aspidoceratidae (Aspidoceratinae and Peltoceratinae) are characterized by significant differences in their inner whorls (including presence of ‘parabolic nodes’ in aspidoceratins) suggesting that the Aspidoceratidae, as conventionally recognized, is polyphyletic and two subfamilies evolved from different groups of pseudoperisphinctins (Page 2008). Aptychi of Late Jurassic peltoceratins are unknown, but their Callovian ancestors (*Binatisphinctes*) are associated with *Praestriptychus anglicus* (Page 1991; Rogov 2004a, b). The single known record of an aptychus within the body chamber of *Peltoceras* (Frerichs 2004, Fig. 1) is preserved as an imprint of the inner surface and its identification as

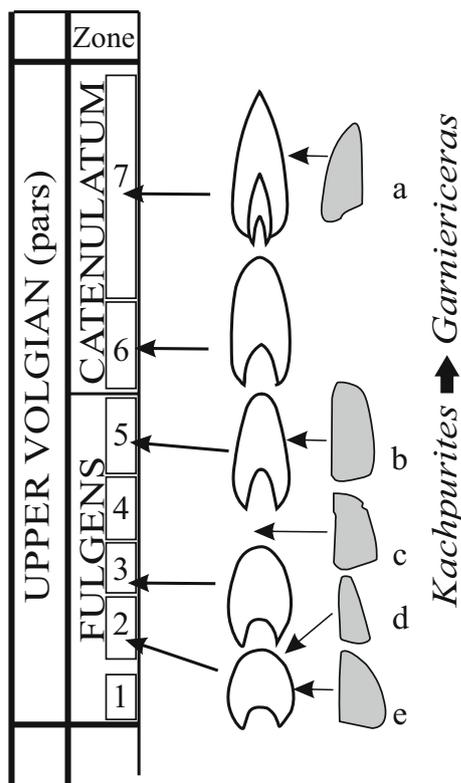


Fig. 4 Changes of shell cross-section and aptychi outline within the lineage of the Late Volgian Garniericeratinae. Biohorizons are marked by numerals (1 *evolutum*, 2 *tenuicostatum*, 3 *cheremkhensis*, 4 *subfulgens*, 5 *involutum*, 6 *internicarinatum*, 7 *catenulatum*). Outline of praestriptychi is given without scale: a aptychus of *Garniericeras catenulatum* (Fisch.), MSU, Ivanovskoe; b aptychus of *Kachpurites involutum* Rogov, in litt., MSU6503, Marievka; c aptychus of *Kachpurites subfulgens* (Nik.), MSU 121/12, Kashpir; d, e aptychus of *Kachpurites tenuicostatum* Rogov, in litt., d MSU 121/42, Marievka; e MSU 116/5, Eganovo = Mironenko (2014, pl.II, Fig. 5)

Praestriptychus is only preliminary. Aspidoceratins developed very thick aptychi (*Laevaptychus* Trauth 1927), which clearly differ from aptychi of other ammonoid groups by their remarkable porous outer surface (Rogov 2004a, b), albeit the imprints of their inner surface could be compared with those of praestriptychi (Fig. 2r). These aptychi are known from nearly all levels of the Subboreal Callovian and Upper Jurassic, which are characterized by aspidoceratins, i.e. from the Upper Callovian, Upper Oxfordian, Lower and Upper Kimmeridgian and uppermost Lower Volgian (Rogov 2004a, b). However, aptychi of microconchiate aspidoceratins were poorly known and their taxonomy remains controversial. Ziegler (1974) ascribed aptychi of *Sutneria apora* (Opp.) as *Laevilamellaptychus* Trauth, 1930, while Schweigert (1998) suggested that aptychi of *Sutneria* should be considered as small-sized *Laevaptychus*. Here, we are presenting a first report of aptychi found in situ within the body chamber of

