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Latest Campanian to Early Maastrichtian (Cretaceous) nautiloids from the white chalk of Kronsmoor, northern Germany

MARKUS WILMSEN[1] & KLAUS J.K. ESSER[2]

[1]*Institut für Paläontologie der Bayerischen Julius-Maximilians-Universität, Pleicherwall 1, D - 97070 Würzburg, Germany. E-mail: m.wilmsen@mail.uni-wuerzburg.de*
[2]*Pommernweg 4, 25479 Ellerau/Holstein, Germany. E-mail: kjkesser@online.de*

ABSTRACT:

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A well preserved and stratigraphically tightly constrained nautiloid fauna consisting of two species is described from the uppermost Campanian to Lower Maastrichtian white chalk section of Kronsmoor, northern Germany. *Cymatoceras patens* (KNER, 1848) occurs rather frequently in the Kronsmoor section; one specimen is from the Upper Campanian *Micraster grimmensis*/*Cardiaster granulosus* Zone, one from the upper *Belemnella pseudobtusa* to lowermost *Belemnella obtusa* Zone. The bulk of the material (nine specimens) is from the Early Maastrichtian *B. obtusa* and *Belemnella sumensis* zones. The species is known from the Upper Campanian to Lower Maastrichtian of northern Germany, The Netherlands, Poland, the Ukraine, and possibly Denmark. *Cymatoceras loricatum* (SCHLÜTER, 1876) occurs in Kronsmoor (four specimens) in an interval comprising the Early Maastrichtian upper *B. obtusa* to *B. sumensis* zones. The species was hitherto only recorded from the uppermost Lower and Upper Campanian of Westphalia and Lower Saxony, Germany. Both species appear to be restricted to the Central European Subprovince of the temperate North European Province (Boreal Realm).

Key words: Cretaceous, Campanian-Maastrichtian, Northern Germany, Nautiloids, Systematic palaeontology, Palaeobiogeography.

INTRODUCTION

Cretaceous nautiloids are a rather poorly studied invertebrate group, and the phylogeny and systematics of the group are still poorly understood. This is also related to the fact that nautiloids are relatively rare fossils in many formations and show only a few taxonomically significant characters (such as suture and embryonic shell). The most recent comprehensive accounts date back to WIEDMANN (1960) and SHIMANSKY (1975). More recent papers on Upper Cretaceous nautiloids were presented by COBBAN & KENNEDY (1994), MORRIS (1995), WILMSEN (2000), CICHOWOLSKI (2003) and WILMSEN & YAZYKOVA (2003). KENNEDY (2002) presented a brief state-of-the-art summary of British Chalk Nautiloidea.

The aim of the present paper is to document and systematically describe a well preserved and biostratigraphically well constrained nautiloid fauna from the uppermost Campanian to Lower Maastrichtian of Kronsmoor, northern Germany, a key reference section for the Campanian-Maastrichtian boundary interval in northern Europe.

GEOLOGICAL SETTING AND STRATIGRAPHY

Exposures of uppermost Campanian to Maastrichtian strata are rare in northern Germany because marine sedimentation was terminated in many regions by the *Nostoceras polyplocum* regression of the Upper Campanian *Neancyloceras bipunctatum* / *Galerites roemeri* (= *Belemnitella langei*) Zone (NIEBUHR 1995; NIEBUHR & *al*. 1997). Uppermost Campanian strata up to the equivalent of the *B. langei* Zone (NIEBUHR & *al*. 1997) crop out at Ahlten near Hannover (see Text-fig. 1). Apart from the coastal outcrops of Lower Maastrichtian strata at Rügen (e.g., REICH & FRENZEL 2002), excellent exposures of Maastrichtian fossiliferous chalk facies ("Schreibkreide") were available near Lüneburg ("Zeltberg section", see VON STROMBECK 1863; STOLLEY 1896; SCHMID 1962), at Hemmoor-Basbeck (e.g., SCHMID 1982), and at Lägerdorf-Kronsmoor (Text-fig. 1). However, only the white chalk section of Lägerdorf-Kronsmoor (e.g., SCHULZ & *al.* 1984) is accessible today (but will partly be abandoned).

The Alsen and Kröpke quarries of Lägerdorf, ca. 2 km S of Kronsmoor (Text-fig. 1), provide exposures of the Middle Coniacian to Upper Campanian (ERNST & SCHULZ 1974; SCHULZ & *al*. 1984). The Saturn quarry of Kronsmoor is the only available Campanian-Maastrichtian boundary succession of North Germany (Text-figs 1, 2), and it was proposed as a global stratotype for the base of the Maastrichtian Stage. Although this proposal was subsequently rejected, the Kronsmoor section has still a status of a key reference section for the Campanian-Maastrichtian boundary interval (e.g., ODIN 2001; ODIN & LAMAURELLE 2001). A total sediment thickness of ca. 100 m is exposed there, comprising the Upper Campanian *Belemnitella langei* to Lower Maastrichtian *Belemnella sumensis* zones of SCHULZ (1978, 1979). Most macro- and microfossil groups were already monographed (e.g., SURLYK 1982; SCHÖNFELD 1990; NIEBUHR 2003). However, the present paper is the first taxonomic treatment of the nautiloid fauna from this section.

The lower 46 m of the Kronsmoor section (Upper Campanian of belemnite stratigraphy) comprise featureless white chalks with a few thin marly beds, some discontinuous burrow horizons and a single flint bed in the lower part of the *B. langei* Zone (Text-fig. 2). The fossil content is low and predominantly comprises belemnites (*Belemnitella langei* JELETZKY, *Belemnitella schulzi* CHRISTENSEN) as well as irregular echinoids [*Galerites roemeri* (DESOR), *Micraster grimmensis* NIETSCH, *Cadiaster granulosus* (GOLDFUSS)]. The prominent nodular flint layer F 600 (Text-fig. 2) marks the entry of the belemnite genus *Belemnella*, especially *B. lanceolata* (SCHLOTHEIM), and represents the Campanian-Maastrichtian boundary of belemnite

