Evidence for ammonite survival into the Danian (Paleogene) from the Cerithium Limestone at Stevns Klint, Denmark

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Two ammonite species, *Baculites vertebralis* and *Hoploscaphites constrictus*, are recorded from the Cerithium Limestone (lower Danian, Paleogene) at Stevns Klint, Denmark. Most of the specimens represent internal and external moulds of shell fragments, the sole exception being a complete, well preserved internal mould of *H. constrictus.* The infilling of the body chamber and phragmocone of this specimen is indistinguishable from the surrounding limestone. The $\delta^{13}C$ value for the phragmo-cone fill is 1.382, matching Danian values much better than the more positive Maastrichtian values for the fine-fraction $\delta^{13}C$ curve of the Stevns Klint succession. Additionally, the phragmocone infill contains *Operculodinella operculata*, a calcareous dinocyst typical of the Danian at high latitudes. The specimen is thus interpreted to be an indigenous early Danian ammonite. In view of the mass occur-rence of calcitic bryozoans, brachiopods, and bivalves in the topmost Maastrichtian chalk at Stevns Klint, the total absence of brachiopods and near-absence of bryozoans and calcitic bivalves in the Cerithium Limestone provide evidence against significant redeposition of Maastrichtian fossils into the latter unit. Consequently, all ammonites from the Cerithium Limestone studied are interpreted as early Danian survivors.

Key words: Extinction, survival, ammonites, reworking, calcareous dinocysts, stable isotopes, K–Pg boundary, Danian, Maastrichtian, Denmark.

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The hypothesis that an asteroid impact caused a mass extinction at the Cretaceous–Paleogene boundary (Alvarez *et al*. 1980; Alvarez *et al*. 1984; Smit 1999) revived the old dispute between catastrophists and gradualists on the nature of biotic turnovers across major geological boundaries. However, the record of such turnovers is commonly deformed by taphonomic processes, e.g. the piping down of remains of post-boundary biota into pre-boundary sediments by burrowing organisms, or exhumation of pre-boundary biota and their redeposition into post-boundary sediments. The latter process is often invoked to explain the presence of typically pre-boundary biota in younger sediments. However, after more detailed investigations, many of the supposedly reworked fossils have instead been suggested to be remains of short-term survivors ('holdover taxa' of Hallam & Wignall 1997 or 'failed survivors' of Korn *et al*. 2004). For example, Barrera & Keller (1990), using stable-isotopic data, postulated that some foraminifera preserved in the lowest Danian strata at Brazos, Texas, are survivors rather than reworked Maastrichtian specimens.

The problem also concerns the ammonites, which are a text-book example of victims of the end-Cretaceous crisis. Rare specimens of baculitid and scaphitid ammonites have been known for a long time from the lower Danian Cerithium Limestone at Stevns Klint, south of Copenhagen, Denmark (Rosenkrantz 1924; Rasmussen 1971; Birkelund 1979, 1993; Surlyk & Nielsen 1999). Most authors have regarded these to have been derived from the uppermost Maastrichtian chalk (Rosenkrantz 1924; Rasmussen 1971; Birkelund 1979, 1993). However, Surlyk & Nielsen (1999) suggested that the ammonite remains in the Cerithium Limestone might well represent short-term Danian survivors, a view subsequently challenged by Machalski (2002).

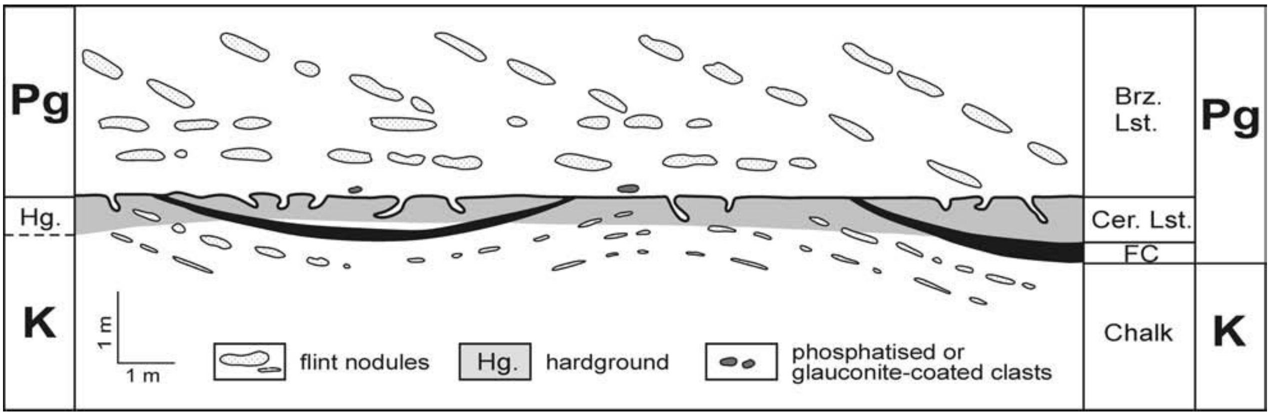

Fig. 1. Details of the K–Pg (Cretaceous–Paleogene) boundary interval at Stevns Klint. K: Cretaceous. Pg: Paleogene. Hg: hardground truncating the crests of the Maastrichtian bryozoan bioherms and the Danian Cerithium Limestone. FC, Fish Clay. Cer. Lst., Cerithium Limestone. Brz.Lst.: bryozoan limestone (modified after Heinberg 1999).

All previous discussions on ammonites from the Cerithium Limestone have suffered from a lack of illustrations and descriptions of these fossils in the literature. The aim of the present paper is to fill this gap. It presents a description and illustrations of an ammonite faunule collected *in situ* from the Cerithium Limestone, and discusses this in the context of reworking and survival hypotheses.

The Cerithium Limestone

The Cerithium Limestone (Cerithiumkalk) is the lowermost carbonate unit of Danian age at Stevns Klint. Together with the underlying iridium-bearing Fish Clay (Fiskeler), of earliest Danian age, it forms infillings of small basins between the crests of the uppermost Maastrichtian bryozoan bioherms (Rosenkrantz 1924; Surlyk 1997; Kunzendorf *et al.* 1990; Surlyk & Håkansson 1999; Hart *et al.* 2004). The basins range from less than ten metres to some tens of metres in width, depending on the direction of section, and the maximum thickness of the Cerithium Limestone is 90 cm. The Cerithium Limestone basins are exposed along the almost entire 12 km long cliff at Stevns Klint.

