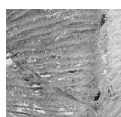


# The endemic and morphologically remarkable nautilid genus *Deltocymatoceras* Kummel, 1956 from the Late Cretaceous of Central Europe

JIŘÍ FRANK, MARKUS WILMSEN & MARTIN KOŠŤÁK



The endemic Late Cretaceous nautilid genus *Deltocymatoceras* Kummel, 1956 is represented by *Deltocymatoceras leiotropis* (Schlüter, 1876) and *D. rugatum* (Fritsch & Schlönbach, 1872). Characteristic for this genus is a bulbous involute shell with strong radial ribbing and a ventral keel, which appears in post-juvenile ontogenetic stages. The combination of these morphological features is unique among post-Palaeozoic nautiloids. Both species are restricted to the Late Turonian–Middle Coniacian of Central Europe and England. Until now, the type species *D. leiotropis* was known based only on the holotype specimen. This specimen is re-described with revised occurrence and for the first time photographically illustrated. The only preserved syntype from the type specimens of *D. rugatum* was re-discovered during this revision and more than thirty other specimens were studied. Representatives of *Deltocymatoceras* show clear morphological changes during their ontogeny and acquisition of maturity, most notably the appearance of a ventral keel in premature stages and its disappearance at maturity. The hypothesis of a close phylogenetic affinity of *Deltocymatoceras* to the genus *Cymatoceras* Hyatt, 1884 is based on similar morphological features such as the suture, ribbing, shell shape and early ontogenetic development. The ventral keel is quite an exceptional feature of morphology in post-Palaeozoic nautiloids. In particular the combination with an involute depressed shell is only shared with representatives of the genus *Angulithes* Montfort, 1808 (Cretaceous–Palaeogene) and *Gryponautilus* Mojsisovic, 1902 (Triassic). The combination with a compressed and evolute planispiral shell is more common in Palaeozoic and some post-Palaeozoic nautiloids. The ventral keel is discussed here in relation to its functional aspects (hydrodynamic stability) in combination with the strong radial ribbing (protection of the shell against mechanical damage). The appearance of the genus concurred with the late Turonian shallowing/cooling associated with the “*Hyphantoceras* Event” and the availability of an ecologic niche (*i.e.*, absence of medium-sized, keeled ammonites at that time). Low abundance, an endemic occurrence, and the very short stratigraphic range of the genus (~3.5 Ma) reflect the limited evolutionary success of the *Deltocymatoceras* lineage.

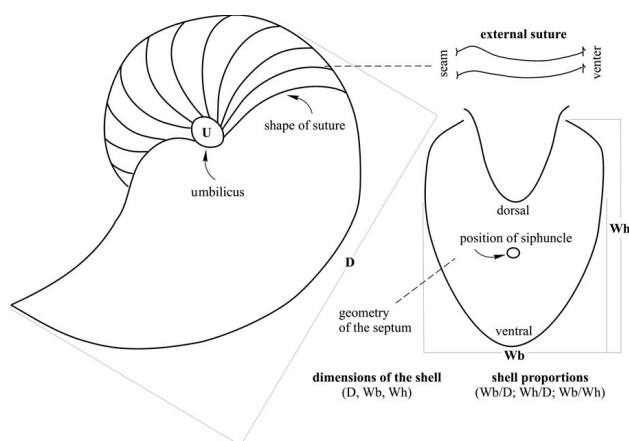
• Key words: Nautilida, taxonomy, phylogeny, ontogeny, palaeogeography, functional morphology, biostratigraphy.

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Jiří Frank, Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Praha 2, and National Museum, Department of Palaeontology, Václavské náměstí 68, 115 79 Praha 1, Czech Republic; jiri\_frank@nm.cz • Markus Wilmsen, Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Sektion Paläozoologie, Königsbrücker Landstrasse 159, D-01109 Dresden, Germany; markus.wilmsen@senckenberg.de • Martin Košťák, Institute of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Praha 2, Czech Republic; martin.kostak@natur.cuni.cz

Late Cretaceous nautilids are morphologically much less diverse and fairly long-ranging compared to contemporaneous ammonites. Thus they seem less attractive for systematic and stratigraphic studies. The genus *Deltocymatoceras* is an exception due to the conspicuous strong radial ribbing, the prominent ventral keel, short stratigraphic range and endemic occurrence. The ventral keel especially is a rare morphological feature within nautilids, particularly in combination with a depressed shell. There are only

a few known genera with this combination of features such as *Gryponautilus* Mojsisovic, 1902 (Triassic) and *Angulithes* Montfort, 1808 (Cretaceous). In contrast, ribbing is a common feature especially within the Cretaceous nautilids of the genus *Cymatoceras*. In the same epoch as *Deltocymatoceras*, nautilids with prominent ventral keels such as *Angulithes* and with various types of radial ribbing such as *Cymatoceras* occurred. However, only *Angulithes galea* (Fritsch & Schlönbach, 1872; see discussion in Frank



**Figure 1.** Morphological features in nautilid biometry and systematics (modified from Wilmsen & Esser 2004, Frank 2010).

2010) displays this combination of characters on the last third of the living chamber of mature shells. Furthermore, the fold-like-ribs of *A. galea* occur when the keel is reduced and disappeared. In our opinion, these traits indicate a close phylogenetic relationship between *Angulithes* and *Cymatoceras* rather than shell convergence (polyphyly – homoplasy). In this paper we discuss the phylogeny of the genus and its affinity to *Cymatoceras* [see Kummel 1956; probably *C. radiatum* (Sowerby, 1822)], and *Angulithes* [*A. triangularis* (Montfort, 1808); see Wilmsen 2000]. Despite the low diversity of *Deltocymatoceras* with only two species and its limited geographic distribution, it is retained as a separate genus based on its specific morphological characters. Ontogenetic trends during the acquisition of maturity are comparable to those documented in recent nautilids (Collins & Ward 1987, Frank 2010). Nevertheless, mature shell modifications are more common and more strongly developed in several early Palaeozoic nautiloids (e.g. Teichert 1964, Stridsberg 1985, Manda 2008). Furthermore, we also discuss the functional morphology of *Deltocymatoceras*. Finally, we evaluate paleoecology and distribution pattern of the genus *Deltocymatoceras*.

## Material and methods

This study has involved the majority of all known specimens of the genus housed in European institutional collections in Europe and new records from field sampling. *Deltocymatoceras rugatum* is currently represented by 22 specimens and *Deltocymatoceras leiotropis* by 10 specimens. Eight specimens are in open nomenclature (see appendix).

The studied material is repositied in the following institutions: Národní muzeum, Prague, the Czech Republic (NM); Chlupáčovo muzeum historie Země, Institute of

Geology and Palaeontology, Faculty of Science, Charles University, Prague, the Czech Republic (CHM UGP); Polabské muzeum, Nymburk, the Czech Republic (PMN); Muzeum Českého ráje, Turnov, the Czech Republic (MCR); Orlické muzeum, Choceň, the Czech Republic (OM); Úpohlavy quarry, the Czech Republic; Regionální muzeum v Teplicích, the Czech Republic (RMT); Muzeum Železnice, the Czech Republic (MZ); Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Germany (MMG); Goldfuss-Museum, Bonn, Germany (GMB). Ruhr-Museum Essen, Germany (RME); Museum für Naturkunde, Berlin, Germany (MfN); Naturhistorisches Museum Wien, Austria (NMW); Natural History Museum London, the United Kingdom (NHM); British Geological Survey, Keyworth, the United Kingdom (BGS). The material from Wittler *et al.* (1999) is not kept in a recognized institution but has been evaluated based on the illustrations provided in the aforementioned paper.

Standard measurements of all specimens were obtained using a sliding calliper (see Fig. 1).  $D$  = maximum diameter;  $Wb$  = maximum width of the whorl;  $Wh$  = maximum height of the whorl; ratios are  $Wb/D$ ,  $Wh/D$  and  $Wb/Wh$  (shells with  $Wb/Wh > 1$  are depressed, those with  $Wb/Wh < 1$  are compressed). The most important features for taxonomic analyses are: the position of the siphuncle; the suture pattern; general form of the shell and the whorl cross-section; the character and width of the umbilicus, and the surface ornamentation of the shell; detailed morphological features and terms as in Teichert (1964). However, most of the specimens are deformed or only partly preserved, and thus biometric data are often incomplete.

## Systematic palaeontology

Order Nautilida Agassiz, 1847

Family Nautilidae Blainville, 1825

### Genus *Deltocymatoceras* Kummel, 1956

*Type species.* – *Nautilus leiotropis* Schlüter, 1876.

*Emended diagnosis.* – Nautilonic, involute, depressed to slightly compressed shells with convex, broadly arched and convergent sides. Whorl cross-section with rounded to sharply angular venter, overlapping approximately one third of the preceding whorl. With prominent, slightly rounded ventral keel appearing in post-juvenile stage, smooth or moderately wrinkled by crossing radial ribs. Shell ornamented with strong radial ribs, bifurcating in approximately the middle of the flanks. Suture moderately sinuous with narrowly rounded saddle on the inner flanks,

broad, more or less shallow lateral lobe on the outer flanks and narrowly rounded to pointed ventral saddle. Position of siphuncle central/ventro-central.

**Discussion.** – Kummel (1956, p. 439) considered *Deltocymatoceras* as being derived from *Cymatoceras* due to the corresponding radial ribbing and he combined both genera in the subfamily Cymatoceratinae Spath, 1927, later he included both genera in the family Cymatoceratidae Spath, 1927 (Kummel 1964, p. 454). Kummel (1956, p. 439) described *Deltocymatoceras* as homeomorphic with *Angulithes* with respect to the shape of the shell and suture line. Wiedmann (1960, pp. 149, 174) regarded *Deltocymatoceras* as a subgenus of *Angulithes* and *D. leiotropis* as well as *D. rugatum* as sculptured forms of the subgenus. Shimansky (1975) discarded the family Cymatoceratidae and grouped *Deltocymatoceras* and *Cymatoceras* together in the family Nautilidae and synonymized *Angulithes* with *Deltoideonautilus*, including the latter genus in the family Hercoglossidae Spath, 1927. Matsumoto & Muramoto (1983, p. 89) proposed that *Deltocymatoceras* (of the family Cymatoceratidae) is convergent with *Angulithes* based on the specific suture line and shell shape. They compared the type species *Deltocymatoceras leiotropis* with that of *Angulithes*, *A. triangularis*. Dzik (1984, p. 180) also discussed the affinity of *Deltocymatoceras* and *Angulithes*, and noted the close relationship between the two type species. Based on the radial ribbing, Wilmsen (2000, pp. 37–38) supported separation of *Deltocymatoceras* and *Angulithes*, but he proposed keeping the two genera in one family, Nautilidae Blainville, 1825. We agree with the interpretation that *Deltocymatoceras* is derived from *Cymatoceras* but we are also aware of inconsistencies in the systematics of the family Cymatoceratidae (Tintant 1989, Frank 2010). The relative importance of traits such as radial ribbing, the suture, the keel or the position of the siphuncle for systematic classification is still under debate.