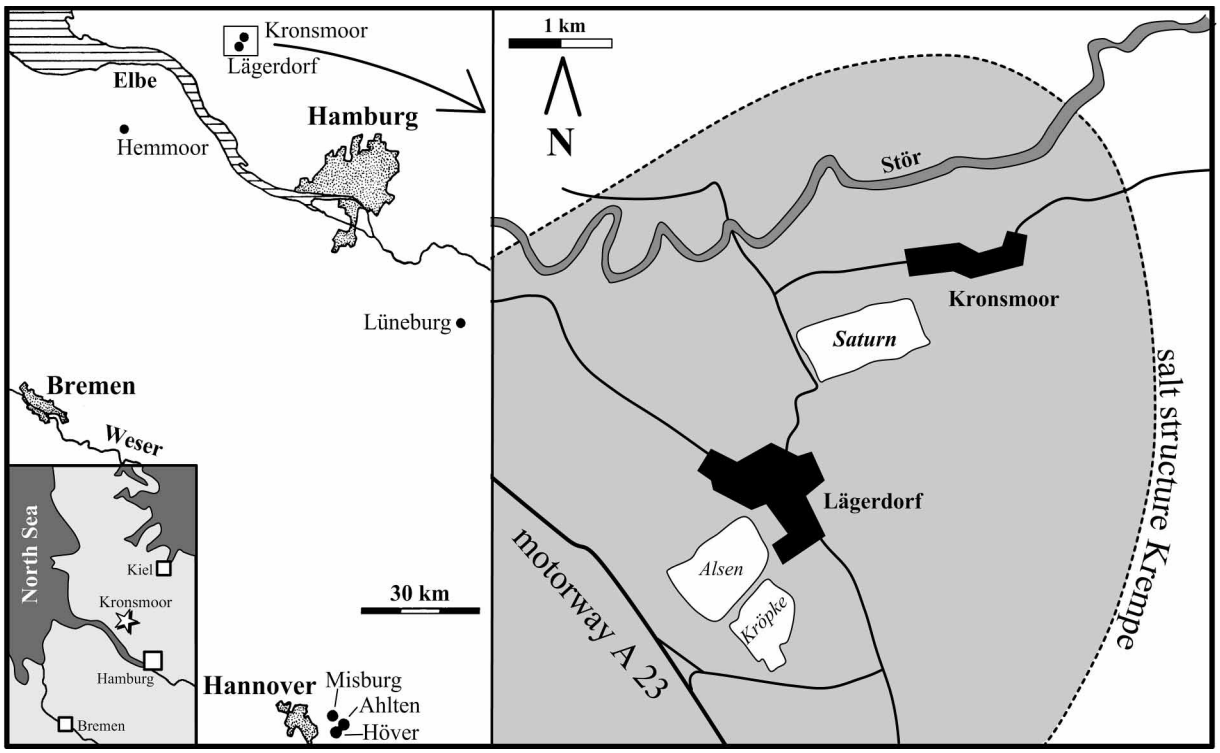

Fig. 1. Locality map of Kronsmoor also showing other German Campanian-Maastrichtian localities mentioned in the text

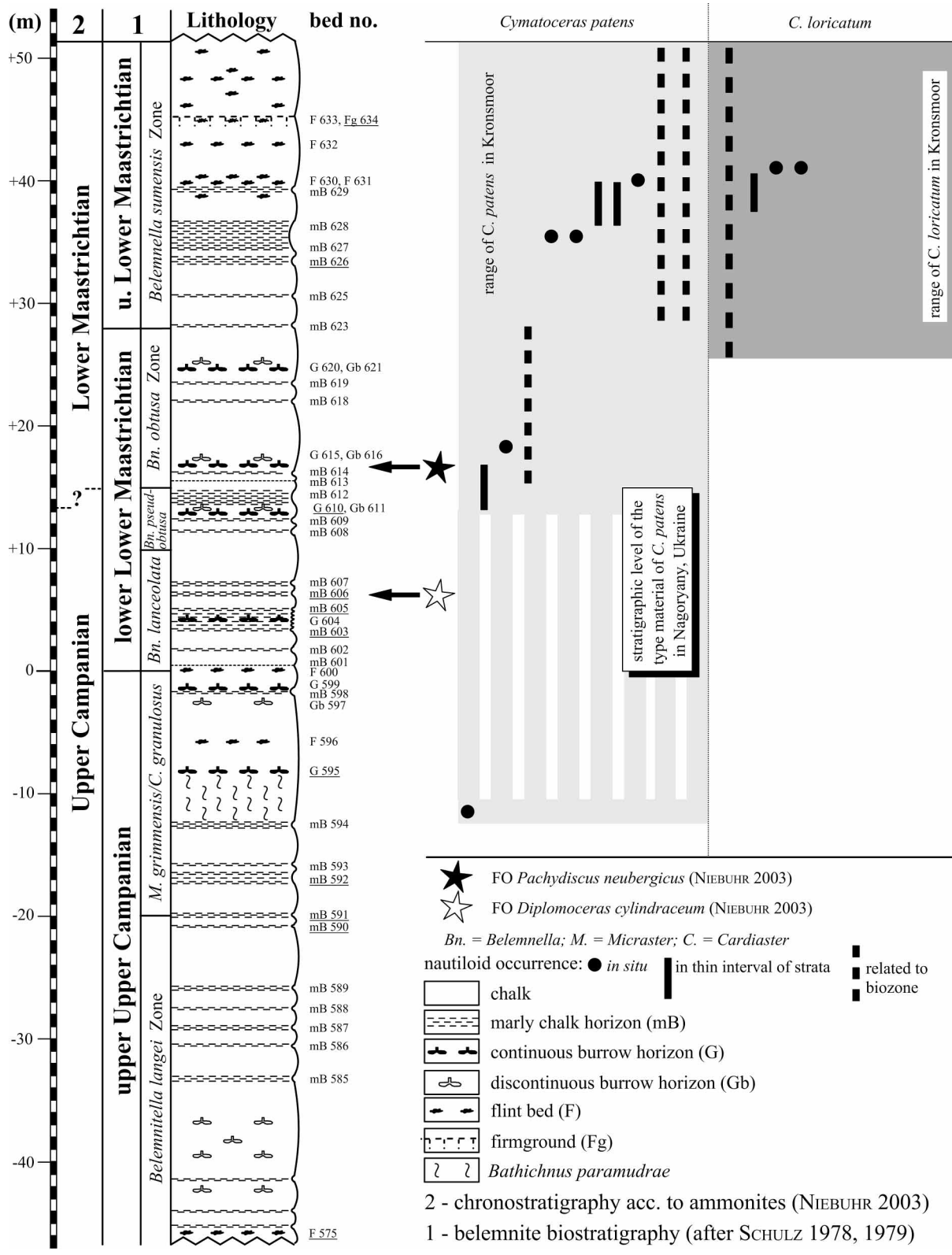

Fig. 2. Stratigraphic log of the Kronsmoor section, northern Germany, showing biostratigraphy, marker beds and nautiloid occurrences (log after Niebuhr 2003)

stratigraphy (SCHULZ 1978, 1979). Of the above mentioned fossils, only *Galerites roemeri* passes the boundary. In the upper 53 m chalk interval (Lower Maastrichtian of belemnite stratigraphy), three distinct marly intervals appear which can be traced across the quarry. The fossil content of the lowermost 3 to 4 m of the *B. lanceolata* Zone is extremly low. From the first marly interval, the index belemnite occurs more frequently. Ammonites and nautiloids, however, remain rare up to the boundary between the *Belemnella pseudobtusa* and *Belemnella obtusa* zones. The *Belemnella sumensis* Zone is the most fossiliferous part of the section, yielding belemnites, ammonites, nautiloids, irregular echinoids, crinoids, and a few bivalves (SCHULZ *& al.* 1984). Only the topmost 14 m of the *B. sumensis* Zone contain more or less discontinuous nodular flint layers. The white chalk has an average carbonate content of 92 to 97 % (EHRMANN 1986) and was deposited in an open epicontinental sea.