The Cerithium Limestone and the crests of the Maastrichtian bioherms are truncated by an intra-Danian hardground, overlain by the lower Danian bryozoan limestone (Fig. 1). Clasts of the Maastrichtian chalk and the Cerithium Limestone, phosphatised or glauconite-coated, are sporadically present in the basal part of the bryozoan limestone (Figs 1, 4C; see Rasmussen 1971; Surlyk & Håkansson 1999; Heinberg 1999).

The Cerithium Limestone itself is a hard yellow limestone unit, penetrated by numerous *Thalassinoides* burrows filled with skeletal hash piped down from the bryozoan limestone (Rasmussen 1971; Bromley 1975; Ekdale & Bromley 1984; Surlyk & Håkansson 1999). The Cerithium Limestone is a microsparite which may have formed as a direct precipitate from sea water (Hansen 1990). In terms of the standard foraminiferal biostratigraphy, the Cerithium Limestone ranges from the P0 to the P1C zones (Schmitz *et al.* 1992; Heinberg *et al.* 2001). However, the base of the unit is older in southern parts of the Stevns Klint and younger to the north as demonstrated in a quantitative biostratigraphic study based on planktonic foraminifera (Rasmussen *at al.* 2005).

The Cerithium Limestone is highly fossiliferous and therefore important for studying the K–Pg turnover (Rosenkrantz 1939, 1960; Heinberg 1999, 2005). The bulk of its fauna is composed of originally aragonite-shelled gastropods and bivalves; calcitic bivalve shells and other calcitic fossils, e.g. bryozans, being extremely rare (Heinberg 1999, 2005).

Material

The complex stratigraphy across the K–Pg boundary at Stevns Klint was deciphered by Rosenkrantz (1924, 1939). Earlier, the name ‘Cerithiumkalk’ (or ‘Faxoelaget’) was applied to the whole indurated zone, including both the Cerithium Limestone *sensu stricto* and the crests of the intervening Maastrichtian bioherms (see Gravesen 1979 for a historic review of stratigraphic terminology). Thus, it is possible that many specimens from older collections, labelled 'Cerithiumkalk' or 'Faxoelaget', were actually collected *in situ* from the indurated portions of the Maastrichtian chalk. Material collected prior to 1924 is accordingly not included in the present study.

The material studied, eleven specimens in total, is deposited at the Geological Museum, Copenhagen (abbreviation MGUH). It comprises the following specimens:

Six specimens, including four *Baculites* and two *Hoploscaphites* (MGUH 27359–27364), coming from various locations along the cliff (Højerup, Eskesti, Mandehoved, Holtug). All these specimens are fragmentary; some of them are preserved as part and counterpart.

The specimens were collected by the second author, along the three other *Baculites* individuals not included in the present study, during processing of 64 bulk samples of the Cerithium Limestone from various locations. These bulk samples totalled more than 258 kg in weight (not all samples were weighed). Occurrence of nine ammonites in this relatively small amount of rock suggests that these cephalopods are not so uncommon in the Cerithium Limestone as previously thought.

One specimen of *Hoploscaphites* (MGUH 27366), a well-preserved complete mould and its counterpart, coming from south of Højerup. This specimen was found by Thomas Blume and was earlier mentioned by Surlyk & Nielsen (1999, p. 117).

A single, poorly preserved specimen of *Hoploscaphites* (MGUH 27368), coming from south of Højerup, preserved as part and counterpart. This specimen was mentioned by Rasmussen (1971, p. 195).

One specimen of *Baculites* (MGUH 27369), preserved as several fragments, the original label (in Danish) stating '*Baculites* over [= above] Fiskeler, Stevns Klint'. This specimen was collected by Alfred Rosenkrantz in 1924.

A single, slightly phosphatised specimen of *Baculites* (MGUH 27367) from Rødvig, preserved as several fragments. The specimen was collected by Eckart Håkansson.

Additionally, a single specimen of *Hoploscaphites* (MGUH 27365), found by the second author in a Maastrichtian clast at the base of the bryozoan limestone at Eskesti, was studied for comparison with the material from the Cerithium Limestone.

Taxonomy

The ammonite faunule from the Cerithium Limestone comprises two genera, *Baculites* and *Hoploscaphites* (Figs 2–3, 6). Only a few specimens are well enough preserved to be identified at the specific level, as *B. vertebralis* Lamarck, 1801 and *H. constrictus* (J. Sowerby, 1817). As no other species of *Baculites* and *Hoploscaphites* have so far been found in the uppermost Maastrichtian of Denmark (Birkelund 1993, text-fig. 3), the remaining material is tentatively assigned either to *B. vertebralis* or to *H. constrictus.*

Baculites vertebralis Lamarck, 1801

All specimens of *Baculites* from the Cerithium Limestone are fragmentary (Figs 2A, B, D–H). The largest piece, MGUH 27369, is 16 mm long (Fig. 2E). In their dimensions and proportions all specimens correspond to those of *Baculites vertebralis*, which is the most abundant ammonite species in the uppermost Maastrichtian chalk at Stevns Klint (Birkelund 1993). Only specimen MGUH 27369 (Fig. 2E) is well enough preserved to show the egg-shaped cross-section, diagnostic of the species (Birkelund 1993).

Hoploscaphites constrictus (J. Sowerby, 1817)

Specimen MGUH 27366 (Figs 3A–C, 6A–C) is probably the most complete ammonite ever found in the Cerithium Limestone. It is a small adult macroconch, as seen by the presence of an umbilical bulge, typical of adult scaphitid macroconchs (e.g. Cobban 1969; Kennedy 1989; Machalski 1996). The specimen is 39 mm in maximum diameter. The apertural angle is obtuse, distinct ribs cover the flanks and venter. There are nine ribs on the last centimetre of the body chamber, fourteen pairs of ventrolateral and three pairs of umbilical tubercles. The ventrolateral tuberculation extends almost to the end of the body chamber.