the Late Oxfordian aspidoceratid *Mirosphinctes* [m] (Figs. 2o, p, 3a). Surprisingly these aptychi differ from those of associated macroconchs *Euaspidoceras* not only by size and shape, but also by their structure. Laevaptychi associated with macroconchs are characterized by a clearly visible porous structure, whereas aptychi of microconchs have a relatively homogenous calcitic layer (Fig. 3b, c) and could be classified within the paragenus *Laevilamellaptychus*. Published data on laevilamellaptychi microstructure (Farinacci et al. 1976, pl. 7–8) indicates the presence of a tubular structure in this taxon, which was not found in our specimens. It should be noted that the shape of laevilamellaptychi, which co-occurred with *Mirosphinctes* is identical to those known as an imprint of the inner surface in the body chamber of *Epipeltoceras* (cf. Enay 1962, pl. IV, Fig. 3). In contrast to *Laevaptychus*, which are only associated with aspidoceratin macroconchs, *Laevilamellaptychus* are known in association with clearly separated ammonoid clades, such as Stephanocerina (Aspidoceratidae) and Haplocerina (Haploceratidae, see Trauth 1934). It is worth noting that the laevaptychi, which were found inside the body chambers of two Late Oxfordian *Euaspidoceras* are significantly smaller than the apertures of these ammonites (in both recorded shells the height of aptychi is approximately 80 % of the height of the aperture), whereas in brevidomic microconchs *Mirosphinctes* the size of aptychi is nearly equal to the size of the aperture (Fig. 2o).

Simbirskitidae

Aptychi of simbirskitid ammonites have been known since the end of the nineteenth century when Weerth (1884) depicted *Aptychus inverselobati* (Weerth 1884, pl. VII, Fig. 2), recovered from the body chamber of “*Olcostephanus inverselobatus* Neum. et Uhl.”, presently considered to belong to the simbirskitid genus *Speetonicerias* (Rawson 1971). This aptychus was included by Trauth (1937) in the paragenus *Praestriptychus*. Additional records of simbirskitid aptychi were reported recently. Engeser and Keupp (2002, Fig. 7) and Frerichs (2004, Figs. 10–12) have described Late Hauterivian *Simbirskites* from Northern Germany with *Praestriptychus* in their body chambers, while some years later Baraboshkin and Shumilkin (2010) described aptychi of *Simbirskites* from the coeval strata of the Volga area, ascribed to the new species *Praestriptychus simbirskense* (*Synaptychus* after Baraboshkin and Shumilkin 2010, Fig. 2). New in situ aptychi were found in the body chamber of *Speetonicerias* (Fig. 5). This aptychus could be determined as *Praestriptychus inverselobatus* (Weerth). It should be noted that the length of this aptychus slightly exceed the measured whorl height of the ammonite (54.1 and 50.5 mm,

Fig. 5 *Praestriptychus inverselobatus* (Weerth), MSU 121/40, Upper Hauterivian, Versicolor Zone, Ulianovsk