NIEBUHR (2003) recently demonstrated that the Campanian-Maastrichtian boundary at Kronsmoor as recognized by means of ammonite biostratigraphy [first appearance of *Pachydiscus neubergicus* (VON HAUER)] is somewhat higher than formerly thought. It is placed at the base of the *Belemnella obtusa* Zone of belemnite stratigraphy, at the 13-15 m level of the displayed log (see Text-fig. 2).

MATERIAL AND METHODS

The preservation of the fauna is mostly excellent, most specimens are (composite) internal moulds. The nautiloids were measured with a sliding caliper. The shape of the suture, the position of the siphuncle on the septal plane with respect to venter and dorsum, measurements of shell dimensions (D = maximum diameter; Wb = maximum breadth of last whorl; Wh = maximum height of last whorl; U = diameter of umbilicus; all values in mm) and calculations of proportions (Wb/D, Wh/D, Wb/Wh, and U/D) are considered as the most important features for taxonomic analyses (see Text-fig. 3, and TEICHERT 1964 for morphological terms). The material described and figured herein is stored in the collection of Klaus J.K. Esser (repository KJKE + no.) and will later be transferred to the collection of the Bundesanstalt für Geologie und Rohstoffe (BGR), Hannover.

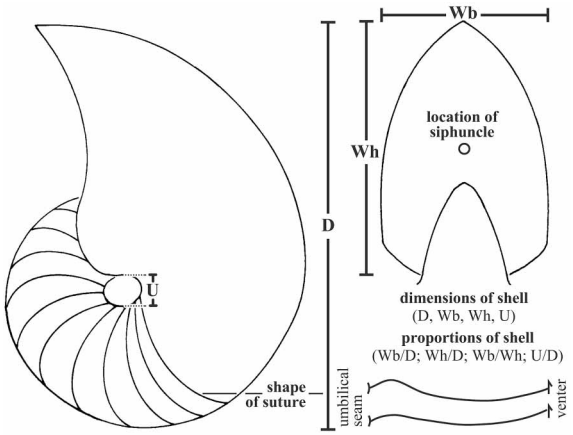

Fig. 3. Criteria used herein for systematic classification of nautiloids

SYSTEMATIC PALAEONTOLOGY

Important contributions on the taxonomy of post-Triassic nautiloids have been presented by KUMMEL (1956, 1964), WIEDMANN (1960), and DZIK (1984). SHIMANSKY (1975) and MATSUMOTO *& al.* (1984) focused mainly on Cretaceous nautiloids and their phylogenetic relationships. Family and genus level classification is still controversial, especially with respect to the family Cymatoceratidae SPATH 1927 (see discussion in WILMSEN 2000 and WILMSEN & YAZYKOVA 2003). Here, the classification of SHIMANSKY (1975) is followed, and we include most of the cymatoceratid genera in the family Nautilidae DE BLAINVILLE 1825. As the described taxa are well known from northern Europe, synonymies are brief.

Order Nautilida AGASSIZ, 1847
Superfamily Nautilacea DE BLAINVILLE, 1825
Family Nautilidae DE BLAINVILLE, 1825

Genus *Cymatoceras* HYATT 1884

TYPE SPECIES: *Nautilus pseudoelegans* D'ORBIGNY (1840 p. 70, pl. 8, by original designation).

DIAGNOSIS: Involute, generally subglobular with rounded whorl cross-section. Degree of involution variable from occluded to slightly evolute. Suture slightly sinuous, position of siphuncle variable. Shell with conspicuous, sigmoidal, commonly flattened ribs covering flanks and venter.

Plate 1. Nautiloids from the Upper Campanian-Lower Maastrichtian white chalk of Kronsmoor, northern Germany. **1a, b** – *Cymatoceras loricatum* (SCHLÜTER, 1876); KJKE 94, Lower Maastrichtian (*Belemnella sumensis* Zone; × 0.8). **2** – *Cymatoceras loricatum* (SCHLÜTER, 1876); KJKE 93, Lower Maastrichtian (upper *Belemnella obtusa* to *Belemnella sumensis* zones; × 0.5). **3 -** *Cymatoceras patens* (KNER, 1848); KJKE 100, Lower Maastrichtian (*Belemnella sumensis* Zone; × 0.7)

REMARKS: The genus was extensively reviewed by KUMMEL (1956); it reached its peak diversity during the Cretaceous. Due to their characteristic ('*Cymatoceras*-like') ribbing and moderately sinuous suture, representatives of *Cymatoceras* are easy to identify. According to KUMMEL (1956, p. 420), at least 64 species are known.

DISTRIBUTION: The genus is cosmopolitan in distribution and ranges from the Upper Jurassic into the Oligocene (KUMMEL 1956).

Cymatoceras loricatum (SCHLÜTER 1876)
(Pl. 1, Figs 1a-b, 2)

*1876 *Nautilus loricatus* sp. n.; SCHLÜTER, p. 180, pl. 51, figs 1, 2.
1956 *C. loricatus* (SCHLÜTER) 1876; KUMMEL, p. 425.
1999 *Cymatoceras loricatus* (SCHLÜTER 1876); WITTLER, ROTH & LEGANT, p. 44, text-figs 54a, b, 55a, b.

TYPES: Holotype should be the specimen figured by SCHLÜTER (1876) on p. 51, figs 1, 2 which, however, could not be located yet. Locus typicus is Haldem (Stemweder Berg) near Osnabrück. Stratum typicum is the "Mucronaten-Kreide" (*Belemnitella mucronata* Zone, lower Upper Campanian).

MATERIAL: 4 specimens from the Saturn pit, Kronsmoor (KJKE 93, 94, 448, 466).

Specimen	Bed no. or biozone	D	Wb	Wh	U	Wb/D	Wh/D	Wb/Wh	U/D
KJKE 93	up. *obtusa* to *sumensis* Z.	215	~110	121.5	—	0.51	0.57	0.91	—
KJKE 94	F631+50cm	145	~80	91	—	0.55	0.63	0.87	—
KJKE 448	F630-1-3m	~80	~54	56.8	~4.0	0.68	0.71	0.95	0.05
KJKE 466	F631+50cm	~109	69.0	~77	~4.0	0.63	0.71	0.90	0.04

DESCRIPTION: Involute, nautiliconic nautiloid with a slightly compressed whorl cross-section (Wh/Wb ~0.90). The umbilicus is very narrow to closed and the umbilical shoulders are rounded. The flanks are only weakly convex, grading into broadly rounded ventrolateral shoulders and venter. Maximum breadth of whorl is in the lower part of the flanks. The ornament is relatively coarse and consists of broad ribs (up to 6mm wide) and narrow grooves (<1mm; Pl. 1, Fig. 1b). The ribs are prosiradiate on the lower flank and show a broad backwards arc across the upper flank and ventrolateral shoulder, crossing the venter in moderate concavity. They do not branch but widen considerably towards the venter. The most distinct aspect of the ornament is that the ribs are asymmetric: they gradually rise from a groove towards the aperture and abruptly terminate at the next groove. At the venter, this ribbing pattern resembles imbricate roofing tiles (Pl. 1, Fig. 1b). The ornament seems to be strongest on the last chambers of the phragmocone and the adult body chamber. The suture is weakly sinuous and only poorly visible; it displays a saddle on the lower flank followed by a shallow lobe and saddle towards the venter. The position of the siphuncle is not visible.