Specimen MGUH 27368 is not illustrated here due to its poor preservation. It is a cast of an adapertural fragment of the hook of a fairly large individual, most probably an adult macroconch. Ventrolateral tubercles extend to the aperture, and there are six ribs on the last centimetre of the body chamber.

The remaining specimens from the Cerithium Limestone (MGUH 27359 and MGUH 27360) are imprints of small fragments of outer flanks of the body chamber with ventrolateral tubercles (MGUH 27359 is illustrated in Fig. 2C).

Specimens MGUH 27366 and 27368 are within the range of variation of adult macroconchs of *Hoploscaphites constrictus* from the indurated portions of the topmost Maastrichtian chalk at Stevns Klint as documented by Birkelund (1993, p. 57–59, pl. 17, 16–23). The rib density on the last centimetre of the body chamber in MGUH 27366 and 27368 is within the

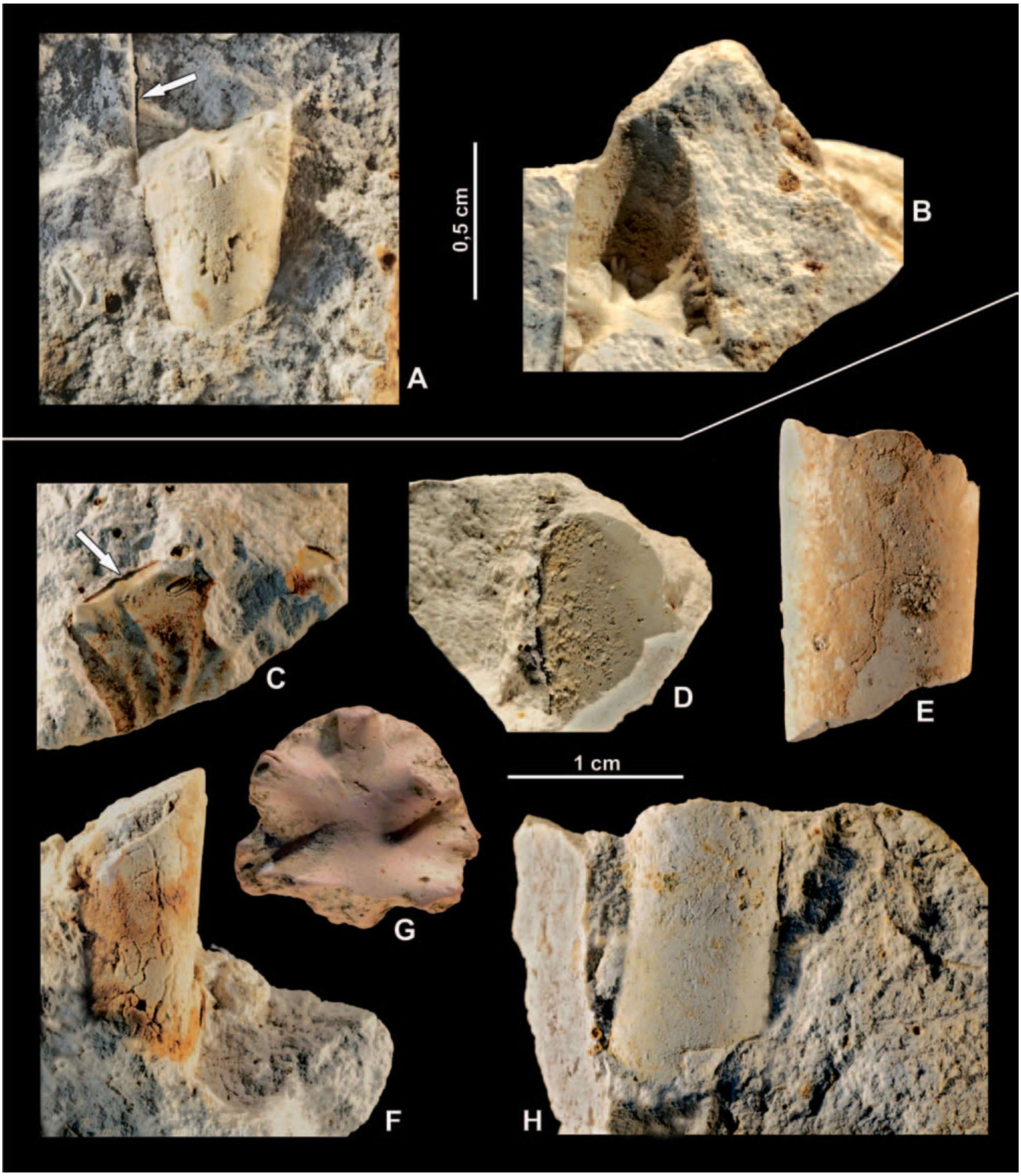

Fig. 2. Ammonite remains from the Cerithium Limestone at Stevns Klint. A, B and D–H, *Baculites vertebralis*. C, *Hoploscaphites constrictus*. A–B, MGUH 27361, Holtug quarry. C, MGUH 27359, Eskesti. D, MGUH 27362, north of Mandehoved. E, MGUH 27369, location only generally indicated as Stevns Klint. F, MGUH 27363, north of Højerup church. G, MGUH 27367, Rødvig. H, MGUH 27364, south of Mandehoved. Voids left after dissolution of the original aragonitic shell are arrowed in Fig. 2A and 2C.