**Stratigraphic and geographic range.** – Both species occurred in the early Late Turonian of the Czech Republic and Germany; *D. rugatum* also occurred in the early Late Turonian of Poland; *D. leiotropis* also occurred in the Late Turonian of England and Germany, in the Early Coniacian of the Czech Republic and in the Middle Coniacian of Germany and Poland.

#### ***Deltocymatoceras leiotropis* (Schlüter, 1876)**

Figures 3, 8J–K

- 1876 *Nautilus leiotropis*; Schlüter, p. 175, pl. 47, figs 1, 2.
- 1934 *Nautilus leiotropis* (Schlüter). – Andert, pp. 390–392, text-fig. 91.

- 1956 *Deltocymatoceras leiotropis* (Schlüter). – Kummel, pp. 438–439, pl. 22, figs 1, 2.
- 1960 *A. (Angulithes) leiotropis* (Schlüter). – Wiedmann, p. 193.
- 1964 *Deltocymatoceras leiotropis* (Schlüter). – Kummel, p. 454, pl. 334, fig. 5a, b.
- 1975 *Deltocymatoceras leiotropis* (Schlüter). – Shimansky, pp. 122–123, tab. 31.
- 1983 *Deltocymatoceras leiotropis* (Schlüter). – Matsumoto & Muramoto, p. 89.
- 1983 *Deltocymatoceras leiotropis* (Schlüter). – Kabamba, pp. 90–91.
- 1983 *Deltocymatoceras* n. sp.; Kabamba, pp. 91–93, pl. 7, fig. 5a, 5b.
- 1984 *Deltocymatoceras leiotropis* (Schlüter). – Dzik, p. 180.
- 1999 *Deltocymatoceras leiotropis* (Schlüter). – Wittler, Roth & Legant, pp. 32–35, text-figs 45a, b, 46a, b.
- non 2000 possible transitional form between *Angulithes* and *Deltocymatoceras* Kummel, 1956; Wilmsen, pp. 37–38 [*A. triangularis*].
- 2009 *Deltocymatoceras leiotropis* (Schlüter). – Frank, p. 13.
- 2010 *Deltocymatoceras leiotropis* (Schlüter). – Frank, p. 494, fig. 5e, f, g.

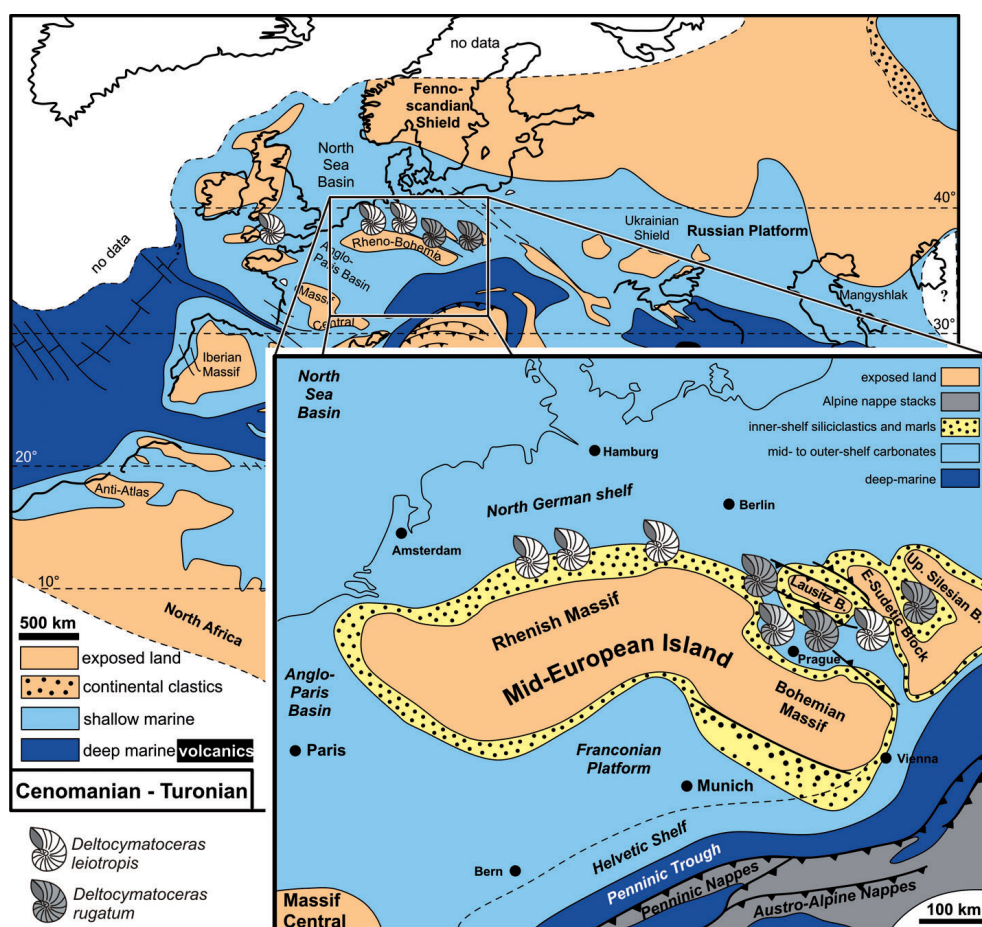
**Holotype (by monotypy).** – Specimen GM 96 figured by Schlüter (1876) on pl. 47 as fig. 3; Goldfuss-Museum, Bonn, Germany (Fig. 3).

**Type locality.** – Hercules mine near Essen, Germany.

**Type horizon.** – In the original description of *Nautilus leiotropis*, Schlüter (1876, p. 175) stated that the single specimen is from the Emscher-Mergel (Emscher Formation, Middle Coniacian–Santonian) of the coal mine Hercules shaft in the centre of Essen. However, the Emscher Formation does not reach that far south in the area of Essen (see Pieper 1990) and the approximately 30 m deep shaft went through Middle–Upper Turonian marly-glaucconitic sediments (Salder and Oerlinghausen formations in proximal greensand facies), Lower Turonian marls (Büren Formation) and Cenomanian greensands (Essen Greensand Formation) before reaching the coal-bearing Carboniferous. Thus, the stratigraphic assignment by Schlüter (1876) is incorrect and the holotype is of Turonian, most likely Late Turonian age.

**Description.** – The shell is nautiliconic, involute and oval with an almost closed umbilicus. The whorl-section is slightly depressed (Wb  $\approx$  170 mm, Wh  $\approx$  130 mm; Wb/Wh  $\approx$  1.3) in late ontogeny and adulthood (maturity). The flanks are convex and the maximum width of the whorl cross-section is on their inner part. The whorl cross-section is more or less triangular in late ontogeny due to the ventral keel. The ventral keel is very prominent, narrowly





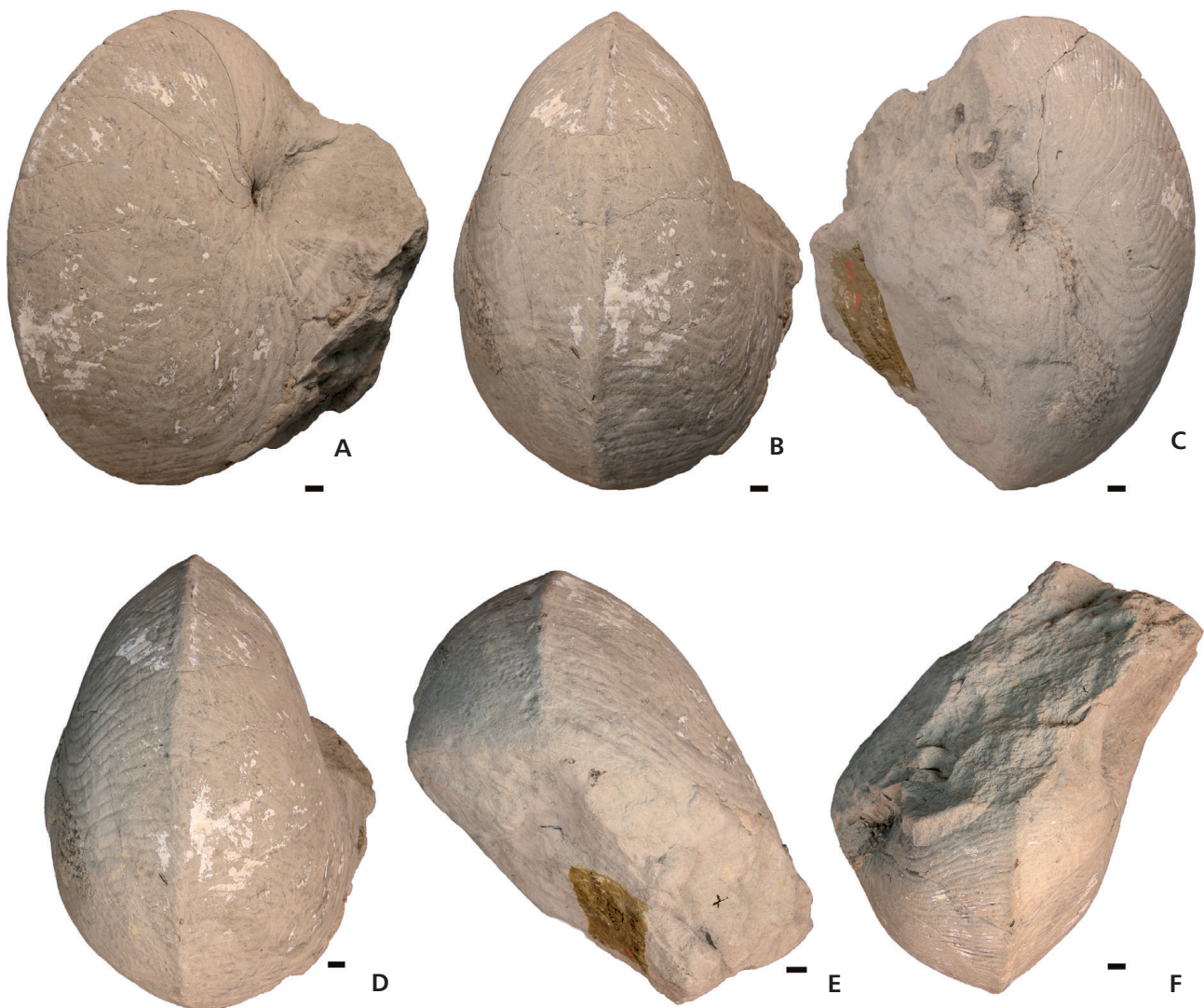
**Figure 2.** Palaeogeographic maps (modified from Philip & Floquet 2000 and Ziegler 1990) with occurrences of *Deltocymatoceras*.

rounded, smooth or weakly wrinkled by crossing radial ribs. The keel appears on the last and probably also on the penultimate whorl. The keel on the fully-grown shell ( $D \geq 290$  mm) gradually decreases in the apertural area. The maximum size ( $D$ ) of the shell is estimated to exceed 300 mm. The whole shell is covered by strong radial ribs, which originate at the umbilicus. They are initially thin and widen on the flanks with a broad, shallow, convex sinus, irregularly bifurcating predominantly on the inner and mid-flank. Ventro-laterally and ventrally, the ribs reach their maximum width ( $\sim 6$  mm). They cross this area with a broad shallow sinus. In the middle of the venter, the ribs are crossed by the keel or they weakly traverse it. The ribs become broader on the body chamber in late ontogeny. The suture (Fig. 4A) is sinuous with a small shallow umbilical lobe, a narrow and regularly rounded saddle on the umbilical margin and on the inner flank, and with a broad shallow ventro-lateral lobe, and a prominent ventral saddle, which is accentuated by the ventral keel. The septa are relatively distant from each other, approximately 16–18 per whorl in the type specimen, creating large phragmocone chambers. The position of the siphuncle is unknown.