REMARKS: The specimens are clearly characterized by their characteristic ornament which allows an assignment to *Cymatoceras loricatum* (SCHLÜTER). The species, which was based by SCHLÜTER on a single specimen, is characterized by a very narrow to closed umbilicus, a slightly compressed whorl cross-section and an only weakly sinuous suture. The siphuncle is located nearer to the venter than to the dorsum (SCHLÜTER 1876, p. 180). The peculiar ornament was described by SCHLÜTER as 'intercalated armour-plating-like bands' ["*Man kann bei derselben* (Ornamentik) *nicht im gewöhnlichen Sinne von Rippen und Furchen reden, da sie den übereinandergelegten Schienen eines Panzers ähnlich ist*"; SCHLÜTER, p. 180). A similar imbricated ribbing pattern is shown by *Cymatoceras imbricatum* (CRICK 1907, p. 220, pl. 14, figs 6, 6a), known from the Cenomanian of Zululand. This species, however, is more compressed and less involute than *C. loricatum*. *Cymatoceras pseudoatlas* (YABE & SHIMIZU 1924) from the Santonian-Campanian of Hokkaido (Japan) and Sakhalin (far-east Russia) is a generally similar species. It shows, however, a depressed whorl cross-section and 'regular' (i.e., non-asymmetric) ribs which branch on the flanks (see WILMSEN & YAZYKOVA 2003).

DISTRIBUTION: The material described herein is from the Early Maastrichtian, upper *B. obtusa* to *B. sumensis* zones. *Cymatoceras loricatum* was hitherto recorded from the Upper Campanian (*mucronata* Zone) of the Stemweder Berg (Haldem), Westphalia, and Königslutter, Lower Saxony (SCHLÜTER 1876). WITTLER & *al.* (1999) described a specimen from the uppermost Lower Campanian of Coesfeld, Westphalia. The range of the species thus comprises the uppermost Lower Campanian to Lower Maastrichtian.

Cymatoceras patens (KNER 1848)
(Pl. 1, Fig. 3; Pl. 2, Figs 1a-c, 2a-b; Pl. 3, Figs 1a-b, 2a-b, 3-4, 5a-b, 6-7; Pl. 4, Figs 1a-c, 2-3, 4a-b)

Plate 2. *Cymatoceras patens* (KNER, 1848) from the Upper Campanian-Lower Maastrichtian white chalk of Kronsmoor, northern Germany (all figures in natural size). **1a-c** – KJKE 444, Lower Maastrichtian (*Belemnella sumensis* Zone). **2a, b** – KJKE 89, Lower Maastrichtian (*Belemnella sumensis* Zone)

*1848. *N. patens, m.*; KNER, p. 7, tab. 1, figs 2, 2a.
1859. *Nautilus patens,* KNER; PICTET & CAMPICHE, p. 121.
1876. *Nautilus patens*, KNER; SCHLÜTER, p. 178, pl. 50, figs 1-5.
1932. *Nautilus patens* KNER; WOLANSKI, p. 8.
1956. *Cymatoceras patens* (KNER) 1850; KUMMEL, p. 426.
1975. *Cymatoceras patens* (KNER, 1850); SHIMANSKY, p. 111, text-fig. 23a, b. [reproduction of the type of KNER 1848]

TYPES: The holotype is a fully septate internal mould in the collection of the Naturhistorisches Museum Wien (specimen NHMW 2004z0117/0001), herein re-figured on Pl. 4. Locus typicus is Nagoryany near Lvov, the Ukraine. Stratum typicum is the "Kreidemergel von Lemberg" (*B. lanceolota* and *B. pseudobtusa* zones *sensu* SCHULZ 1979).

MATERIAL: 11 specimens from the Saturn pit, Kronsmoor (KJKE 89, 97, 100, 444, 445, 447, 619-623).

Specimen	Bed no. or biozone	D	Wb	Wh	U	Wb/D	Wh/D	Wb/Wh	U/D
KJKE 89	mB627-628	95.4	~45.0	52.6	15.9	0.47	0.55	0.85	0.17
KJKE 97	mB628-F630	110.1	~52.0	68.9	11.0	0.47	0.63	0.75	0.10
KJKE 100	*sumensis* Z.	131.5	~60	~68	21.5	0.46	0.52	0.88	0.16
KJKE 444	F630	90.7	42.6	54.6	15.5	0.47	0.60	0.78	0.17
KJKE 445	mB627-628	51.9	25.2	27.5	8.4	0.49	0.53	0.92	0.16
KJKE 447	G610-G615	89.6	~43	56.0	~11.0	0.48	0.63	0.77	0.12
KJKE 619	*sumensis* Z.	56.2	28.4	35.2	7.4	0.51	0.63	0.81	0.13
KJKE 620	mB594+1m	53.4	21.9	29.8	6.0	0.41	0.56	0.73	0.11
KJKE 621	*obtusa* Z.	46.1	~25	29.1	6.0	0.54	0.63	0.86	0.13
KJKE 622	G615+1-2m	140	~66	82.5	12.2	0.47	0.59	0.80	0.09
KJKE 623	mB628-F630	127.5	~56	64.0	20.0	0.44	0.50	0.88	0.16
mean		—	—	—	—	**0.47**	**0.58**	**0.82**	**0.14**

DESCRIPTION: Relatively evolute nautiliconic nautiloid with a compressed whorl cross-section. The umbilicus is open and rather deep with a steep to overhanging umbilical wall. The umbilical shoulder is narrowly rounded, giving rise to nearly flat, slightly converging flanks. Maximum width is at the transition from the lower to the middle flank. The ventrolateral shoulder is broadly rounded. The venter is narrowly rounded in smaller specimens, becoming more broadly rounded in larger ones. The ornament consists of fine and sharp ribs (Pl. 3, Figs 1b, 2b, 4, 5a) which are prosiradiate on the lower flank and then strongly curve backwards in a broad arc at mid-flank. They cross the external part in concavity, forming a narrowly rounded ventral sinus. Ribs are ca. 1mm wide and are separated by 2-5mm wide interspaces showing fine lirae (e.g., Pl. 3, Figs 4, 6). One specimen suffered from a non-fatal shell injury at the venter (Pl. 3, Fig. 5b). The siphuncle is located slightly nearer to the venter than to the dorsum. The suture is of moderate sinuosity and shows a weak saddle at the umbilical shoulder and a broad, shallow lobe on mid-flank rising to a broad ventral saddle.