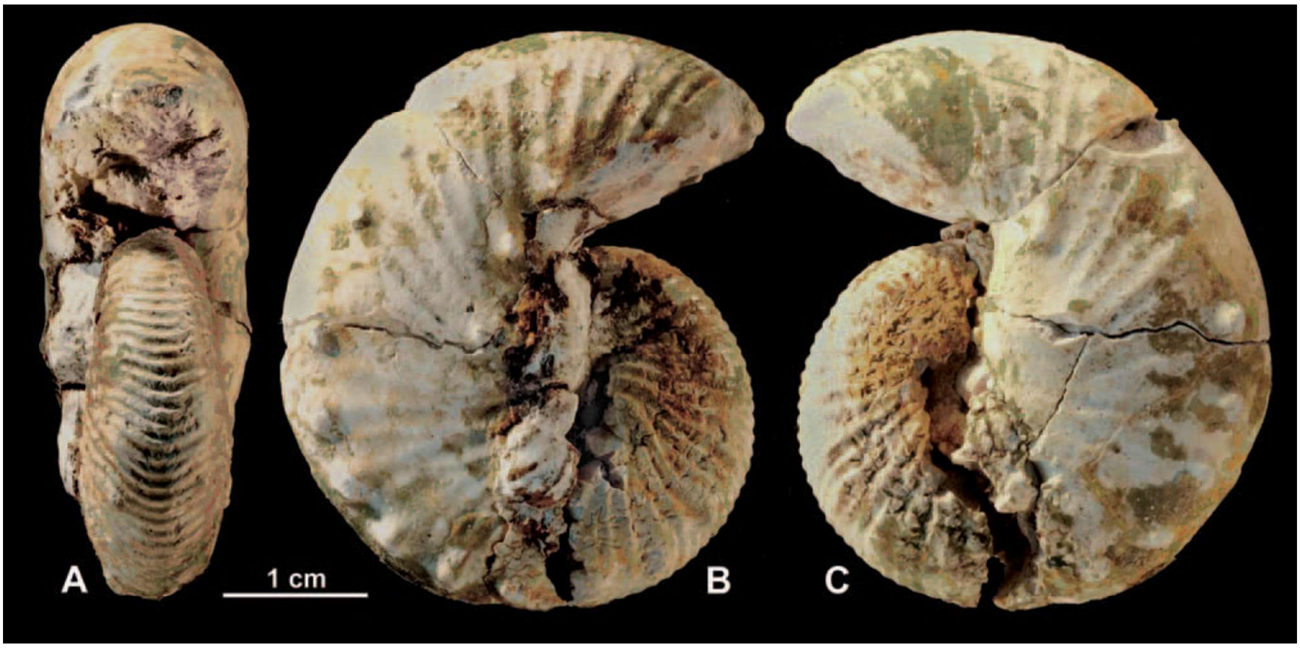

Fig. 3. A–C, *Hoploscaphites constrictus* (MGUH 27366) from the Cerithium Limestone south of Højerup, Stevns Klint. A, adapertural view. B–C, lateral views.

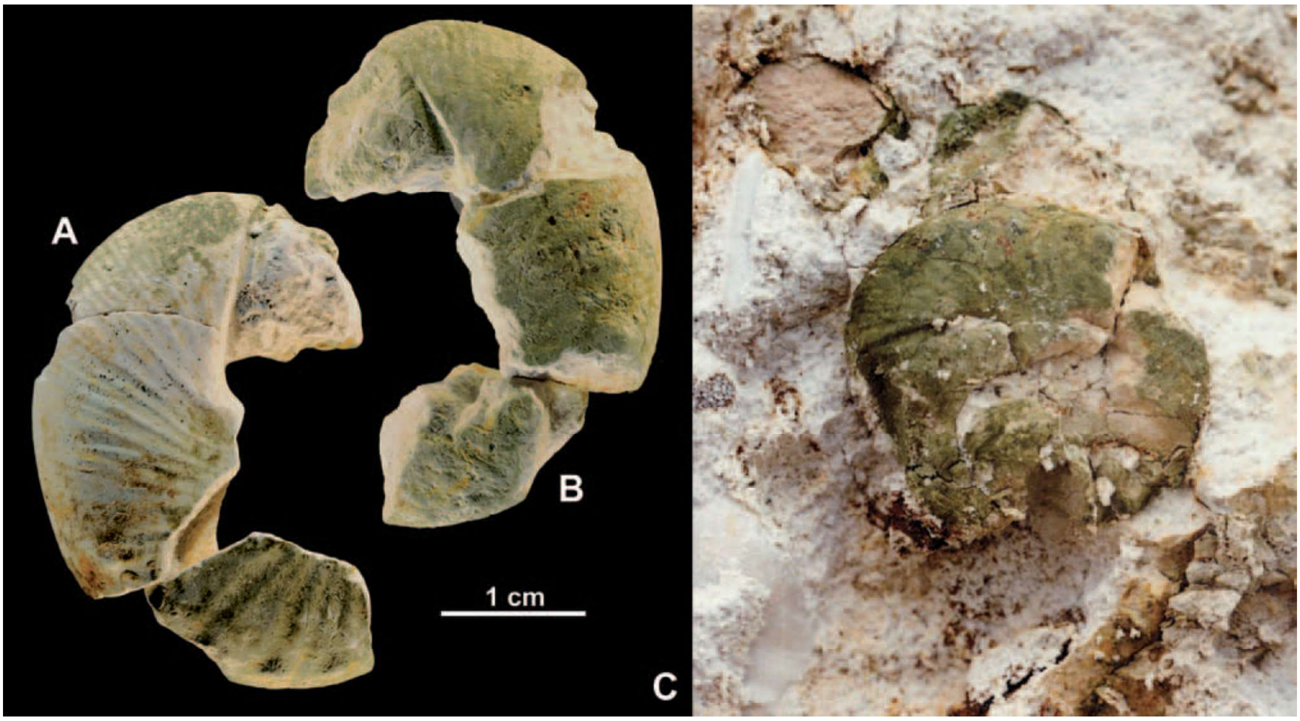

Fig. 4. *Hoploscaphites constrictus* (MGUH 27365), preserved in a glauconite-coated clast of the Maastrichtian indurated chalk, from the base of the bryozoan limestone at Eskesti, Stevns Klint (photograph by Claus Heinberg). A–B, lateral views. C, field photograph of the specimen still embedded in the glauconite-coated clast; note phosphatised (brown) limestone clast in the upper left corner of the photo.

range of this character for the sample of *H. constrictus* from the indurated chalk (Fig. 5).

Specimen MGUH 27365 (Fig. 4A–C), from the base of the bryozoan limestone, is a body chamber of a small adult macroconch, 34 mm in maximum diameter. The umbilical bulge, typical of macroconchs of the species, can only be seen in the field photograph (Fig. 4C), as the specimen was damaged during extraction. The flanks and venter are covered with relatively faint, dense ribs. There are ten ribs on the last centimetre of the body chamber. The ventrolateral tubercles disappear well before the aperture. MGUH 27365 matches the sample from the indurated chalk as overall morphology and rib density (Fig. 5) are concerned.