The holotype GM-42 (96) (Fig. 3) is deformed and slightly askew. The ventral keel is very prominent. The sur-

face of the keel is smooth and no ribbing is preserved on it. The ribs cover the rest of the shell and are remarkably large on the body chamber ( $\approx 6$  mm) in contrast to the width of the ribs on the previous phragmocone chambers ( $\approx 3$  mm) on the ventral side. The last relatively large septa are not approximated, which could indicate that this specimen ( $D \approx 250$  mm) had not attained maturity when it died. This is corroborated by the ventral keel, which is still prominent on the whole body chamber (but has faded away in adult specimens). The aperture is not preserved. Accordingly, 250 mm is not the maximum shell diameter of this species.

Specimen MB.C.15024 (Fig. 8J, K) is described based on an excellent quality plaster cast of the specimen from the Halberstadt Formation (Middle Coniacian) at the Lehofsberg near Quedlinburg (Saxony-Anhalt, Germany). This specimen has prominent ribs and the ventral keel preserved, and it probably represents a full body chamber with the last 2–3 phragmocone chambers being present. The ventral keel is somewhat less prominent compared to the holotype and the ribs are only weakly visible on the keel. This specimen is probably mature or almost mature due to the reduced ventral keel in the apertural area, the shape of the body chamber and the diameter of the shell ( $D \approx 290$  mm).



**Figure 3.** *Deltocymatoceras leiotropis* (Schlüter, 1876), holotype GM 96 (the scale bar is 10 mm). • A – right lateral side; B – ventral side; C – left lateral side; D – ventral side partly posterior view with septa; E – ventral side anterior view; F – ventral side posterior view.

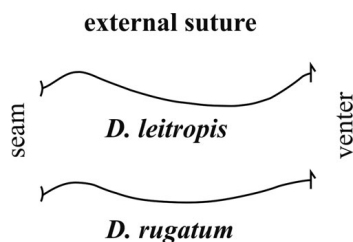
**Discussion.** – *D. leiotropis* differs (Table 1) from *D. rugatum*, in having a one third larger maximum shell size, relatively less wide/thick (strength) ribs, a more prominent ventral keel and different shape of the suture line. The ribs of *D. rugatum* are more robust (thicker and taller) and cross the less prominent ventral keel.

The early Campanian *Angulithes westphalicus* (Schlüter, 1872) is similar to *D. leiotropis* in shell diameter size in the fully grown shell ( $D \approx 250$  mm) and shape of the slightly depressed whorl cross section. The appearance of the ventral keel is also similar. *A. westphalicus* differs in the shape of its suture line which is more sinuous. The most noticeable difference is the lack of radial ribbing in *A. westphalicus* which has a smooth surface covered only by growth lines. An exception is the early Late Turonian *Angulithes galea* (Fritsch & Schlönbach, 1872), in which strong radial rib-like-folds appear in the adapertural area in

the late premature stage, followed by a reduction of the keel (Frank 2010). This keel reduction is similar in *D. leiotropis* and *D. rugatum*. Furthermore, the Late Cenomanian *A. vascogothicus* (Wiedmann, 1960) develops ventral folds on the last whorl (Wilmsen 2000), but these undulations have a different shape and morphology compared to the ribs in *Deltocymatoceras*. *A. galea* differs from *D. leiotropis* in having a shallower lateral lobe and a very shallow ventral saddle on the suture line. Matsumoto & Muramoto (1983, p. 89) and also Dzik (1984, p. 180) compared *D. leiotropis* to *A. triangularis*. These species are similar in their sinuous sutures, which have a relatively deep lateral lobe and narrow ventral saddle. Nevertheless, the suture line of *A. triangularis* is slightly more sinuous, the whorl cross section is more triangular and less depressed than in *D. leiotropis*. Furthermore, *A. triangularis* has a somewhat smaller maximum shell size and the shell is smooth.

**Table 1.** Comparison of different features in *Deltocymatoceras leiotropis* and *D. rugatum*.

<i>Deltocymatoceras leiotropis</i>	<i>Deltocymatoceras rugatum</i>
Maximum size of the shell (D) ~290 mm	Maximum size of the shell (D) ~200 mm
Size and form of ribs on the ventral side: flattened; ~3 mm on the phragmocone in late ontogenetic stage; ~6 mm on the living chamber of same stage; space between ribs ~1 mm.	Size and form of ribs on the ventral side: rounded; ~4–5 mm on the phragmocone in late ontogenetic stage; ~8–9 mm on the living chamber of same stage; space between ribs ~2–3 mm.
Ventral keel: very prominent, narrow, smooth or slightly wrinkled by crossing ribs.	Ventral keel: less prominent, broader, crossed by strong ribs.
Suture line: narrow saddle on the venter; shallow lobe on the outer part of lateral side; narrow prominent saddle on umbilical wall.	Suture line: broad shallow saddle on the venter; broad lobe on the lateral side; shallow saddle on the umbilical wall.

**Figure 4.** Suture lines of *Deltocymatoceras leiotropis* and *D. rugatum*.

*Cymatoceras patens* (Kner, 1848) has a compressed whorl cross section in combination with moderately strong ribbing, but the ribs are not as robust as those in *Deltocymatoceras*. *Cymatoceras loricatum* (Schlüter, 1876) is likewise very involute with an almost closed umbilicus. Its whorl cross section is only weakly compressed ( $Wb/Wh \approx 0.9$ ) and it is characterized by prominent cymatoceratid ribbing (see Wilmsen & Esser 2004 for details). As in *C. patens*, there is no keel during any growth stage.

Large specimens of *D. leiotropis* and *D. rugatum* are easy to identify, but juvenile specimens can easily be misinterpreted as representatives of *Cymatoceras* because of the radial ribbing and depressed whorl cross section. If the ribbing is not preserved, juveniles could even be misinterpreted as specimens of *Eutrophoceras* or *Angulithes* (Frank 2010).

**Occurrence.** – Late Turonian to Middle Coniacian of Germany, England, Poland and the Czech Republic (Fig. 2).

### ***Deltocymatoceras rugatum* (Fritsch & Schlönbach, 1872)**

Figures 6, 8A–I

- ?1845–1846 *Nautilus elegans* Sow. – Reuss, p. 21.  
 1872 *Nautilus rugatus*; Fritsch & Schlönbach, p. 23, pl. 12, fig. 2, pl. 15, fig. 2.  
 non 1872–1875 *Nautilus rugatus* (Fritsch & Schlönbach). – Geinitz, pp. 181–182, pl. 31, fig. 16 [= *Angulithes galea*].  
 ?1876 *Nautilus* cf. *rugatus* (Fritsch & Schlönbach). – Schlüter, pp. 173–174.

- 1883 *Nautilus rugatus* (Fritsch & Schlönbach). – Frič, p. 90, text-fig. 50.  
 1885 *Nautilus rugatus* (Fritsch & Schlönbach). – Frič, p. 85, fig. 50.  
 non 1889 *Nautilus rugatus* (Fritsch & Schlönbach). – Frič, p. 70 [= *Angulithes galea*].  
 non 1893 *Nautilus rugatus* (Fritsch & Schlönbach). – Frič, p. 73 [= *Deltocymatoceras leiotropis*].  
 non 1897 *Nautilus rugatus* (Fritsch & Schlönbach). – Frič, p. 36 [= *Angulithes galea*].  
 1910 *Nautilus rugatus* (Fritsch & Schlönbach). – Spengler, pp. 130–131.  
 1934 *Nautilus rugatus* (Fritsch & Schlönbach). – Andert, pp. 390–392.  
 1960 *A. (Angulithes) rugatus* (Fritsch & Schlönbach). – Wiedmann, p. 193.  
 ?1999 ?*Cymatoceras sharpei* (Schlüter). – Wittler, Roth & Legant, p. 22, text-fig. 26a, b.  
 ?2002 *Deltocymatoceras* sp. – Kennedy, p. 230, pl. 42, figs 4–6, text-fig. 10-1e.  
 2007a *Deltocymatoceras rugatus* (Fritsch & Schlönbach). – Frank, pp. 112–113, text-fig. 1(3).  
 2007b *Deltocymatoceras rugatus* (Fritsch & Schlönbach). – Frank, pp. 35–36, text-fig. 1(3).  
 2009 *Deltocymatoceras rugatus* (Fritsch & Schlönbach). – Frank, p. 13.  
 2010 *Deltocymatoceras rugatus* (Fritsch & Schlönbach). – Frank, p. 494, pl. 5, figs a–d.

**Type.** – Fritsch & Schlönbach (1872) mentioned several specimens in the original description of *D. rugatum*. According to a previous revision (Frank 2010), several of these specimens belong to *Angulithes galea*. Unfortunately, all the specimens assigned to *D. rugatum* by Fritsch & Schlönbach (1872) are missing, except for specimen O 3164 (Fig. 6G–I) from Choroušky, which was originally illustrated and is located in the collections of the National Museum in Prague (note that the figure in Fritsch & Schlönbach 1872 is horizontally orientated). The surface morphology of this specimen is only partly preserved. Furthermore, the ventral side is in some parts fixed by plaster



and the ribs in this area are partly sculptured. The ventral keel is also poorly preserved. Even after a number of years, we were not successful in re-locating the other syntypes from the Frič collection, but we found additional specimens in the collection of the National Museum, which correspond well with the original description of *Nautilus rugatus*. From these specimens we selected a neotype candidate (O 6039, Fig. 6A–F). We recommend requesting the international commission on zoological nomenclature under its plenary power to set aside the existing name-bearing type (syntypes O 3164) and to designate a neotype (O 6093) in terms of retaining stability and universality of this taxon. This specimen is the best candidate as it exhibits all the taxonomic features described in Fritsch & Schlönbach (1872). Furthermore, it is from the same locality and horizon as specimen O 3164. This specimen was, with high probability, studied by Frič himself and could be considered as a part of his collection. The specimen is deposited in the National Museum, Prague, the Czech Republic.