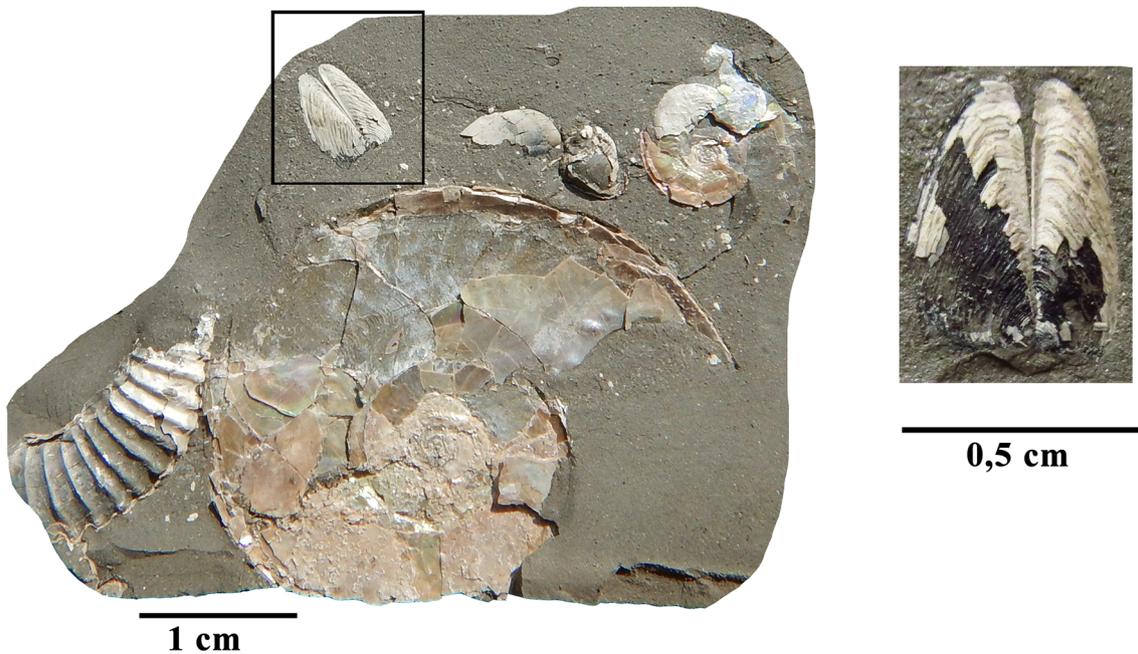
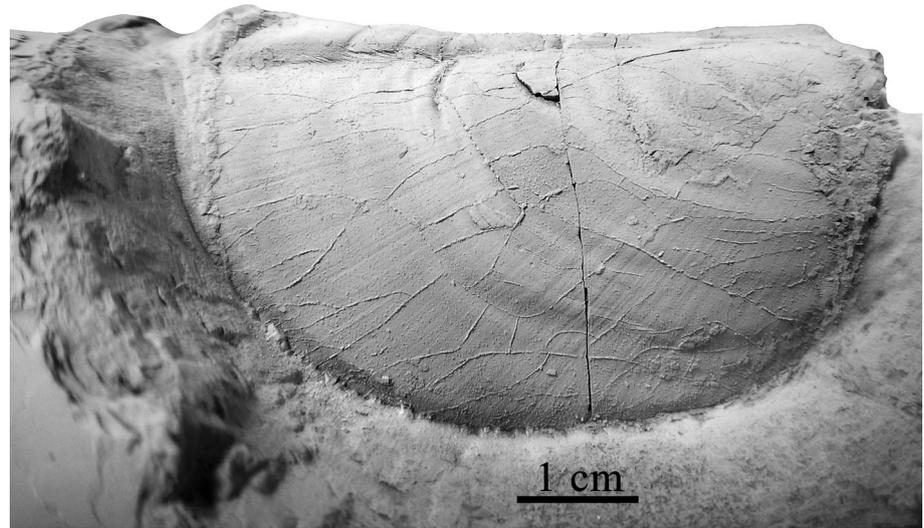


Fig. 6 Aptychi co-occurring with *Sinzovia sasonovae* Wright (left photograph made in field, right the same specimen photographed in laboratory with well-visible inner organic black layer), MSU 121/45, Lower Aptian, Volgensis Zone, Shirokij Buerak, member 3

respectively), while the width of both valves are ~ 1 cm narrower compared to whorl breadth.

Desmoceratoidea

Desmoceratidae

Aptychi of Late Cretaceous desmoceratid ammonites are relatively well known (Tanabe 1983) and they consist of a single valve (anptychus), which, however, shows remains

of the symphysis (“intermediate type”, showing transition from anptychus-type to the aptychus-type, see Tanabe et al. 2015) and possibly it originated not from a true *Anptychus*, but from bivalved aptychi. This hypothesis is supported by a recently described aptychus associated with the desmoceratid ammonite *Grantziceras* from the Lower Albian of Kamtchatka (Cape Hajryuzova, see Palechek et al. 2005). This aptychus is represented by two clearly isolated valves and possibly could be ascribed to as *Praestriptychus*, while its original assignment to

Synptychus Basse, 1953 (*S.?* *hairyusovi* Baraboshkin in Palechek et al. 2005, pl. 1, Fig. 4) seems to be incorrect.

Hoplitoidea

Hoplitidae

Engeser and Keupp (2002) wrote that hoplitids are characterized by praestriptychi, but in support of this view the authors cited Trauth (1927, 1930), who used the generic name *Hoplites* for all Early Cretaceous tuberculated forms, now included in Berriasellidae, Himalayitidae, Neocomitidae, Hoplitidae, Deshayesitidae and Parahoplitidae. Among the aptychi mentioned by Trauth, there are some Early Cretaceous praestriptychi characterized by the presence of radial striae (*P. columbi*: Trauth 1937, pl. 11, Fig. 2; *P. subtriangularis*: Trauth 1937, pl. 11, Figs. 3–4), but they are Neocomian in age and associated with berriasellid and neocomitid ammonites. Similar Berriasian aptychi were recently described in association with berriasellid ammonites from the Western Bermuda Rise (Renz 1979, pl. 1, Figs. 1, 9–10). The only record of an aptychus in association with Albian hoplitids was mentioned by Baraboshkin (in Palechek et al. 2005, p. 89) who compared desmoceratid aptychi with those from the Middle Albian of the Moscow region. As aptychus-bearing beds of this area are characterized exclusively by hoplitid ammonites (Baraboshkin and Mikhailova 1987), the mentioned aptychus very likely belongs to hoplitids, but its true taxonomy remains unclear.