REMARKS: All described features and shell parameters are very similar to those of the holotype figured by KNER (1848, tab. 1, fig. 2; see Pl. 4 herein) from the Lower Maastrichtian of Nagoryany, south of Lvov (the former Lemberg, Ukraine) (see KENNEDY & SUMMESBERGER 1987), and the specimens of SCHLÜTER (1876, pl. 51, figs 1-5) from the Upper Campanian of northern Germany.

From the original description of KNER (1848, p. 7) it is clear that he was dealing with two specimens when he erected the species, but it was unclear whether his two figures (figs 2 and 2a on his tab. 1) showed one or two specimens (which then have to be regarded as syntypes). However, investigation of the type material in the collection of the NHM Wien showed that fig. 2a of KNER represents the apertural view of the medially split specimen shown in fig. 2, and that the two views of that single specimen were figured at different scales (albeit KNER stated that both were × 0.5). Unfortunately, part of this specimen is lost, and it is now represented only by the greater part of the phragmocone. However, the diagnostic features of the species (shape of suture, shell dimensions and proportions, position of siphuncle, ribbing pattern) are sufficiently well represented by this remaining part of the original type specimen, which must be regarded as the holotype by monotypy of *C. patens*. It has the following shell dimensions and proportions (see also Pl. 4):

D	Wb	Wh	U	Wb/D	Wh/D	Wb/Wh	U/D
~114	55	67.5	~15	0.48	0.59	0.81	0.13

SCHLÜTER (1876, p. 179) gives the dimension of two specimens:

D	Wb	Wh	U	Wb/D	Wh/D	Wb/Wh	U/D
70	31	38	12	0.44	0.54	0.82	0.17
103	51	60	17	0.50	0.58	0.85	0.17

The material figured by SCHLÜTER (1876, pl. 50) also shows that the venters of larger specimens (as in the Kronsmoor material) are not as narrowly rounded as in

Plate 3. *Cymatoceras patens* (KNER 1848) from the Upper Campanian-Lower Maastrichtian white chalk of Kronsmoor, northern Germany (all figures × 1 except for Fig. 4 which is × 0.75). **1a, b** – KJKE 620, Upper Campanian (*Micraster grimmensis*/*Cardiaster granulosus* Zone). **2a, b** – KJKE 621, Lower Maastrichtian (*Belemnella obtusa* Zone). **3** – KJKE 619, Lower Maastrichtian (*Belemnella sumensis* Zone). **4** – KJKE 622, Lower Maastrichtian (*Belemnella obtusa* Zone). **5a, b** – KJKE 445, Lower Maastrichtian (*Belemnella sumensis* Zone). **6** – Close-up of the venter of KJKE 447 showing well developed lirae between sharp ribs, Campanian-Maastrichtian boundary interval (upper *Belemnella pseudobtusa* to lower *Belemnella obtusa* Zone). **7 -** KJKE 97, Lower Maastrichtian (*Belemnella sumensis* Zone)

the type specimen of KNER (1848; see Pl. 4). The mean shell proportions of *C. patens* from Kronsmoor are: Wb/D = 0.47; Wh/D = 0.58; Wb/Wh = 0.82; U/D ~0.14.

Cymatoceras patens var. *intrasiphonata* (ŁOPUSKI 1912, pl. 1, figs 5, 6) from the Upper Maastrichtian of Poland (Kazimierz Dolny, Polanówka, Chełm) is a generally similar form (see also MACHALSKI 1995 for an illustration). However, it differs from *C. patens* KNER in the position of the siphuncle and a more flexuous suture line near the umbilicus. Furthermore, it appears to be more involute. At the moment it can not be decided whether it falls into the intraspecific variation of "true" *C. patens* (from which it appears to be stratigraphically separated) or whether it represents a separate (i.e., younger) species. *Cymatoceras loricatum* (SCHLÜTER 1876, p. 180, pl. 51, figs 1, 2) is more involute, less compressed and has a completely different ornament (see above). *C. bayfieldi* (FOORD & CRICK 1890, p. 405, fig. 7) from the Campanian of Great Britain is similar with respect to the relatively large umbilicus. However, it has a depressed whorl cross-section and a stronger ribbing. The Maastrichtian *Epicymatoceras vaelsense* (BINKHORST 1861, p. 15, pl. 5c, fig. 2) is more evolute and compressed (U/D ~0.26, Wb/Wh ~0.60; see SCHLÜTER 1876, p. 177-178), and is clearly separated by its narrowly rounded ventrolateral shoulders and flattened venter.

DISTRIBUTION: One of the Kronsmoor specimens is from the Late Campanian *Micraster grimmensis*/*Cardiaster granulosus* Zone. Another specimen comes from the upper *B. pseudobtusa* to lowermost *B. obtusa* Zone (uppermost Campanian according to NIEBUHR 2003). The bulk of the material is from the Early Maastrichtian *Belemnella obtusa* and *Belemnella sumensis* zones. The types from Nagoryany (Ukraine, KNER 1848) are probably of latest Campanian to earliest Maastrichtian age: CHRISTENSEN (1987) described *Belemnella* (*Pachybelemnella*) *inflata* (ARKHANGELSKY) from this locality, which occurs in Kronsmoor in the *Belemnella lanceolata* and *B. pseudobtusa* zones (SCHULZ 1979). *Cymatoceras patens* is known from Upper Campanian (Ahlten Opoka near Hannover) to Lower Mastrichtian of northern Germany (chalks of Lüneburg and Rügen; SCHLÜTER 1876; WOLANSKI 1932; REICH & FRENZEL 2002), the upper Lower to lower Upper Maastrichtian Vijlen Member (Gulpen Formation) of the Maastrichtian type area (The Netherlands; JAGT & *al*. 1999), and the uppermost Campanian *Nostoceras hyatti* Zone of the Piotrawin quarry, Vistula River valley, Poland (written com. M. MACHALSKI, 05/2004). SCHLÜTER (1874) reports the species from the 'chalk' of Denmark. The range of *Cymatoceras patens* thus extends from the Upper Campanian to the Lower Maastrichtian.

PALAEOBIOGEOGRAPHIC IMPLICATIONS

Cymatoceras patens (KNER 1848) and *C. loricatum* (SCHLÜTER 1876) appear to be restricted to the Central European Subprovince of the temperate North European Province (Boreal Realm, Text-fig. 4) as defined by belemnites (CHRISTENSEN 1976, 1997). The southernmost occurrence of *C. patens* is that of Nagoryany, located in ca. 35° northern palaeolatitude near to the boundary to the Tethyan Realm (Text-fig. 4). The northernmost occurrence known to date is from Denmark, representing ca. 43°N. *C. loricatum* is so far only known from northern Germany (ca. 40°N). This rather narrow palaeolatitudinal distribution pattern may indicate a preference of the two nautiloid species for the warm-temperate areas of the Boreal Realm, and their restriction to the Central European Subprovince suggests some endemism.