*Type locality.* – Choroušky near Mělník, Central Bohemia, the Czech Republic.

*Type horizon.* – *Trigonia*/Choroušky Beds (*sensu* Frič 1885), Jizera Formation, lower Upper Turonian, probably *Subprionocyclus neptuni* and *Inoceramus perplexus* zones.

*Description.* – Nautiliconic, involute and oval shell, with closed umbilicus. Depressed whorl cross-section ( $Wd \approx 110$  mm;  $Wh \approx 95$  mm;  $Wd/Wh = 1.2$ ) with convex lateral sides, broadly rounded venter and slightly trigonal shape in late ontogeny due to the ventral keel. Maximum width is on the inner flank. The ventral keel appears on the last and penultimate whorl. The keel is blunt, narrowly rounded and weakly to moderately wrinkled by crossing radial ribs. The height of the keel gradually decreases in the apertural area on the fully-grown shell ( $D \approx 190$  mm). In this area, the whorl cross-section is depressed with a broadly rounded venter. The maximum size ( $D$ ) of the shell is  $\approx 210$  mm. The ventral keel did not develop during early growth stages, but the whole shell was crossed by robust radial ribs throughout ontogeny. Ribs originate at the umbilicus, where they are thin, and broaden across the flanks with a broad shallow convex curve, irregularly bifurcating, predominantly on the inner and mid-flank. Close to and on the venter, the ribs reach their maximum width ( $\approx 8$ – $9$  mm during the stage of late ontogeny) and cross this area with a broad shallow sinus. The ribs weakly traverse the ventral keel. The suture (Fig. 4B) is moderately sinuous with a small shallow umbilical lobe, a shallow umbilical saddle on the inner flank, followed by a very shallow lateral lobe, and a saddle on the venter. The position of the siphuncle is central to ventro-central.

The syntype O 3164 (Fig. 6G–I) ( $D = 120$  mm) has strong radial ribs on part of the left lateral side and on part of the frontal venter. The ribbing or other ornamentation is not preserved on the rest of the shell. The ventral side has in some parts been repaired by plaster and the ribs in this area are partly reconstructed. The whorl cross-section is depressed. The ventral keel is hardly recognisable due to poor preservation. The candidate neotype specimen O 6093 (Fig. 6A–E) is from the same locality and horizon as the syntype. Very strong radial ribbing is preserved on the shell and is more concentrated in the apertural area. This concentration is accompanied by a reduction of the ventral keel, interpreted as a character associated with the attaining of maturity. Its adult aperture is preserved with a noticeable constriction. Accordingly, this specimen shows more or less maximum shell size ( $D \approx 200$  mm). A similar smaller specimen O 6417 (Fig. 8A–C) from the same collection and locality, displays the absence of a ventral keel on the younger whorl and its appearance during ontogeny. Specimens MMG SaK 8469 (Fig. 8D, E) and MMG SaK 8471 (Fig. 8F, G) are of a smaller size ( $D \approx 70$ – $80$  mm) and represent early ontogenetic stages of *D. rugatum* with very strong ribbing. Unfortunately, both specimens are deformed, although the dorso-ventral deformation indicates the absence of a keel.

*Discussion.* – Several specimens of *Angulithes galea* were interpreted as *D. rugatum* due to the strong radial rib-like folds in the apertural area in late ontogeny ( $D \approx 290$  mm; Frank 2010). This ribbing is interpreted by Frank (2010) as a mature character. *A. galea* differs from *D. rugatum* in the maximum diameter of the shell ( $D \approx 290$  mm versus  $D \approx 190$  mm) and by a smooth shell surface covered by growth lines. Both species have a conspicuous ventral keel. *Angulithes vascogothicus* is medium-sized ( $D = 130$ – $150$  mm) and only weakly compressed, characterized by an ovoid to triangular whorl cross-section with maximum breadth on the inner flank. *A. vascogothicus* has coarse fold-like undulations on the outer flanks of the last whorl (Wilmsen 2000). However, these undulations are not real ribs but folds restricted to a specific part of the shell; furthermore, they are much broader than in *D. rugatum*. The suture is more sinuous than in *D. rugatum*. The ribbing is robust even on juveniles of *D. rugatum* and is a feature, which differs from that in juveniles of *Cymatoceras*. Exceptions are juveniles of *C. radiatum* (Sowerby, 1822), *C. huxleyanum* (Blanford, 1861), *C. columbinum* (Fritsch & Schlönbach, 1872) and *C. delongchampsianum* (d'Orbigny, 1840). The latter species has characteristic strong ribs crossed by linear lines creating a reticular structure throughout ontogeny. However, these fine structures are not always preserved. Nevertheless, *C. delongchampsianum* differs from *D. rugatum* by a significantly sharp umbilical wall. Very strong radial ribs and a depressed shell

are typical for *Cymatoceras pseudoelegans* (d'Orbigny, 1840) from the Early Cretaceous, but the ribbing of *D. rugatum* in late ontogeny is much stronger, also when compared to other representatives of *Cymatoceras* from the Late Cretaceous. *C. columbinum* has strong, but less robust ribs than *D. rugatum*. The suture line is similar with a slightly more prominent umbilical saddle and a shallower lateral lobe. The distance between septa (length of phragmocone chambers) is greater than in *D. rugatum* at the same ontogenetic stage. *C. radiatum* has very robust ribbing even in juveniles, which is comparable to *D. rugatum*. It has a depressed, rounded to slightly trapezoidal whorl cross-section and a centro-dorsal siphuncle. *C. radiatum* has no keel, but it is a suitable candidate as an ancestor of *D. rugatum*.

**Occurrence.** – Early Late Turonian of the Czech Republic, Germany and Poland.

### Phylogeny of *Deltocymatoceras*

*Deltocymatoceras* may have evolved either from *Cymatoceras* (i.e., *C. radiatum*) or from *Angulithes* (*A. triangularis*). We support the former interpretation that it evolved from *Cymatoceras* as suggested by Kummel (1956, homeomorphism with *Angulithes*) and we agree partly with Dzik (1984, derivation from *Cymatoceras*). However, *Angulithes* and its possible phylogenetic affinity to *Cymatoceras* or *Cimomia* Conrad, 1866 need to be revised in the future.

Coarsely ribbed “cymatoceratid” nautilids are known from the Late Jurassic and range throughout the Cretaceous into the Palaeogene with a possible ancestry from *Cenoceras* Hyatt, 1883 (e.g., Kummel 1964, Dzik 1984). *Angulithes* appeared in the Albian and flourished throughout the Late Cretaceous and Palaeogene with a possible derivation from *Cimomia* or *Hercoglossa* Conrad, 1866 (Kummel 1956, p. 453). According to Wilmsen (2000, pp. 37–38, fig. 5), *Deltocymatoceras* is derived from *Angulithes* based on a potential transitional form between both genera. However, a re-evaluation of the questionable specimen showed that it represents more likely a fully grown specimen of *A. triangularis* with a strongly inflated shell. Regarding the presence of the prominent ribs that characterize and are considered as a primary character of *Deltocymatoceras*, it thus appears more likely that the genus was derived from *Cymatoceras radiatum*.

The genus *Cymatoceras* represents a rather diverse group containing approximately 64 species (Kummel 1956). It has been considered recently as polyphyletic (Matsumoto & Muramoto 1983, Wilmsen 2000, Wilmsen & Yazykova 2003, Cichowolski 2003). The main common character of *Cymatoceras* are the radial ribs, but the species differ in shell shape, suture lines and position of siphuncle.

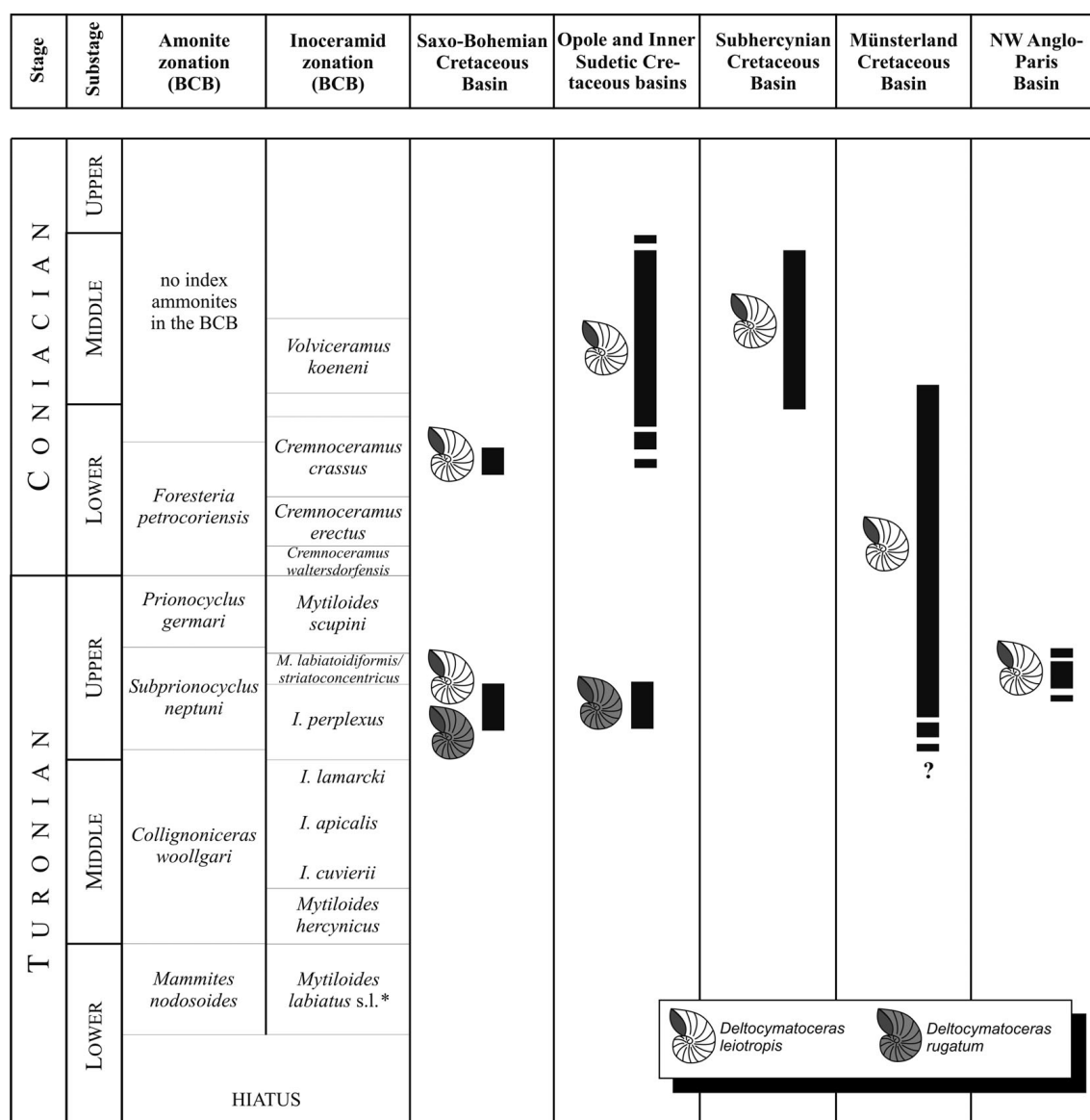
However, if one compares early ontogenetic stages (up to 3–4 whorls) of the type species of the genus, *C. pseudoelegans*, or of *C. radiatum* with juveniles of *D. rugatum*, it is difficult to distinguish between them according to their shell shape, ornamentation and suture lines. *C. pseudoelegans* and especially *C. radiatum* have very strong ribs and depressed whorl cross-sections, very similar to *D. rugatum*, and a ventral keel is not present in early ontogenetic stages of both genera. The keel appears only in *Deltocymatoceras* during post-juvenile ontogeny. It was acquired later in phylogeny and is a secondary character, which is combined with the inherited strong radial ribs.