Haploceratoidea

Aconeceratidae

Aptychi, which belong to pre-Barremian Haploceratoidea are so well known, numerous and diverse in pelagic carbonate deposits of the Tethys that the succession of these aptychi (generally called lamellaptychi, which now are subdivided into a few separate genera, see Měchová et al. 2010) are used for zonal subdivision and correlation. In contrast to “Neocomian” deposits, the Barremian is mainly lacking in lamellaptychi: only few records are known from the Upper Barremian of the Eastern Carpathians (Gräf and Turculeț 1988) and their relation with certain ammonoid groups remains unclear. Although aptychi belonging to Aptian aconeceratids are relatively well known, some uncertainties concerning their systematic position remain. Aptychi of *Sinzovia* from the Early Aptian of the Volga area, studied in thin sections, showed some calcification of their apical part (Doguzhaeva and Mutvei 1990), which led to ascribing these aptychi to rhynchaptychi (Engeser and

Keupp 2002). However, such interpretation contradicts known records of aptychi within or close to the body chambers of aconeceratids (Thomson 1972, Fig. 3; Riccardi et al. 1987, pl.11, Fig. 13; Lehmann 1995), as these aptychi show outlines and sculptures typical for lamellaptychi. Unfortunately, aconeceratid aptychi recorded from the Early Aptian concretions (Fig. 3d, e) of the Volga area generally lack a calcitic layer due to taphonomic loss and their classification is unclear. Aptychi recorded from black shales are commonly preserved with remains of a calcitic layer (Fig. 3j, k), but also cannot be precisely determined due to their small size. However, by analogy with lamellaptychi of Antarctic aconeceratids, which are characterized by a backward rib direction near the symphysis (Thomson 1972, Figs. 2–3) and taking into account new records (Fig. 6), these aptychi could be tentatively referred to as *Didayilamellaptychus* Turculeț, 1994. It should be noted, however, that rib curvature in aptychi of *Sinzovia* is rather close to the earliest members of this genus (Měchová et al. 2010, Fig. 11A–C) or to some *Thorolamellaptychus* (Měchová et al. 2010, Fig. 10E), and the systematic position of these aptychi remains unclear. Additional records of aptychi in the body chamber of *Sinzovia* supports the latter interpretation that calcification of the apex could be partially caused by taphonomic processes as well as by remains of well-calcified embryonic aptychi (Mironenko and Rogov 2015). It should be noted that one of the figured aconeceratid aptychi has healed injuries (Fig. 3d), which strongly resemble abnormalities documented in jaws of modern *Nautilus* (Kruta and Landman 2008). The same kind of healed injuries is also known in some Late Cretaceous *Scaphites* (Landman et al. 2010, Fig. 13E).

Ancyloceratoidea

Crioceratitidae

Aptychi of crioceratids were recently figured and briefly described in Hauterivian *Aegocrioceras* and *Crioceratites* from Northern Germany by Engeser and Keupp (2002, Figs. 5–6) and Frerichs (2004, Figs. 6–9). All these aptychi are characterized by prominent radial ribs and were ascribed by Engeser and Keupp (2002) to anaptychi. It should be noted, however, that these aptychi differ from typical anaptychi by the presence of remains of the symphysis and should be further considered as a separate genus as well as aptychi of Late Cretaceous desmoceratids (see above). However, this is not the only type of aptychi known in crioceratitids. In the Lower Hauterivian of Kelevudagh Mt (Azerbaijan), early crioceratitids (*Criosarasinella* and *Crioceratites*) were associated with *Praestriptychus* (Figs. 2t, 3j).