Preservation of specimens

All ammonite remains from the Cerithium Limestone are devoid of their original, aragonitic shells, as elsewhere along Stevns Klint. Most of the specimens are internal and external moulds of shell fragments (Fig. 2). Voids left after dissolution of the original aragonitic shells are visible on some specimens (e.g. Fig. 2A, C). Their presence suggests that the ammonite fragments were buried in the Danian sediment with the shell material still preserved. The rusty yellow stain visible on the surface of some specimens (e.g. Fig. 2C, F) may be linked to iron-oxide impregnation, clearly a post-burial phenomenon, typical of many moulds and casts in the Stevns Klint succession.

In view of the aragonite survival across the K–Pg boundary at Stevns Klint (Birkelund 1993; Machalski 2002), the preservation of the specimens mentioned above does not offer any definitive clues as for their origin. These fossils may either represent fragments of ammonite shells derived from the soft Maastrichtian chalk or remains of indigenous Danian ammonites, fragmented on the seafloor (e.g. by durophagous predators). It is impossible to say which of these scenarios should be favoured, based solely on preservation of these specimens.

The fragmentary baculitid MGUH 27367 (Fig. 2G) is phosphatised which might suggest reworking (compare Kennedy & Garrison 1975). It is impossible to decide, however, whether the reworking was inter-formational (from the Maastrichtian into the Danian) or intra-formational (within the Danian).

The specimen MGUH 27366 of *Hoploscaphites constrictus* figures prominently in the studied collection, being a well-preserved, complete internal mould (Figs 3A–C, 6A–C). Its preservation is so good, that even the circumapertural constriction, typical of the species, is present (Figs 3C, 6B–C). MGUH 27366 was intact just after its recovery from the host rock (Fig. 6B), but subsequently broke down into several fragments due to lack of proper conservation. Still later,

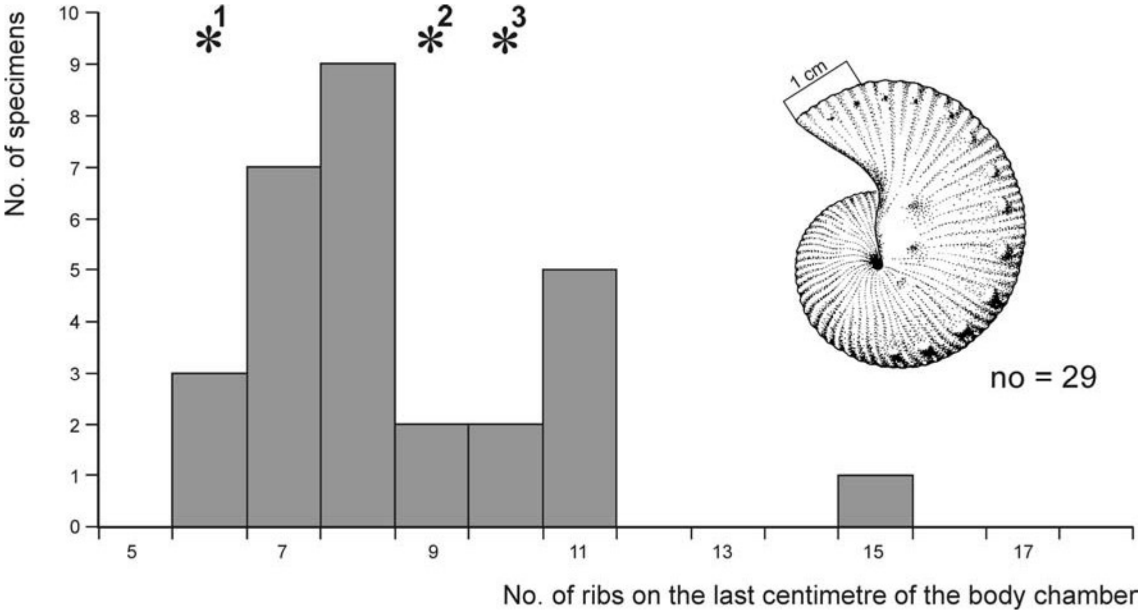

Fig. 5. Variation in rib density on the last centimetre of the body chamber of adult macroconchs of *Hoploscaphites constrictus* from the indurated Maastrichtian chalk at Stevns Klint (based on collections of the Geological Museum, Copenhagen). Positions of the identifiable specimens of this species collected from the Cerithium Limestone (MGUH 27368 and 27366) and from the base of the bryozoan limestone (MGUH 27365) are indicated: 1, MGUH 27368. 2, MGUH 27366. 3, MGUH 27365.