The limited evolutionary success of the genus *Deltocymatoceras* is reflected in its low diversity, endemic distribution and narrow stratigraphic range (Late Turonian–Middle Coniacian = approximately 3 million years according to the Geological Timescale 2012, Ogg & Hinnov 2012). We speculate that the evolutionary experiment to combine an inflated, strongly ribbed shell with a prominent keel represented an evolutionary “blind alley”.

### Functional morphology and ontogeny

The combination of a prominent keel and strong ribbing in *Deltocymatoceras* is unique in post-Palaeozoic nautilids (*Angulithes galea* has these features but separately during ontogeny with folds-like-ribs). Thus, any interpretation of the functional morphology is difficult. With the exception of *Deltocymatoceras* and *Angulithes*, a keel in combination with a depressed shell appeared only in mature shells of *Gryponautilus galeatus* (Mojsisovics, 1873) from the late Triassic. Functional interpretations of a keel were usually related to hydrodynamics (Chamberlain & Westermann 1976, Frank 2010), although such hypotheses are difficult to test. Such a keel might hypothetically have provided greater hydrodynamic stability for the shell and thus saved energy during inactivity (Westermann 1996, Frank 2010), and the keel ornamentation may have increased streamlining (Spath 1919). Keels are, however, usually developed in smooth, mainly compressed nautiloids (except for *Deltocymatoceras*), which are typical for pelagic, low-energy environments (Tintant & Kabamba 1985, Wilmsen 2000). The ventral keel has variable shapes (usually flattened) and dimensions. Usually, the whole ventral side has an angular shape, narrowly rounded as for example in *Heminautilus* Spath, 1927 from the Cretaceous, or in *Phacoceras* Hyatt, 1884 from the Carboniferous and Permian. The angular shape of the narrowly rounded venters already appeared in nautiloids from the Early Ordovician (evolute shells of *Pilotoceras* Cullison, 1944). *Oxygonioceras oxynotum* (Barrande, 1865) and *O. discoideum* (Barrande, 1866) from the late Silurian (see Manda & Frýda 2010) also developed a prominent ventral keel on the depressed, evolute and





**Figure 5.** Stratigraphic distribution of *Deltocymatoceras* within European basins. Ammonite and inoceramid zonation after Košťák *et al.* (2004). The dashed lines indicate the approximate extension of the occurrence.

slightly trochospiral shell. Keeled venters are also commonly found in ammonoids, for example in representatives of the order Prolecanitida. Barskov *et al.* (2008, p. 1228) mentioned that streamlined (compressed) shell shape together with a keel indicates good manoeuvrability in various shelf environments. The keel in several cephalopod groups thus played a different role, but the basic function seems to be stability control. Ribbing and tuberculation, however, result in decreased swimming abilities (Tsujita & Westermann 1998).

In some Late Cretaceous ammonites – predominantly in placenticeratids with oxyconic shells (and many others), the elevated keel and the ornamentation (in some species – *i.e.* nodes) are developed only in immature specimens

(compare the analogy with *Deltocymatoceras*). The function of ribbing is still controversially discussed (*e.g.* Spath 1919, Westermann 1971, Chamberlain & Westermann 1976, Tintant & Kamamba 1985, Wilmsen & Yazykova 2003, Chirat & Bucher 2006). Certainly, it affects the hydrodynamic properties of any shell, but this effect will be less important for forms, which were poor swimmers (Chamberlain & Westermann 1976), especially nautilids with depressed shells (Chamberlain 1976). When ribbing evolved in depressed forms such as in *Deltocymatoceras*, its function is thus probably not functionally related to hydrodynamics, especially when the ornamentation is more robust and prominent throughout ontogeny (Chamberlain & Westermann 1976). Hypothetically, this kind of ribbing

was a defensive trait (strengthening of the shell), either protecting the shell against mechanical damage in shallow turbulent water (Tintant *et al.* 1982, Tintant & Kamamba 1985, Frank 2010, Wilmsen & Mosavinia 2011) or against predators (*e.g.* Ward 1981, Signor & Brett 1984, Wilmsen & Yazykova 2003). Both interpretations could apply because *Deltocymatoceras* occurred in shallow environments and predation pressure by durophagous vertebrates increased throughout the Cretaceous (Vermeij 1977, Ward 1981, Gregory 2001). Highly elaborated sculptures occur in Devonian rutoceratoid nautilids and reflect an adaptation to life in high-energy environments (Manda & Turek 2009a, 2011) rather than an anti-predatory feature (Signor & Brett 1984). However, it is very difficult to test these hypotheses in *Deltocymatoceras*, partially because of the limited number of available specimens and their poor preservation.

The change in morphology of the *Deltocymatoceras* shell during ontogeny consists of the development and reduction of the ventral keel. The keel appears in an advanced ontogenetic stage as shown by specimen O 6417 (Fig. 8A–C). The keel persists into the late ontogenetic stage and its loss is interpreted as a consequence of the rounded broadening of the body chamber and subsequent weak apertural contraction. This stage is also followed by approximation of the last phragmocone chambers, but septal crowding usually occurs shortly before attaining maturity (Collins & Ward 1987). These features are thus expressions of the approach of maturity, shared with some features of recent nautilids (Collins & Ward 1987), and also comparable to the ventral keel of *Angulithes* (Frank 2010).

## Stratigraphic distribution

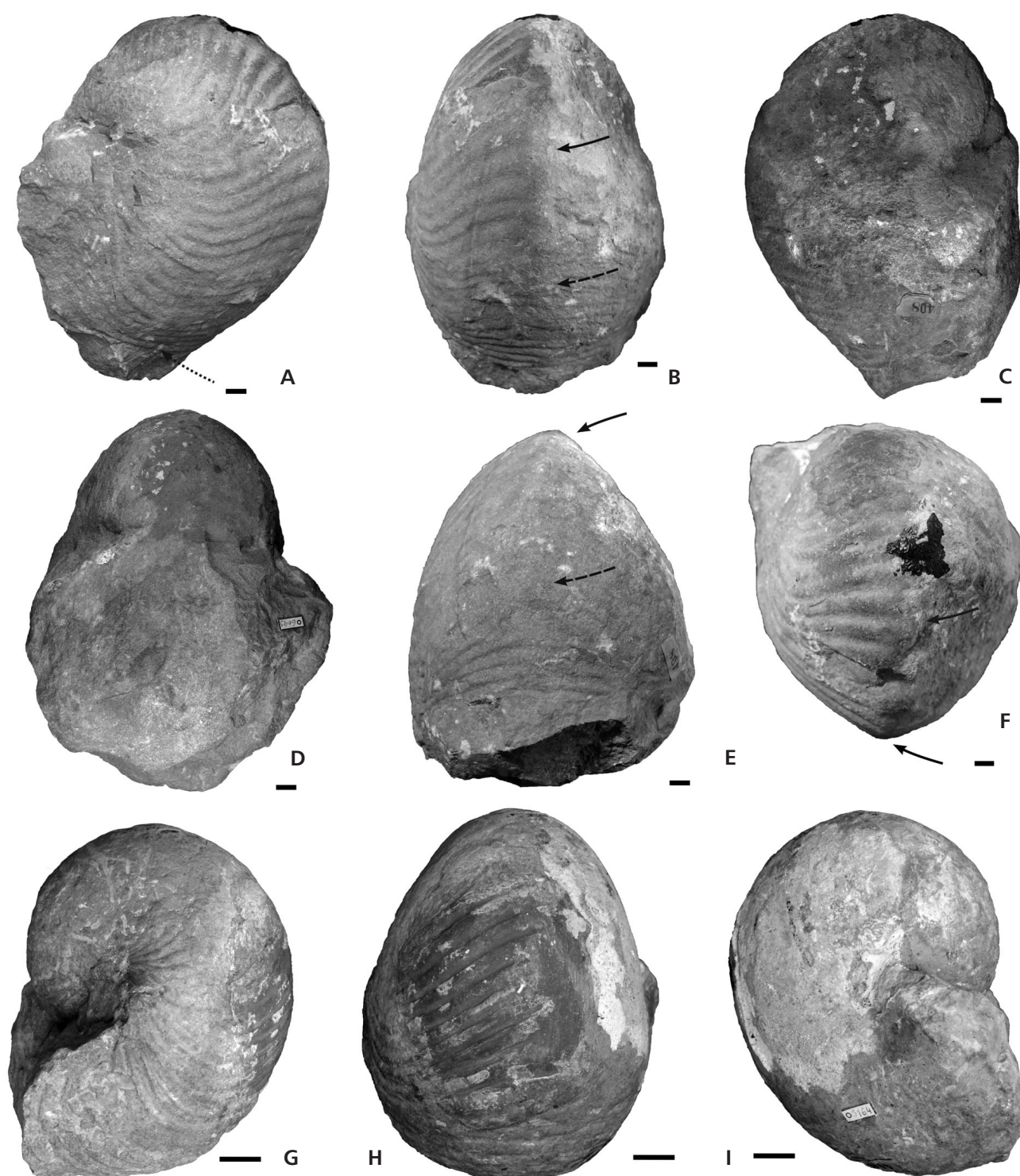
The stratigraphic range of the genus *Deltocymatoceras* is very narrow. The first record is from the latest Middle?–early Late Turonian of Germany and the Czech Republic and the lineage ranges into the Mid-Coniacian. According to Ogg & Hinnov (2012), this interval lasted about 3.5 million years. Compared to other long-ranging nautilid genera and even species [*e.g.*, *Angulithes fleuriausianus* (d’Orbigny, 1840): Cenomanian–Coniacian, 15 million years] this is a very short period of time. This short stratigraphic range of the genus corresponds well with its endemic distribution (Fig. 2).