Cymatoceras patens and *C. loricatum* occur in a variety of epicontinental facies comprising hemipelagic marl-limestone rhythmites (e.g., at Coesfeld, Westphalia), opoka (spiculitic chalks, e.g., at Stemweder Berg and Ahlten, NIEBUHR & *al*. 1997), sandy opoka (at Nagoryany, KNER 1848), marly-glauconitic chalks (Maastricht area; JAGT & *al*. 1999), and pure nannofossil chalks ("Schreibkreide", e.g., at Kronsmoor), indicating a rather facies-independent distribution. In most localities, they co-occur with smooth-shelled nautiloids of the genus *Eutrephoceras* HYATT (e.g., at Nogoryany; see KNER 1848). Also in Kronsmoor, the two *Cymatoceras* species are associated with representatives of the genus *Eutrephoceras*, the poor preservation of which, however, does not allow a specific determination.

Plate 4. Holotype of *Cymatoceras patens* (KNER, 1848), from the "Kreidemergel von Lemberg" at Nagoryany near Lvov, the Ukraine (*Bn. lanceolota* and *Bn. pseudobtusa* zones *sensu* SCHULZ 1979). The specimen is in the collection of the Naturhistorisches Museum Wien (NHMW 2004z0117/0001). **1a-c** – 1a, apertural view; 1b, lateral view; 1c, ventral view. Note the faint ribs visible on the internal mould (natural size). **2** – Reconstruction of the whorl cross-section of the holotype (approximately × 0.9). **3** – Suture lines of the holotype; left side indicates umbilical seam, arrow marks the external side (not to scale). **4a, b** – Reproduction of KNER's (1848) original illustrations (approximately × 0.5). 4a, KNER's fig. 2 on tab. 1; note that the left part of the holotype is missing (compare to Pl. 4, Fig. 1b). 4b, KNER's fig. 2a on tab. 1; apertural view of the right part of the holotype, indicating that it was already split into two parts when KNER first described the species (compare to Pl. 4, Fig. 1a)

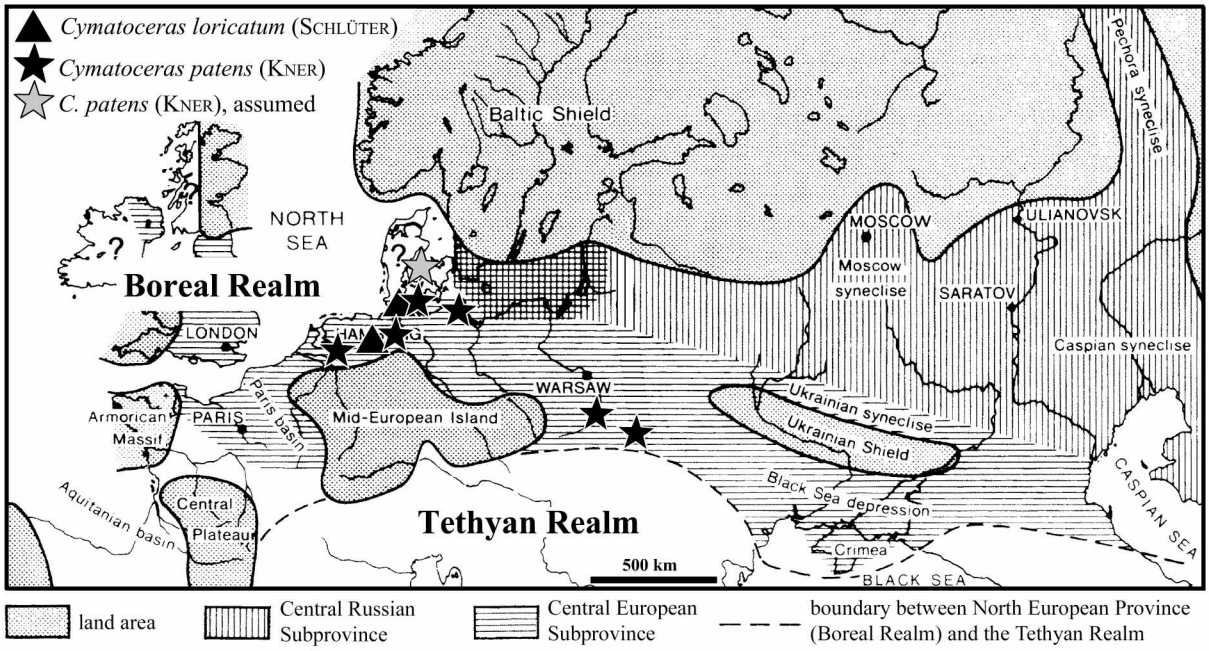

Fig. 4. Palaeobiogeographic distribution of *Cymatoceras patens* (KNER 1848) and *C. loricatum* (SCHLÜTER 1876) in the Late Campanian and Early Maastrichtian (map modified from CRISTENSEN 1997)