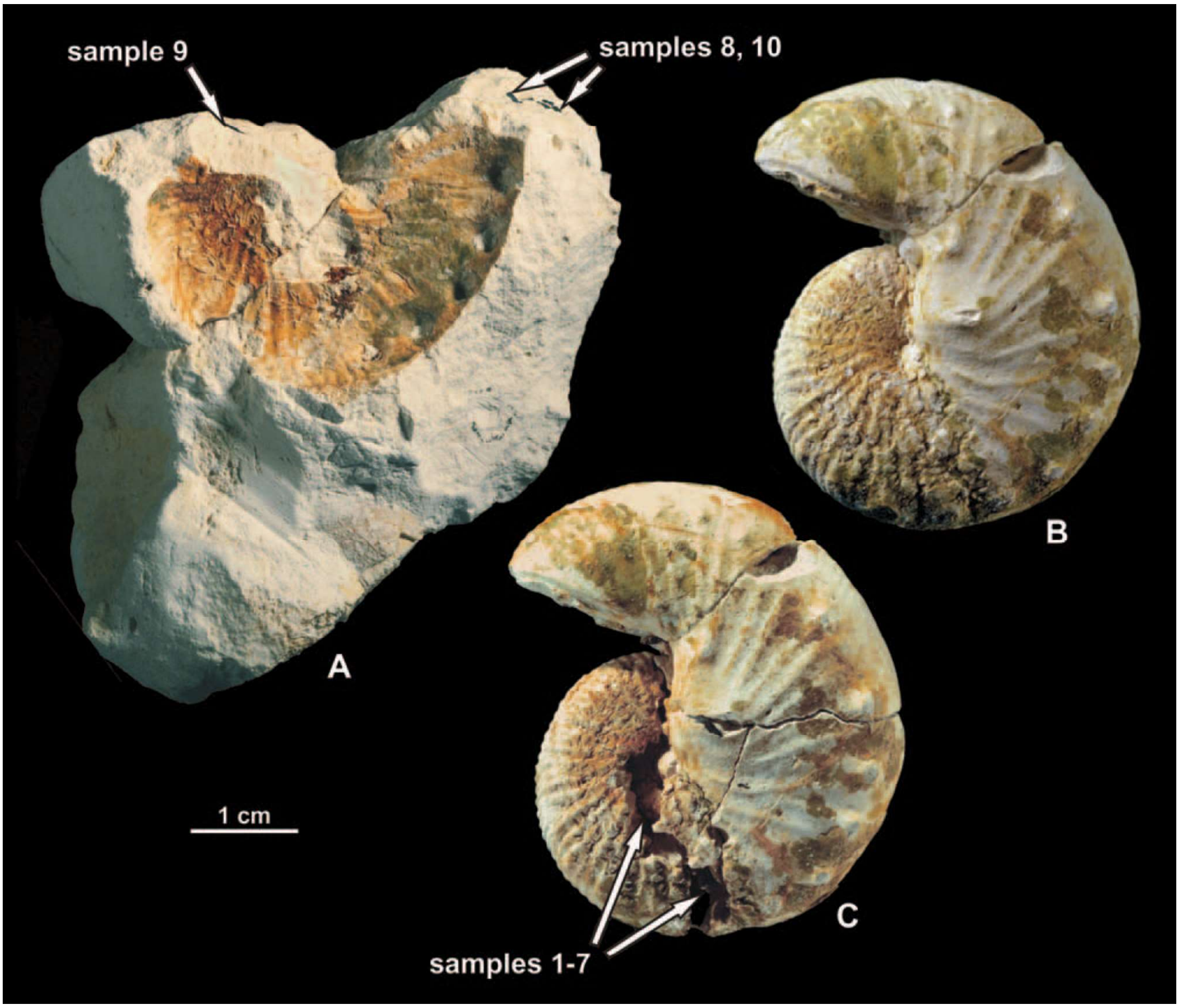

Fig. 6. *Hoploscaphites constrictus* (MGUH 27366) from the Cerithium Limestone south of Højerup, Stevns Klint. A, a fragment of the limestone with the counterpart of the specimen. B, the specimen in lateral view just after its recovery from the rock (photograph courtisy of Eckart Håkansson). C, the present state of the specimen in the same view as in B. Arrows indicate position of samples for nannofossils and stable isotopes.

the specimen was impregnated with a resin and carefully glued together by the museum preparator (Fig. 6C).

The surface of MGUH 27366 is covered locally with a thin, green crust of Fe-rich aluminosilicate (as evidenced by EDS analysis), most probably glauconite. It is impossible to decide whether the crust results from transformation of the original ammonite shell or formed subsequent to its dissolution.

Superficially, MGUH 27366 with its green, possibly glauconitic dots (Figs 3A–C, 6A–C), looks like a reworked fossil. However, comparison with the conspecific glauconite-coated mould MGUH 27365 (Fig. 4A–C) from the base of the bryozoan limestone reveals significant differences. The latter specimen is worn on one side (Fig. 4B) and formed part of a larger, glauconite-coated clast (Fig. 4C). The glauconite coating is more intense on the worn side of the specimen (Fig. 4B) than on the opposite one (Fig. 4A). This mode of preservation implies reworking and temporal exposure on the seafloor (Kennedy & Garrison 1975), MGUH 27365 obviously having lain with its worn and more intensively glauconite-affected side upwards.

The matrix of the clast comprising specimen MGUH 27365 provides additional clues for identification of its source. These are abundant bryozoan fragments present in its matrix. This allows to iden-