*D. rugatum*, after its systematic and taxonomic revision excluding related taxa, exhibits an even more limited stratigraphic distribution, *i.e.* it is confined to a narrow horizon in the early Late Turonian. A potential latest Middle Turonian occurrence is reported from East Bohemia (in the vicinity of Choceň).

The majority of records are from the lower part of the Teplice Formation in NW Bohemia and from the upper-

most parts of the Jizera Formation (so called “Trigonia/Choroušky” beds by Frič 1885) in Central and East Bohemia. In the Teplice Formation, the stratigraphic range of *D. rugatum* corresponds to the “*Hyphantoceras* event” (Wiese *et al.* 2004) in the middle part of the *Subprionocyclus neptuni* Zone and the uppermost part of the *Inoceramus perplexus* Zone (Fig. 5). The stratigraphic data are supported by the ammonite fauna including *Hyphantoceras reussianum* (d’Orbigny), *Subprionocyclus* cf. *branneri*, *Allocrioceras* sp., and others (see Wiese *et al.* 2004), associated with the belemnite *Praeactinocamax bohemicus* (Stolley) (Košťák *et al.* 2004, Košťák & Wiese 2011). New records from Úpohlavý (the Czech Republic) constrain the stratigraphic range and the FAD of *D. rugatum*. The earliest records from the section are reported herein from the base of the Teplice Formation (“Lower Coprolite Bed” *sensu* Wiese *et al.* 2004 – *i.e.* lithounit Xa *sensu* Zahálka (1900a, b). The highest abundance is recorded from the so-called Hudcov Limestone (Hundorfer Kalkstein *sensu* Frič 1889) or Zahálka’s lithounit Xb<sub>α</sub>. They are reported from former quarries at Čížkovice and Hudcov, and recently, these records have been confirmed from the Úpohlavý working quarry. All these records are from the *S. neptuni* Zone (middle part) and *Inoceramus inequalis* / *I. lamarcki stuemckei* / *I. cuvieri* / *I. perplexus* Zone (upper to uppermost part) *sensu* Wiese *et al.* (2004).

The second population of *D. rugatum* comes from Central and NE Bohemia, from the Jizera Formation. Records from the vicinities of Turnov and Jičín as well as from the Choroušky area are also of Late Turonian age (“Trigonia/Choroušky Beds” *sensu* Frič 1885). In particular the horizons bearing *D. rugatum* from the Jičín area (Železnice, Rovensko pod Troskami, *etc.*) are correlatable to Xb<sub>α</sub> in NW Bohemia. The accompanying ammonite assemblage of *Lewesiceras mantelli* (Wright & Wright), *L. permplum* (Mantell), *Scaphites geinitzi* (d’Orbigny), *Allocrioceras strangulatum* (Wright) and *Baculites* sp. (unpub. data, MK) corresponds to the typical so called “*reussianum* fauna” known from hemipelagic sediments of NW Bohemia (*i.e.* Úpohlavý, Čížkovice). Other records of *D. rugatum* from the Bohemian Paradise Region (NE Bohemia) were mentioned (but not figured) by Ziegler (2003) from Dolánky near Turnov, Hrubý Rohozec, Turnov, Ondříkovice and Sychrov. All these occurrences are of Late Turonian age. The record from East Bohemia (Choceň town) is rather problematic as the locality label was probably exchanged. The records of *D. rugatum* from Saxony (Germany) are mostly from the lower Strehlen Formation, *i.e.* the limestones of Strehlen and Weinböhla (see Tröger & Voigt in Niebuhr *et al.* 2007). These occurrences correspond to the mid-Upper Turonian *Hyphantoceras* Event and are thus equivalent to the Hudcov Limestone in Bohemia. A single specimen comes from the lower

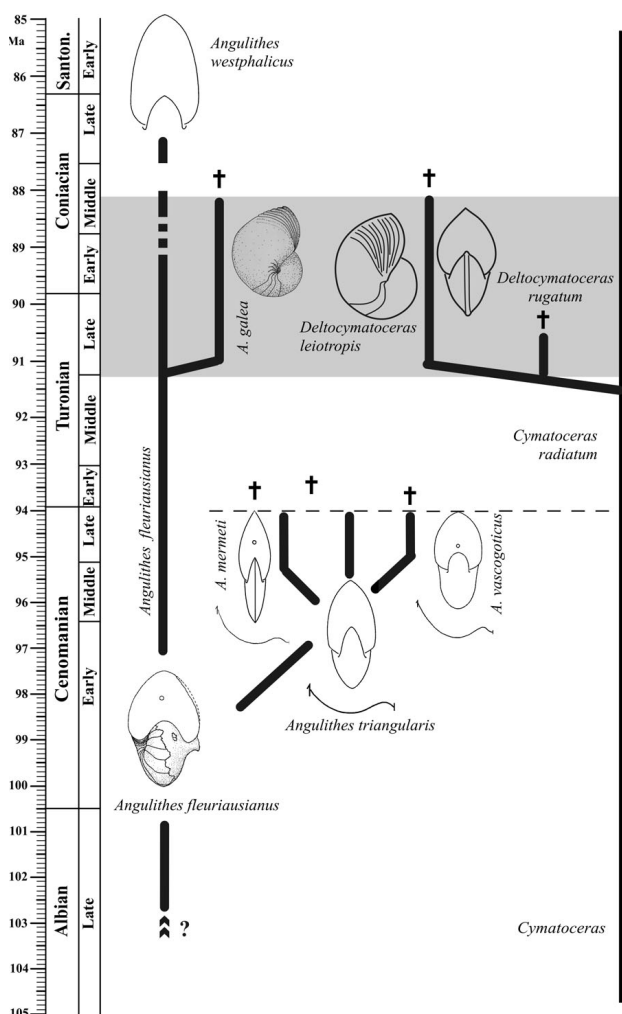


**Figure 6.** *Deltocymatoceras rugatum* (Fritsch & Schlönbach, 1872). • A–F – candidate neotype NM O 6093; A – left lateral side; B – ventral side; C – right lateral side; D – dorsal side; E – ventral side anterior view; F – ventral side posterior view. • G–I – syntype NM O 3164; G – left lateral side; H – ventral side; I – right lateral side. The dotted arrow shows the concentration of ribs in the apertural area. Full black arrows show the position of ventral keel. Dashed black arrows show the position of the disappearing ventral keel. The scale is equal 10 mm.

Schrammstein Formation (Upper Turonian), which overlies the Zeichener Ton (Zeichen clay), an equivalent of the *Hyphantoceras* Event. The few records of *D. leiotropis*

from northern Germany are from the Subhercynian Cretaceous Basin (nearshore sandstones of the Middle Coniacian Halberstadt Formation near Quedlinburg) and the Upper





**Figure 7.** Inferred phylogeny of *Deltocymatoceras*, partly based on data from Dzik (1984) and Wilmsen (2000); absolute ages, after Ogg & Hinnov (2012). The range of *Deltocymatoceras* is shaded in grey.

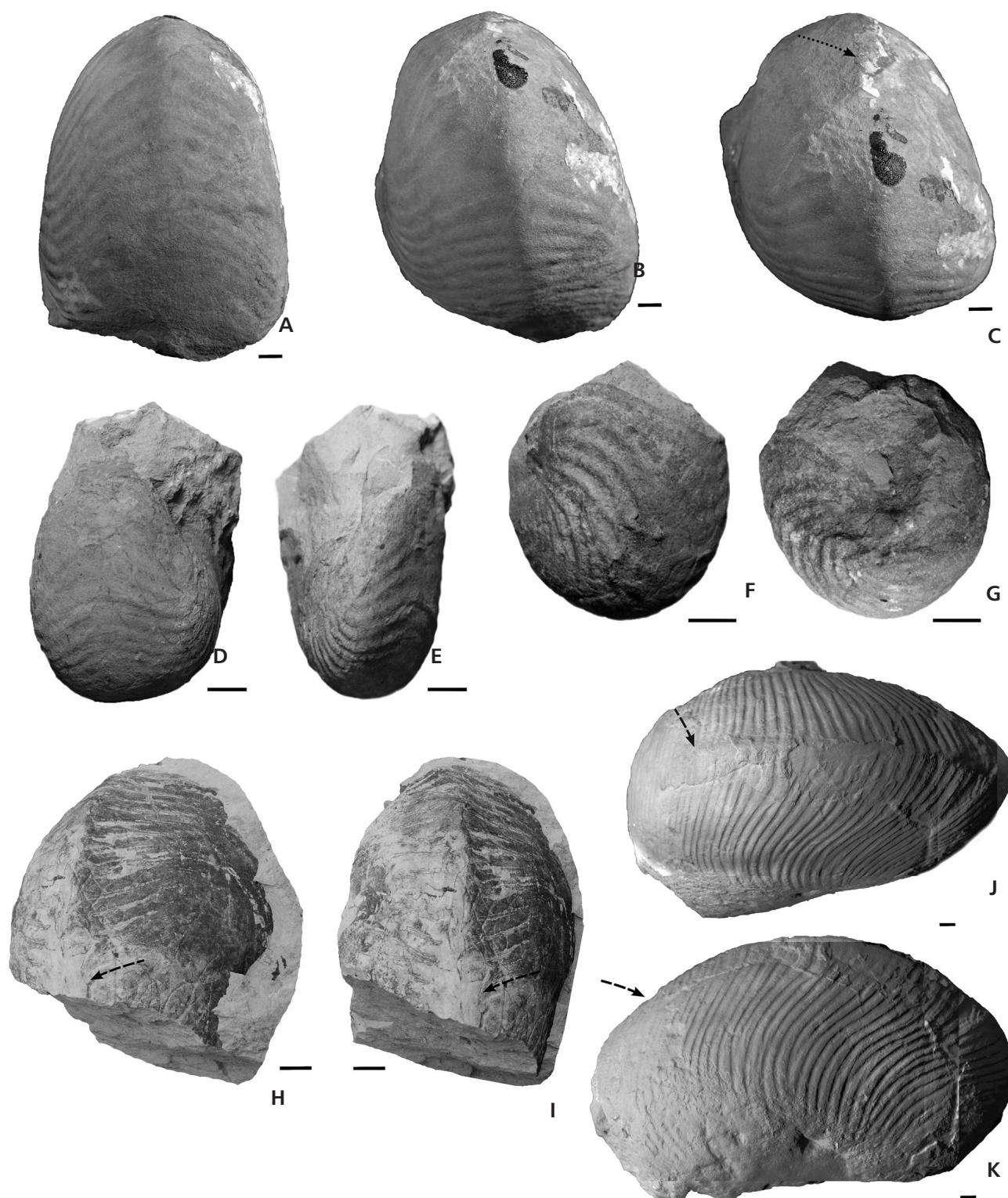
Turonian–Lower Coniacian proximal marly-glaucinitic deposits of the southern Münsterland Cretaceous Basin (Salder and Erwitte formations; see Niebuhr *et al.* 2007). The holotype of *D. leiotropis* is not from the Emscher Formation (Middle Coniacian–Santonian) but most likely also of late Turonian age (see above). There are no records of the genus *Deltocymatoceras* from contemporaneous strata of the Danubian Cretaceous Group, south of the Bohemian Massif, developed in similar lithofacies as in Bohemia (Schneider *et al.* 2011). The single specimen of *D. leiotropis* from SW England is from the Chalk Rock, a condensed Upper Turonian lithostratigraphic unit. Another single specimen of *D. cf. leiotropis* from the BCB is reported from the Březno section (Ohře River) near Louny and is of late Early Coniacian age. It comes from the so-called “Gastropod Beds” *sensu* Frič (1894) of the Březno Formation. Stratigraphically, it belongs to the middle to upper part of the *Cremnoceramus crassus*