Ancyloceratidae

Ancyloceratid ammonites are characterized by the same types of aptychi, which are known from crioceratitids. *Praestriptychi* were mentioned by Wright et al. (1996) as belonging to *Ancyloceras* and praestriptychi were found in the body chamber of *Proaustraliceras*. However, closely related ancyloceratids, such as *Australiceras whitehousei*, are known to bear striated “anptychi” resembling those of crioceratitids (Doguzhaeva and Mikhailova 2002, Fig. 1). In addition to these two types of aptychi, the Early Barremian ancyloceratid ammonite *Karsteniceras* has bivalve aptychi with prominent concentric ribs, which were primarily referred to the “*Lamellaptychus*-type” (Lukeneder and Tanabe 2002). However, concentric ribs at the outer surface of these aptychi are of a different type than those of true lamellaptychi: they are not tile-like, but rather look like thick growth lines (Lukeneder and Tanabe 2002, Figs. 5–6). Therefore, these aptychi should be assigned to a new type, intermediate between lamellaptychi and praestriptychi.

Deshayesitoidea

Deshayesitidae

Deshayesitids represent a group of ammonoids with monomorphic shells, which originated from heteromorph heteroceratids (Mikhailova and Baraboshkin 2009). Aptychi recorded from the body chamber of juvenile *Deshayesites* from the Early Aptian of the Middle Volga area were described and figured by Doguzhaeva et al. (1995, Fig. 1). The shape of this aptychus along with additional records of isolated aptychi, possibly belonging to *Deshayesites* (Fig. 3g), permits its assignment to *Praestriptychus*.

Ammonite shell evolution versus aptychi evolution: a Boreal view

In the course of research on ammonoid aptychi, two general approaches on their significance for reconstruction of ammonoid phylogeny developed. Some scholars considered aptychi as a key for ammonoid evolution (Trauth 1927; Engeser and Keupp 2002), while others suggest an independent development of the similar aptychi within different lineages (Nagao 1932; Rogov 2004a, b). Taking into account documented examples of convergent evolution of ammonoid shells within different lineages (Bayer and McGhee 1984; Monnet et al. 2011; Rogov 2014a, b), one could come to the conclusion that the same evolutionary mode was also possible for other parts of the

ammonoid skeleton such as the aptychi. Evolution of the Jurassic and Cretaceous ammonoids is relatively well-known presently; conclusions about phylogenies, as a rule, are based on a set of morphological (conch and suture form, their changes during ontogeny), stratigraphical (observations on the step by step evolution within lineages) and biogeographical (based on biogeographic affinities of taxonomic units) evidences (Besnosov and Michailova 1991; Page 2008). Our review of aptychi records in ammonoids, which inhabited Boreal or Subboreal seas during the Middle Jurassic–Early Cretaceous, highlights some aspects of aptychi evolution (Fig. 7):

1. Some aptychi types are restricted to certain ammonoid groups (i.e. laevaptychi, which belong to Aspidoceratinae), while other aptychi occurred within different lineages (praestriptychi). In general, Boreal and Subboreal ammonoids were characterized by bivalved aptychi with a poorly developed calcitic layer and an absence of prominent sculpture elements (praestriptychi).
2. Ammonoids, which belong to the suborder Ancylocerina and the superfamily Desmoceratoidea show a presence of two different types of aptychi through their evolution. This could indicate either a presence of independent lineages within these groups, which developed the same aptychi type over a long period irrespective to changes of shell form or easy transition from one type of aptychi (praestriptychi) to another (“anptychi” which originated from praestriptychi and are characterized by remains of the symphysis between both parts of the valve) and vice versa.

Conclusions

Aptychi occurrences in ammonites of Boreal origin or from Boreal/Subboreal basins during the Bathonian to Albian are reviewed. The bulk of the studied ammonoid groups have poorly sculptured *Praestriptychus*, characterized by a thin calcareous layer.

Aptychi of aconoceratid ammonites belong to the same type of aptychi as the ancestral haploceratid ammonites (lamellaptychi sensu lato), while their previous assignment to rhynchaptychi was caused by misidentification.