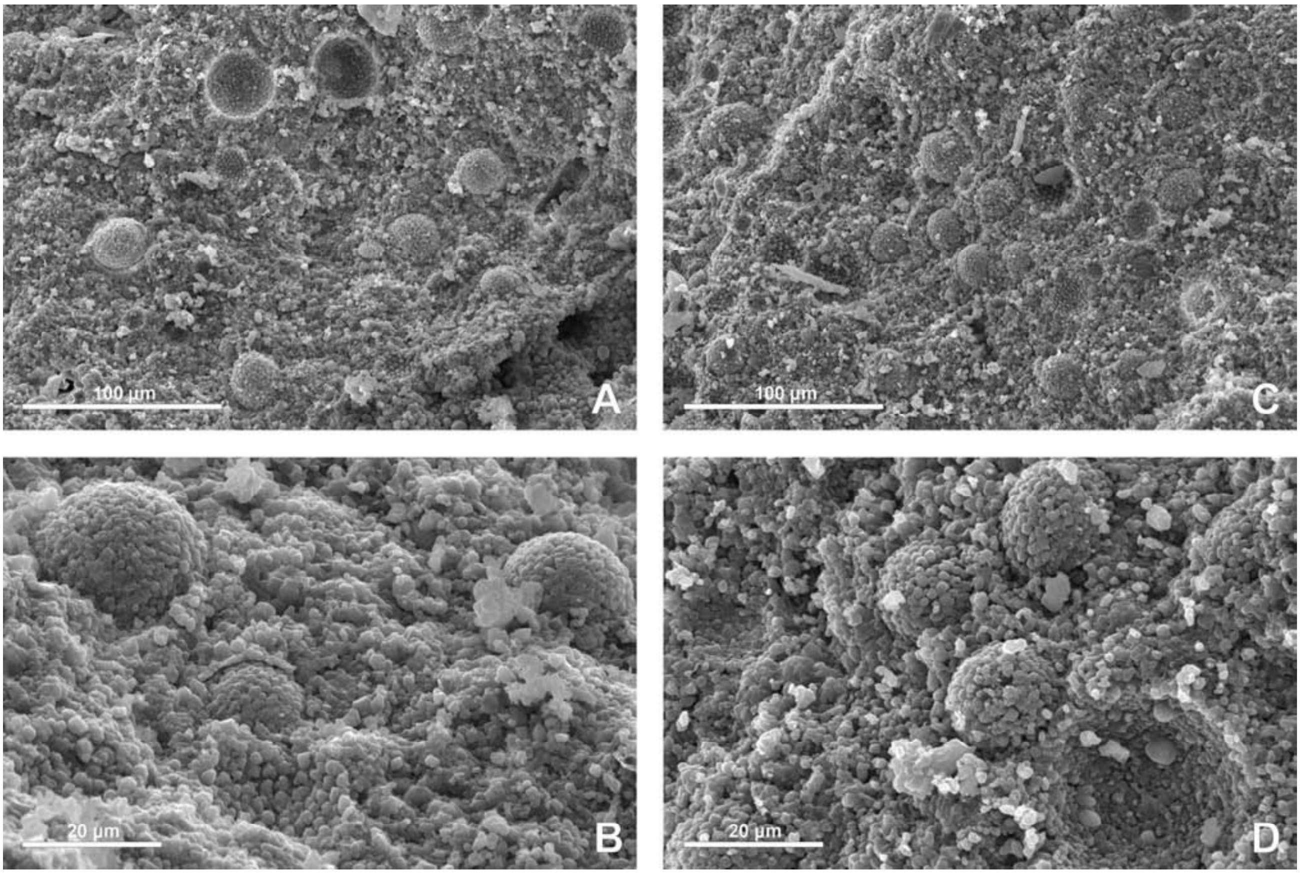

Fig. 7. Calcareous dinocysts set in a fine crystalline matrix as seen in SEM images of the fractured limestone surfaces from Stevns Klint. A–B, sample 8 (limestone surrounding MGUH 27366). C–D, sample 1 (phragmocone infilling of MGUH 27366); see Fig. 6 for location of samples.

tify the matrix as a Maastrichtian chalk (bryozoans are extremely rare in the Cerithium Limestone). There is thus not much room for doubt that MGUH 27365 is a reworked latest Maastrichtian fossil. In contrast, MGUH 27366 does not bear any traces of abrasion or mineralisation of the mould. In particular, the sediment visible in the aperture of MGUH 27366 is not affected by glauconite. Moreover, it contains no bryozoans which suggests that the body chamber of MGUH 27366 is filled with Danian Cerithium Limestone rather than with Maastrichtian chalk.

Structural and nannofossil evidence

Several minute fragments of the sedimentary infill of the phragmocone of MGUH 27366 were left after conserving the specimen. These fragments were examined for their nannofossil content and stable isotopic composition. Only the fragments with preserved casts of the septa were selected for analyses to assure that they actually come from the ammonite phragmocone. Unfortunately, the exact position of particular fragments within the mould could no longer be precisely established.

The fractured surfaces of six samples from the phragmocone of MGUH 27366 were analysed under SEM (samples 1–6) and a single sample (7) was examined for oxygen and carbon isotopes (Fig. 6C). For comparison, three samples from the rock surrounding the specimen were examined: two for nannofossils (samples 8 and 9 in Fig. 6A) and one for stable isotopes (sample 10 in Fig. 6A).

The samples studied, revealed a significant varia-

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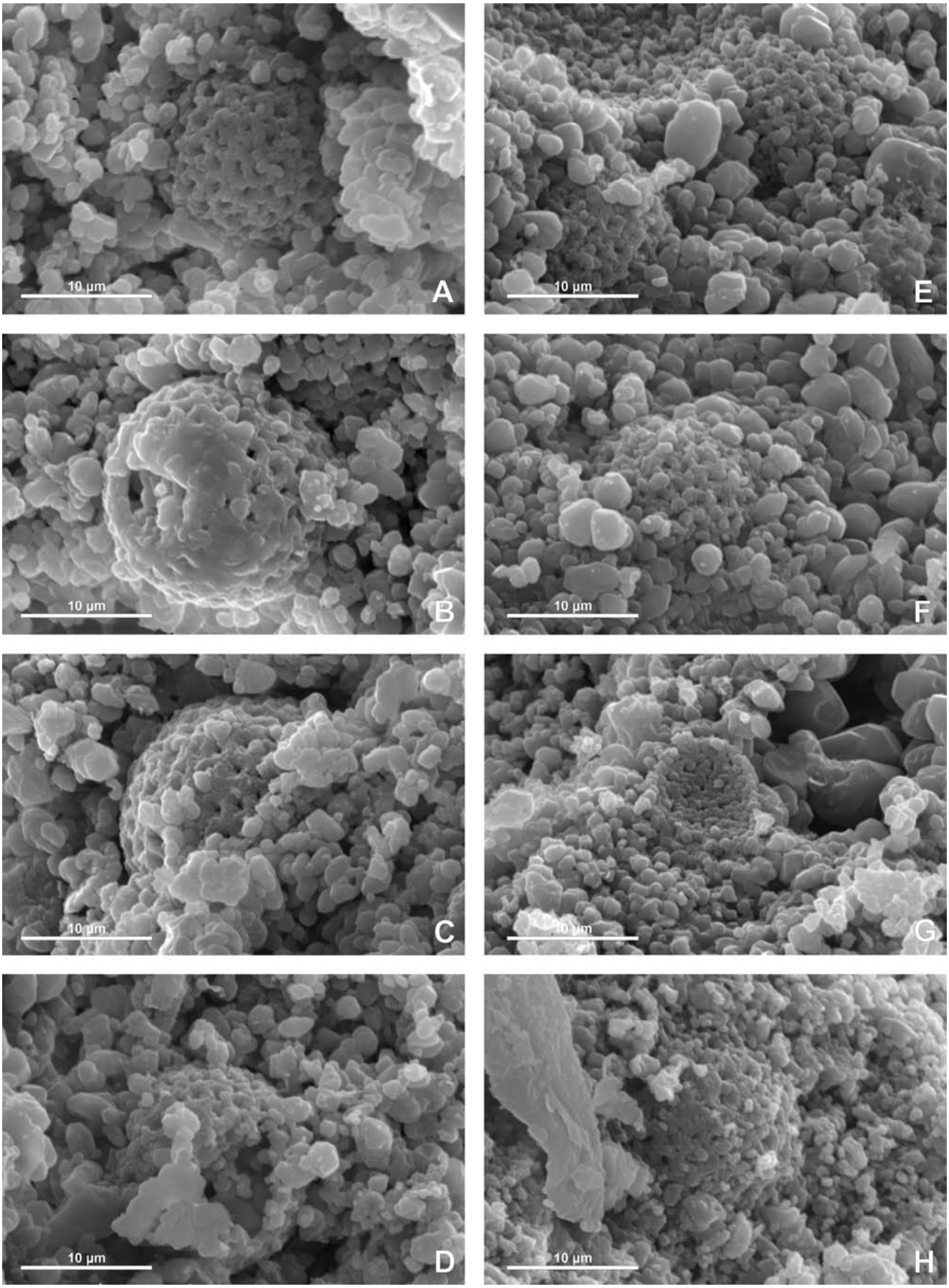
Fig. 8. *Operculodinella operculata* (Bramlette & Martini, 1964), Stevns Klint, as seen in SEM images of the fractured limestone surfaces. A–D, sample 8 (limestone surrounding MGUH 27366). E–H, sample 1 (phragmocone infilling of MGUH 27366); see Fig. 6 for location of samples.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bility in preservation and development of the matrix and larger components. This may result from a differentiated, patchy diagenesis. However, in places where diagenesis was minor, the phragmocone infilling and the limestone surrounding MGUH 27366 are virtually indistinguishable in terms of structure and composition (Figs 7, 8). In several cases, the matrix resembles that described and illustrated by Hansen (1990) from the Cerithium Limestone at Stevns Klint and from the time-equivalent 'dead layer' in Jylland (compare Hansen 1990, fig. 1 with Figs 8B and 8F herein).