inoceramid Zone in the uppermost part of the *Foresteria petrocoriensis* ammonite Zone. Ziegler (2003) recorded *D. leiotropis* from the Bohemian Paradise Region (Hrdoňovice) associated with *Peroniceras tricarinatum* (d'Orbigny), clearly documenting a Middle Coniacian age. Another fragmentary record, probably of *D. leiotropis*, is reported from the Borecké skály and Trosky hills, from the light yellowish-grey marls of the Březno Formation (Soukup 1963).

## Distribution pattern of *Deltocymatoceras* and its implications

*D. rugatum* is exclusively known from the Saxo-Bohemian Cretaceous Basin, with the exception of a single record from the Opole trough in Poland (see Fig. 2). The basin was situated between the Mid-European (Reno-Bohemian) Island in the south and west and the Lausitz and Sudetic blocks in the north (Fig. 2). During the Late Turonian, the Saxo-Bohemian Cretaceous Basin formed a narrow seaway linking the Boreal and the Tethyan Realms, the so-called “gateway to the Tethys”. The basin was influenced several times by trophic changes, *i.e.* enrichment and depletion of nutrients (Wiese *et al.* 2004). The incursions of ribbed nautilids and/or local allopatric speciation are connected to changes in trophic conditions during the cooling phase of the “Hyphantoceras event”, resulting in shallower water conditions in the Saxo-Bohemian Cretaceous Basin. *D. rugatum* occur in the Saxo-Bohemian Cretaceous Basin mainly in two facies reflecting deposition in different environments. While the nautilids inhabited hemipelagic environments (recorded by limestones) in NW Bohemia (Teplice Formation, Hudcov Limestone – Wiese *et al.* 2004) and Saxony (Strehlen and Weinböhla limestones), the other records are from the Jizera Formation indicating shallower water conditions with larger siliciclastic input (Uličný 2001). However, the bathymetric conditions in the two areas may not have been very different. At Úpohlavý (based on macrofossil biofacies), the basin depth probably did not exceed 60 meters, and in Central and NE Bohemia, the average water depth was around 30–40 m (the Trigonía/Choroužky beds).

The occurrence of *D. rugatum* in the Bohemian Cretaceous Basin is probably connected with another cephalopod faunal turnover caused by a marked cooling event in the terminal Middle Turonian or in the Middle/Upper Turonian boundary interval after the Middle Turonian thermal maximum (Voigt & Wiese 2000, Wiese & Voigt 2002, Wiese *et al.* 2004, Jarvis *et al.* 2006). The *D. rugatum* incursion, as in the “*Hyphantoceras* Event”, was connected to the second cooling pulse (Phase III *sensu* Voigt & Wiese 2000) in the middle part of the *Subprionocyclus neptuni*



**Figure 8.** Ontogeny of *Deltocymatoceras*. • A–I – *Deltocymatoceras rugatum* (Fritsch & Schlönbach, 1872); A–C – specimen NM O 6417; C – appearance of the ventral keel. • D–G – juveniles with strong ribbing and without ventral keel; D, E – specimen MMG SaK 8469; F, G – specimen MMG SaK 8471. • H, I – specimen NM1-2010, onset of disappearance of the ventral keel. • J, K – *Deltocymatoceras leiotropis* (Schlüter, 1876), specimen MfN MB.C.15024, disappearance of ventral keel in late ontogeny. The dotted arrow shows the appearance of the ventral keel. Dashed black arrows show the position of the disappearing ventral keel. The scale is equal 10 mm.

ammonite Zone). This cooling event was associated with a marked sea-level lowstand. Probably, these conditions were highly suitable for nautilids including *D. rugatum* as well as other cephalopods (see below). Additionally, this cooling phase was accompanied by a southward shift of “exotic” faunas including Boreal ammonites and especially belemnites, typical inhabitants of the inner shelf areas (Košťák & Wiese 2011).

It is remarkable that not only *D. rugatum* shows a high degree of endemism. Other cephalopods known from *D. rugatum*-bearing horizons in the Saxo-Bohemian Cretaceous Basin, such as the belemnites *P. bohemicus* (Stolley) and *P. aff. strehlensis* (Fritsch & Schlönbach; see Košťák & Wiese 2011) and the heteromorphic ammonites *Allocrioceras strangulatum* Wright and *Eubostrychoceras saxonum* (Schlüter) also show a higher degree of endemism in European shelf seas. The majority of these cephalopod taxa are known from Germany, the Czech Republic, Poland, and partly from the Anglo-Paris Basin (Kaplan 1988, 1989; Košťák *et al.* 2004).

*D. rugatum* became extinct shortly after its appearance (at the top of the Hudcov limestone in the BCB) in the Late Turonian. Strong predation pressure cannot be excluded as a potential reason as Ekrt *et al.* (2001) and Wiese *et al.* (2004) reported the highest vertebrate diversity in the lithounit Xb<sub>α</sub> (at the base). Marine reptiles and larger fishes (Ekrt *et al.* 2008), especially chondrichthyans (sharks and rays, 19 species), occurred (Wiese *et al.* 2004), including malacophagous taxa, which document a relatively high predation pressure. It is notable that this high predator diversity occurred approximately at the same level (base Xb<sub>α</sub>) as the FA of *D. rugatum*.

*Deltocymatoceras leiotropis* is also very restricted in its palaeobiogeographic distribution, being known from northern Germany (Münsterland, Subhercynian area), the Saxo-Bohemian Cretaceous Basin and a single specimen from SW England (Fig. 2). According to the endemic occurrence of both species of *Deltocymatoceras*, there was no significant post-mortem dispersal (Reyment 2008). The single specimen from Chalk Rock (UK) most probably represents a stray individual and documents the low dispersion potential of *Deltocymatoceras*.

*Deltocymatoceras* is one of only a few endemic post-Triassic nautilids while early Palaeozoic cephalopods contain many endemic taxa derived from immigrants. Nevertheless, the vast majority of these endemic taxa are demersal nautilids (e.g. Barskov *et al.* 2008, Manda & Turek 2009b, Turek & Manda 2011) and endemism in coiled nautilids is quite rare. The distribution pattern of Cretaceous *Deltocymatoceras* to some degree corresponds to recent nautilids and reflects a decrease in steered nautilids in late Mesozoic ecosystems.

## Competition – nautilids versus ammonites, and/or ecological substitution?

Ecological interactions between nautilids and ammonoids have recently been discussed including their early co-occurrence in the Early Devonian (Barskov *et al.* 2008, Klug *et al.* 2010, Manda & Turek 2011). Possible interaction between the two groups may aid understanding of the evolutionary pattern of ectocochleate cephalopods. To understand the unusual morphological features in nautilids described herein (depressed shell, prominent keel, strong ribs), a comparison with the only other ectocochleate, morphologically similar and a contemporaneous cephalopod group, i.e. ammonites, may be rewarding. In the case of *D. rugatum*, comprehensive and stratigraphically well calibrated data on the ammonite assemblage from the Úpohlavý working quarry may be used (cf. Wiese *et al.* 2004). Based on a brief morphological analysis, we propose the idea that *D. rugatum* developed the described features as a reaction to the existence of a free ecological niche, i.e. the almost complete absence of medium-sized keeled ammonites (see below).

The ammonite assemblage recorded in the horizon with *D. rugatum* can be subdivided into five basic morphogroups inhabiting different environments:

- 1) Normally coiled (planispiral) ammonites represented by very large non-keeled *Lewesiceras peramplum* (Mantell) (> 50 cm in diameter) and smaller *L. mantelli* (Wright & Wright) (microconchs about 8–10 cm; macroconchs up to 25–30 cm in diameter) and a single specimen (diameter 12 cm) of the keeled ammonite *Subprionocyclus cf. branneri* (Anderson).
- 2) Heteromorphic (orthocone) ammonites (*Baculites* sp.) of different sizes varying between 6–20 cm.
- 3) Heteromorphic (scaphiticone) ammonites including *Scaphites geinitzi* (d’Orbigny) (numerous microconchs of 4–5 cm and macroconchs of 6–7 cm in diameter) and *Yezoites bladenensis* (Schlüter) (only a single specimen known).
- 4) Heteromorphic (open turriliticone to turriliticone) nos-toceratid ammonites (*Hyphantoceras reussianum* (d’Orbigny), *Eubostrychoceras saxonum* (Schlüter); incomplete specimens of about 10–15 cm in diameter).
- 5) Heteromorphic (toxocone) anisoceratid ammonites (*Allocrioceras strangulatum* Wright), only two incomplete specimens are recorded.

Identical ammonite faunas from the *D. rugatum* horizon are fragmentarily known from other parts of the SBCB (see above – Stratigraphic distribution section), for example E and NE Bohemia, where a predominance of *Lewesiceras*, *Scaphites* and some *Baculites* can be observed.

The majority of these taxa are heteromorphic ammonites with inferred planktonic (scaphitids – with different habitats in juvenile and adult stages – see Landman



1987), benthic to nekto-benthic (nostoceratids) and pelagic (baculitids) life-style (e.g., Westermann 1996, Tsujita & Westermann 1998). Only three species with planispiral shell – giant *Lewesiceras peramplum*, medium-sized *L. mantelli* and smaller *S. cf. branneri* were nektonic taxa. Within this group, the niche of medium sized (20–30 cm) ammonites is occupied only by non-keeled *L. mantelli*. Keeled *S. cf. branneri* (characterized by marked ornamentation – strong ribs and tubercles arranged in rows) is known only from a single incomplete specimen (found during the last 15 years of intensive collecting in the quarry – this is probably also the only specimen known from the Bohemian part of the SBCB). These observations suggest the almost complete absence of keeled ammonites in the critical interval inhabited by *D. rugatum*. Thus, we discuss the possibility of an expansion of *Deltocymatoceras* into an ecological niche which was actually not occupied by ammonites. Consequently, the similar morphological features developed in this nautilid genus (i.e. ribs, keel, size) should clearly document convergence with medium-sized, ribbed and keeled ammonites. This development seems to be highly specific for the SBCB and adjacent shelf seas, and it should also explain the high degree of endemism in the genus. However, the data are limited to date and our hypothesis needs to be tested in the future by further quantitative studies.