Differences between aptychi, which belong to microconchs and macroconchs of the same ammonite group, were recognized for the first time. Aptychi of corresponding microconchs and macroconchs of the Aspidoceratinae should be referred to as different genera of aptychi (i.e. *Laevilamellaptychus* and *Laevaptychus*). However, while laevaptychi are only known in aspidoceratins, laevilamellaptychi also occurred in some haploceratids

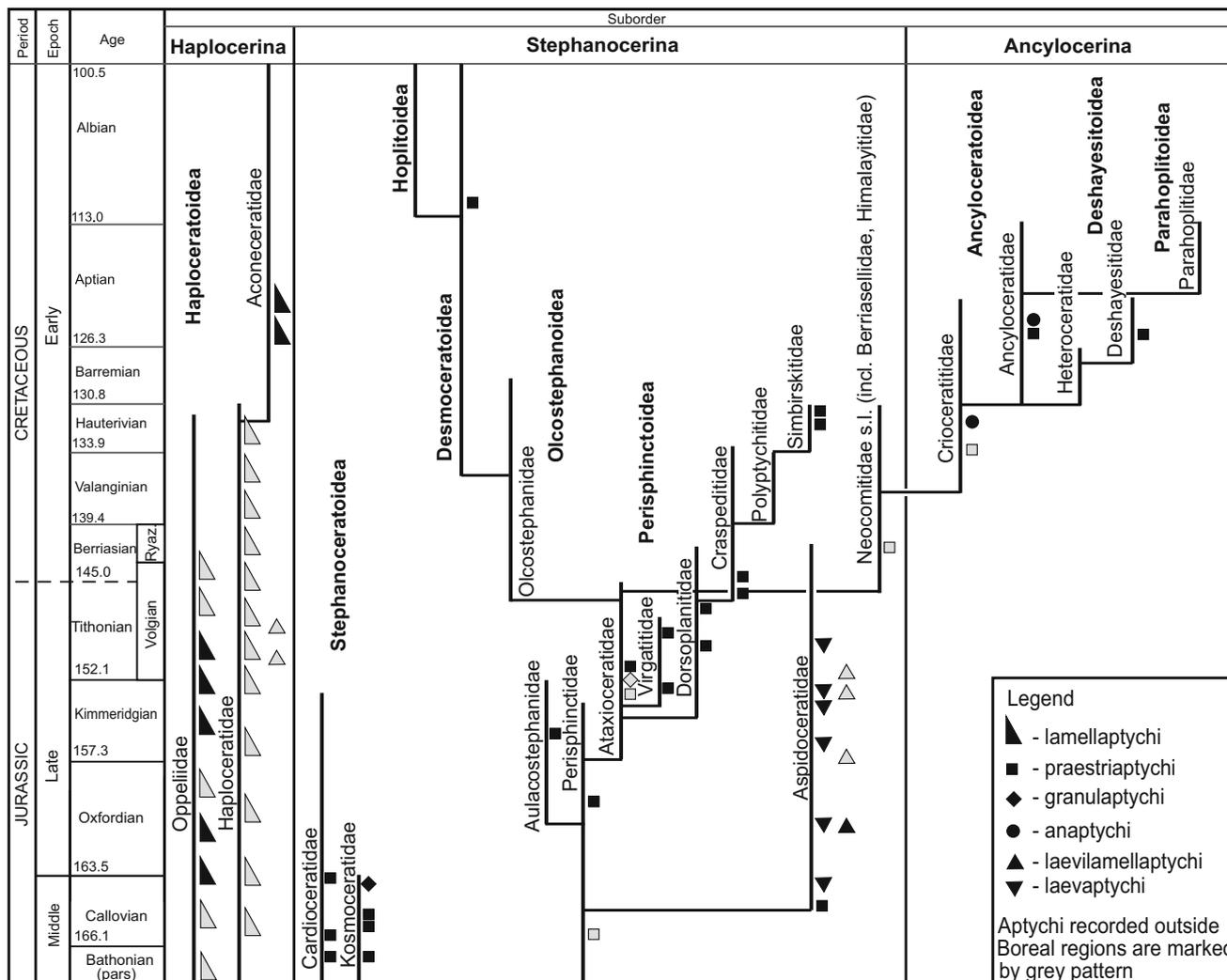


Fig. 7 Aptychi distribution among the selected Middle Jurassic–Early Cretaceous ammonite lineages. Ammonoid suborders and evolution of lineages are given after Besnosov and Michailova (1991), Page (2008) and Shevryev (2006); spelling of suborder is given after Shevryev (2006)

(*Pseudolissoceras*, see Trauth 1930, 1934). For some macroconchs, the relatively small size of aptychi versus whorl height and breadth is recognized (cf. Keupp and Mitta 2013).

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