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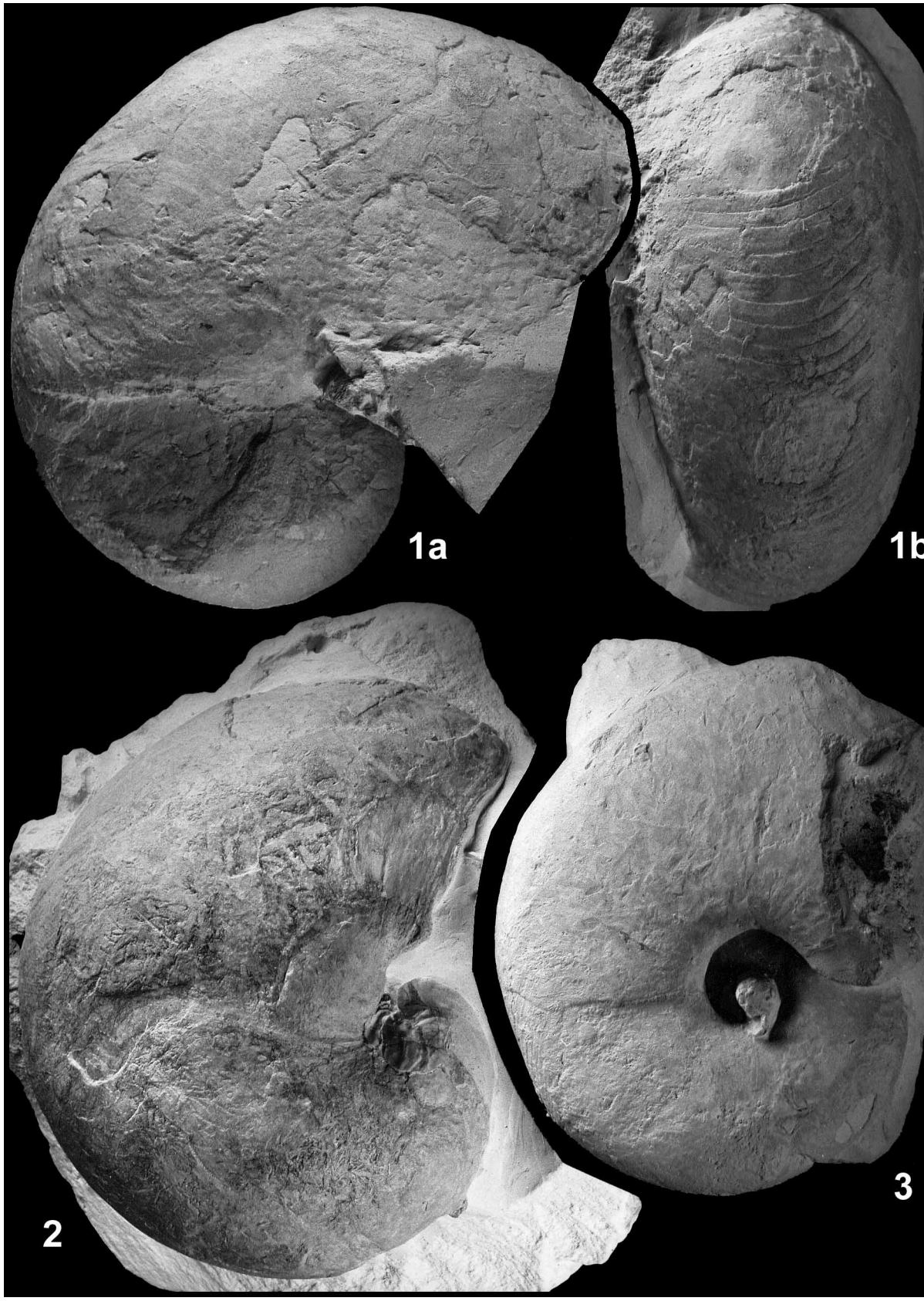
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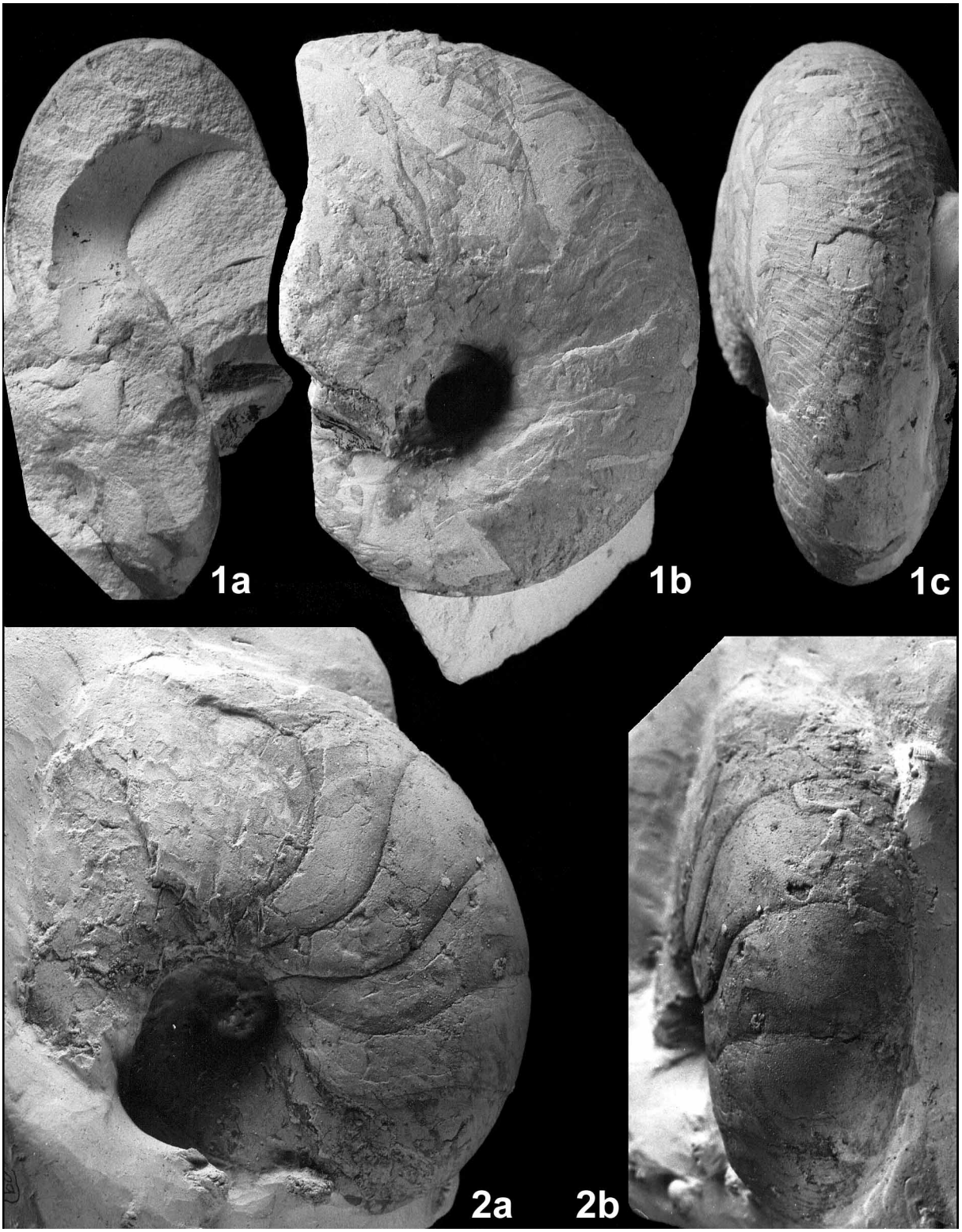