## Conclusions

*Deltocymatoceras* is a rare Late Cretaceous nautilid genus comprising only two species characterized by bulbous shells with strong radial ribs and a ventral keel which appears in post-juvenile ontogenetic stages. This combination of morphological features is unique in post-Palaeozoic nautilids. The holotype of *Deltocymatoceras leiotropis* is for the first time photographically illustrated, accompanied by a detailed re-description. The majority of all known specimens of the species have been included in our revision. The revision revealed a narrow stratigraphic and endemic paleogeographic occurrence of *D. leiotropis*, which ranges from the Late Turonian to the Middle Coniacian with records from Germany, England, Poland and the Czech Republic. It is noteworthy that the type specimen stems from Upper Turonian strata in southern Münsterland (northern Germany) and not from the Middle Coniacian–Santonian. The only preserved syntype of *D. rugatum* is described and, according to its poor preservation and incomplete morphological features, a new candidate neotype is recommended. The species has a very short stratigraphic range (lower Upper Turonian) and occurs only in the Saxo-Bohemian Cretaceous Basin and in Poland. The phylogeny of *Deltocymatoceras* is discussed with two possible ancestors, i.e. *Angulithes* or *Cymatoceras*. Based on the similarity of juveniles of

*Deltocymatoceras* and *Cymatoceras* (inflated, strongly ribbed shells), a derivation from *Cymatoceras radiatum* is proposed. Despite the morphological affinities and presumably close phylogenetic relationship, we keep *Deltocymatoceras* as a separate genus based on its unique combination of strong ribbing and the development of a conspicuous keel. Some morphological changes in *Deltocymatoceras* during late ontogeny such as the disappearance of the ventral keel, the approximation of the last septa, rib crowding in the apertural area, the rounded broadening of the fully matured body chamber and an apertural constriction are comparable to other nautilids, both fossil (e.g., *Angulithes*) and Recent, and are interpreted as an expression of attaining and acquisition of maturity. These morphological changes during ontogeny (e.g. appearance of the ventral keel) are explained as potential adaptations to a change in lifestyle and habitat. The genus is a rare endemic taxon, which inhabited shallow water environments at the northern margin of the Mid European Island and in the vicinity of the Lausitz and the Sudetic blocks. All records come from shallow water siliciclastic environments and/or hemipelagic argillaceous carbonates and marls. A trigger for the appearance of *Deltocymatoceras* may be the sea-level fall associated with the “*Hyphantoceras* event” and the opening of an ecologic niche (i.e., lack of medium-sized, keeled ammonites at that time). The combination of the unusual morphological features developed in *Deltocymatoceras* may thus be a result of convergence with ammonites. However, the very short stratigraphic range of the genus (Late Turonian–Middle Coniacian, ca 3.5 Ma) reflects the limited evolutionary success of the “*Deltocymatoceras* model” combining hydrodynamically inefficient, bulbous, ribbed shells with a ventral keel. The rapid evolution and higher abundance of vertebrate predators in the Late Turonian may also have contributed to the rapid extinction of the genus. The stratigraphic range of *Deltocymatoceras* is very short for Late Cretaceous nautilids, especially for *D. rugatum*, the occurrence of which has the character of a bioevent. Its occurrence seems to be in direct relation to the “*reussianum* fauna” of the “*Hyphantoceras* event” in the middle part of the Late Turonian *S. neptuni* Zone of Central Europe. Thus, *D. rugatum* has a relatively high biostratigraphic potential for intrabasinal correlation.

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## Appendix

### List of specimens

Collections	Specimen	Old determination	New determination	Locality	Stratigraphy	Age
<i>Deltocymatoceras rugatum</i> (Fritsch & Schlönbach, 1872)						
NM Prague – CZ	O 3164 – syntype	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Choroušky; Czech Republic	Jizera Formation	Upper Turonian
NM Prague – CZ	O 6093 – candydate neotype	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Choroušky; Czech Republic	Teplice Formation	Upper Turonian
NM Prague – CZ	new number NM1-2010	<i>D. rugatus</i>	<i>D. rugatum</i>	Úpohlavy; Czech Republic	Teplice Formation, Lower Coprolite Beds	Upper Turonian
NM Prague – CZ	new number NM2-2010	<i>D. rugatus</i>	<i>D. rugatum</i>	Úpohlavy; Czech Republic	Teplice Formation, Lower Coprolite Beds	Upper Turonian
NM Prague – CZ	O 6417	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Choroušky; Czech Republic	Jizera Formation	Upper Turonian
NM Prague – CZ	d44/2006	<i>D. rugatus</i>	<i>D. rugatum</i>	Úpohlavy; Czech Republic	Teplice Formation, Upper Coprolite Beds, Kt3-XbIX	Upper Turonian
ChM ÚGP Prague – CZ IGP 9446		<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Hundorf/Teplice; Czech Republic	Teplice Formation	Upper Turonian
ChM ÚGP Prague – CZ IGP 7913		<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Rovensko pod Troskami; Czech Republic	Jizera Formation	Upper Turonian
ChM ÚGP Prague – CZ IGP 2013/3		<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Hundorf/Teplice; Czech Republic	Teplice Formation	Upper Turonian
PMN Nymburk – CZ	D43	<i>Nautilus</i> sp.	<i>D. rugatum</i>	Hrubý Jeseník; Czech Republic	Jizera-Teplice formations	Upper Turonian
MCR Turnov – CZ	P 543	<i>Nautilus rugatus</i>	<i>D. rugatum</i>			Upper Turonian
OM Choceň – CZ		<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Choceň; Czech Republic	Jizera-Teplice formations	Upper Turonian
M Železnice – CZ	MZ 3/13	<i>Nautilus</i>	<i>D. rugatum</i>	Železnice; Czech Republic	Jizera Formation	Upper Turonian
Úpohlavy quarry – CZ	no number yet	none	<i>D. rugatus</i>	Úpohlavy; Czech Republic	Teplice Formation, Upper Coprolite Beds	Upper Turonian
RME Essen – DE	RE 551.763.320 (A 0708/1)	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Oppeln/Opole; Poland	Opole	Upper Turonian
MMG Dresden – DE	SaK 8469	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Weinböhla; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 8471	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Weinböhla; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 8476	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Weinböhla; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10007	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10009	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10010	<i>Nautilus rugatus</i>	<i>D. rugatum</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10015	<i>Nautilus elegans</i>	<i>D. rugatum</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10016	<i>Nautilus elegans</i>	<i>D. rugatum</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
<i>Deltocymatoceras leiotropis</i> (Schlüter, 1876)						
GMB Bonn – DE	96 (GM-42) – holotype	<i>Nautilus leiotropis</i>	<i>D. leiotropis</i>	Hercules mine in Essen; Germany	Oerlinghausen or Salder Formation	(?Middle to) Upper Turonian
MfN Berlin – DE	MB.C.15024 (A 24 – copy)	<i>Nautilus leiotropis</i>	<i>D. leiotropis</i>	Lehofsberg near Quedlinburg; Germany	Halberstadt Formation	Middle Coniacian
BGS Keyworth – UK	GSM 117523	<i>Deltonautilus</i>	<i>D. leiotropis</i>	Hitch Wood Chalkquarry, St. Paul Walden Heights; UK	Upper Chalk, Chalk Rock, <i>Subprionocyclus neptuni</i> Zone	Upper Turonian

Collections	Specimen	Old determination	New determination	Locality	Stratigraphy	Age
MMG Dresden – DE	SaK 6379	<i>Nautilus leiotropis</i>	? <i>D. leiotropis</i>	Wehlen; Germany	Schrammstein Formation	Upper Turonian
NHM London – UK	C. 15226	<i>Nautilus leiotropis</i>	? <i>D. leiotropis</i>	Halberstadt, Saxony-Anhalt; Germany	lower Emscher Formation	(Lower–Middle) Coniacian
MfN Berlin – DE	MB.C.13922	none	<i>D. leiotropis</i>	Bystrzyca Kłodzka (= Habelschwerdt), Poland	“Emscher”	Coniacian
Wittler <i>et al.</i> (1999) p. 35, text-fig. 45a, b		<i>D. leiotropis</i>	<i>D. leiotropis</i>	Dortmund – Mitte; Germany	Erwitte Formation	Lower Coniacian
Wittler <i>et al.</i> (1999) p. 36, text-fig. 46a, b		? <i>D. sp.</i>	? <i>D. leiotropis</i>	Dortmund – Wambel; Germany	Salder Formation	lower Upper Turonian
NM Prague – CZ	O 6604 (d 169/2005)	<i>Nautilus rugatus</i> – <i>N. leiotropis</i>	– <i>D. leiotropis</i>	Březno; Czech Republic	Brezno Formation	Lower Coniacian
NMW Vienna – AT	NHMW 24	<i>Nautilus sp.</i>	<i>D. leiotropis</i>	Hundorf/Teplice; Czech Republic	Teplice Formation	Upper Turonian
In open nomenclature due to preservation						
RMT Teplice – CZ	PA 1328	<i>Nautilus sp.</i>	<i>D. rugatum?</i>	Hundorf/Teplice; Czech Republic	Teplice Formation	Upper Turonian
NHM London – UK	C. 15578	<i>Nautilus leiotropis?</i>	<i>D. sp.</i>	Wickham, Strood, Kent; UK	zone <i>Holaster planus</i>	Turonian
MMG Dresden – DE	SaK 9994	<i>Nautilus rugatus</i>	<i>D. sp.</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 9995	<i>Nautilus rugatus</i>	<i>D. sp.</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 9996	<i>Nautilus sublaevigatus</i>	<i>D. sp.</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 9997	<i>Nautilus rugatus</i>	<i>D. sp.</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
MMG Dresden – DE	SaK 10006	<i>Nautilus rugatus</i>	<i>D. sp.</i>	Dresden – Strehlen; Germany	Strehlen Formation	Upper Turonian
Wittler <i>et al.</i> (1999) p. 22, text-fig. 26a, b		? <i>Cymatoceras sharpei</i>	<i>D. sp.</i> or <i>A. galea</i>	Dortmund – Wambel; Germany	Salder Formation	Upper Turonian