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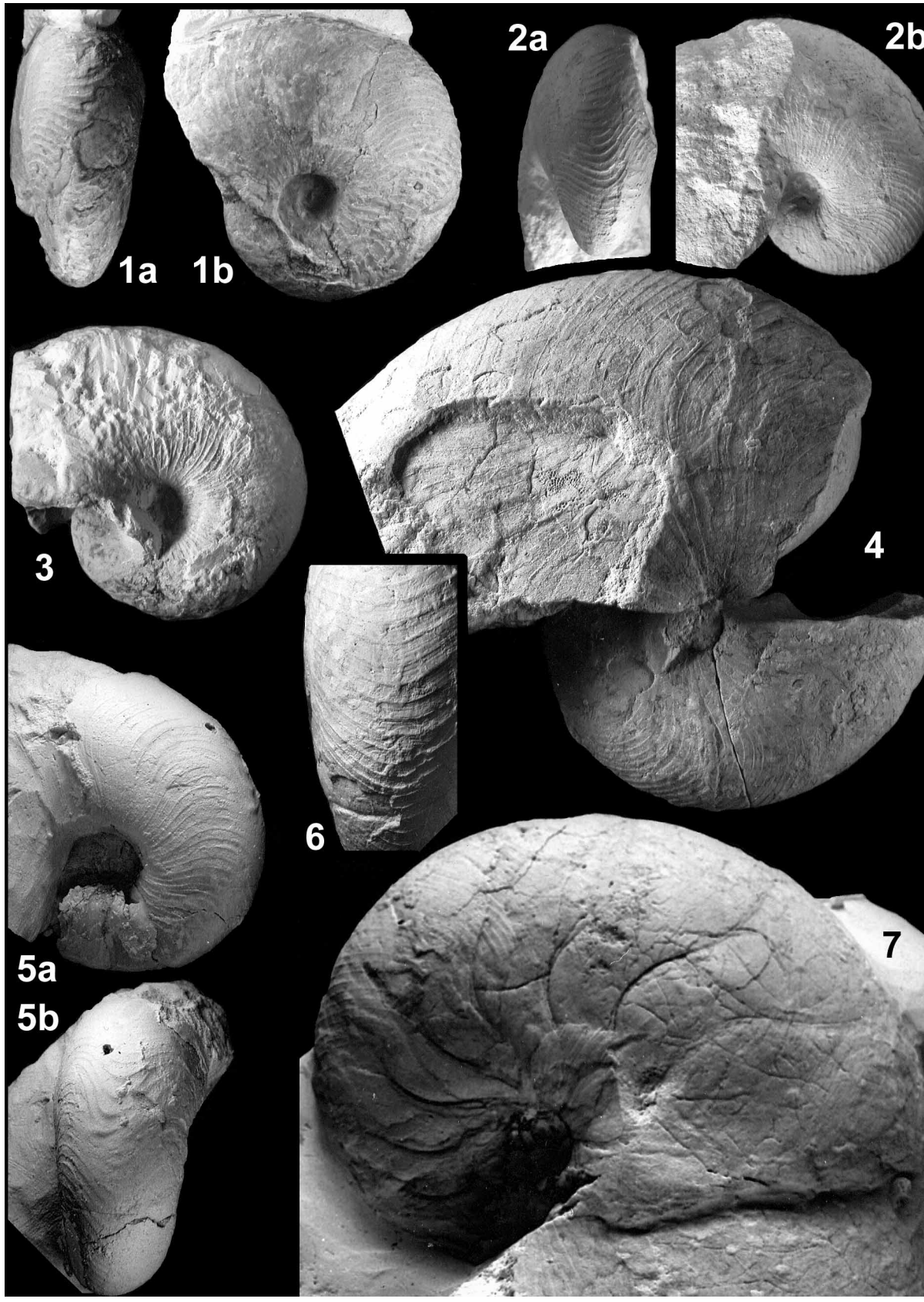
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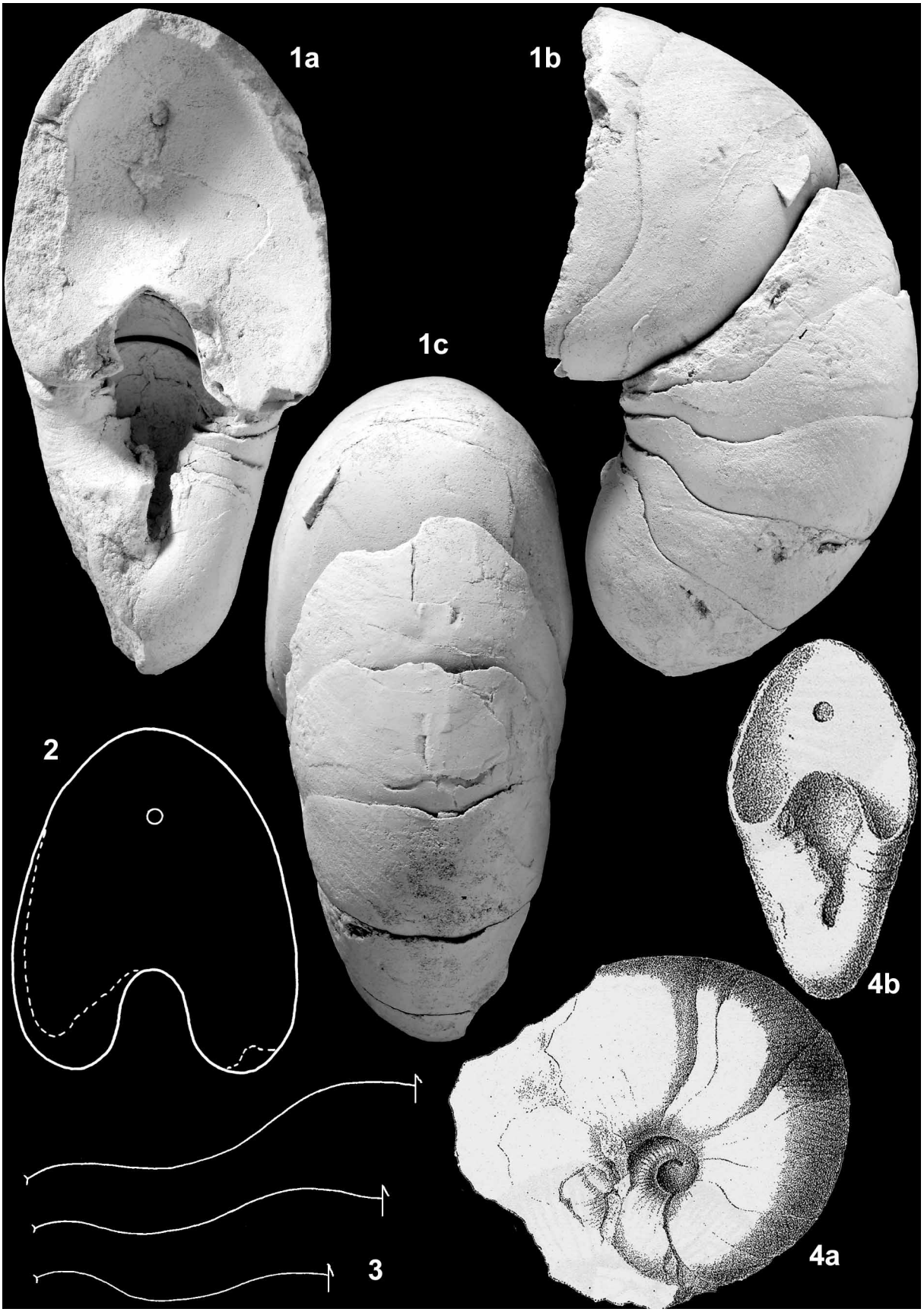
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