Rare coccoliths, usually preserved as fragments, occur in all samples studied. Examination of these coccoliths has revealed late Maastrichtian taxa only (Danuta Peryt, Jens Wendler, personal communications 2005). Their significance is equivocal in the present discussion since most of the 'Cretaceous' coccoliths in the Cerithium Limestone have been argumented to represent short-term Danian survivors (Perch-Nielsen *et al.* 1982). However, the frequency of specimens may be of some importance because coccoliths are usually extremely common in the Maastrichtian chalk (e.g. Surlyk & Håkansson 1999, fig. 6) and markedly less so in the Cerithium Limestone.

The dominating components of the samples studied are calcareous dinocysts (Figs 7, 8), usually referred to as 'calcispheres' in earlier papers (e.g. Bromley 1979). Many specimens are coated by minute calcite crystals, rendering identification of their original ultrastructure and taxonomic assignment impossible (cf. Bromley 1979). The best-preserved dinocysts were found in samples 1 and 8 (Fig. 7A–D).

No taxonomic identification of the calcareous dinocysts was attempted, except for a distinctive form referred to as *Operculodinella operculata* (Bramlette & Martini, 1964) (Fig. 8A–H). The morphology of the specimens studied fully corresponds to the descriptions and SEM illustrations in Perch-Nielsen (1969, pl. 34, fig. 9), Jafar (1977, fig. 2, 1a, b & fig. 3, 4a–d), Gaździcka (1978, pl. 41, figs 3–4), Willems (1996, pl. 2, fig. 20), and Hildebrand-Habel & Streng (2003, pl. 4, figs 8–9). The species was formerly assigned to the genus *Thoracosphaera* (Bramlette & Martini 1964; Perch-Nielsen 1969, 1979 a, b; Perch-Nielsen *et al.* 1982; Jafar 1977; Gaździcka 1978).

According to Perch-Nielsen *et al.* (1982, p. 355): "*Thoracosphaera* is consistently present in Maastrichtian sediments in lower latitude sites, such as Caravaca and El Kef, and becomes common shortly above the boundary in these sections. It is virtually absent in higher latitude localities, such as Stevns and at DSDP Site 524, and starts appearing just above the boundary, increasing in importance upsection. The appearance of *Thoracosphaera* can be used as a marker for the Cretaceous/Tertiary boundary in high latitudes; in low latitudes, its sharp increase in abundance can serve the same purpose". Kienel (1994) did not found *Operculodinella operculata* in the upper Maastrichtian of Stevns Klint either. However, the species occurs as an extremely rare component of the dinocyst associations in the topmost Maastrichtian strata of North Germany (Kienel 1994) and eastern Poland (Gaździcka 1978), not far from the study area.

A single specimen of *O. operculata* has been illustrated from the Maastrichtian part of the Stevns Klint section by Wendler & Willems (2002, fig. 3G). It is from their sample Fi3, taken 2 cm below the Fish Clay (Wendler & Willems 2002, fig. 4). This record is taken here as evidence of the latest Maastrichtian appearance of *O. operculata* in the Stevns Klint area, although the possibility that the specimen has piped down via one of the minute burrows descending from the base of the Fish Clay (Ekdale & Bromley 1984, p. 688, fig. 6) cannot be excluded.

Rare specimens of *Operculodinella operculata* have been identified in samples 8 (Fig. 6A) and 1 (Fig. 6C). Five specimens in total come from sample 1 from the phragmocone infill of MGUH 27366 (four of them are illustrated in Fig 8E–H). No data on the total number of individuals of *O. operculata* from the Maastrichtian chalk are available in Wendler & Willems (2002). However, the evidence published to date indicates that the species is extremely rare in the Maastrichtian at Stevns Klint. Thus, *O. operculata* is still regarded herein as an informal guide fossil for the Danian part of the Stevns Klint succession. Consequently, its presence in the phragmocone infill of MGUH 27366 is suggestive of a Danian age of the latter.

Stable isotopic data

Two samples were analysed for oxygen and carbon stable isotopes: sample 7 from interior of the phragmocone, and sample 10 from the limestone outside the ammonite (see Figs 6A, C for sample location). For sample 7, the $\delta^{18}O$ value is –1.195 and $\delta^{13}C$ value is 1.382; for sample 10, $\delta^{18}O$ value is –1.392 and $\delta^{13}C$ is 1.524. These results can be compared with fine-fraction stable isotope curve for the Stevns Klint succession (Hart *et al.* 2004, fig. 4; redrawn herein in Fig. 9).

The $\delta^{18}O$ values for the phragmocone and the matrix surrounding the ammonite are of no significance to the present problem as the Maastrichtian and Danian parts of the oxygen curve of Hart *et al.*

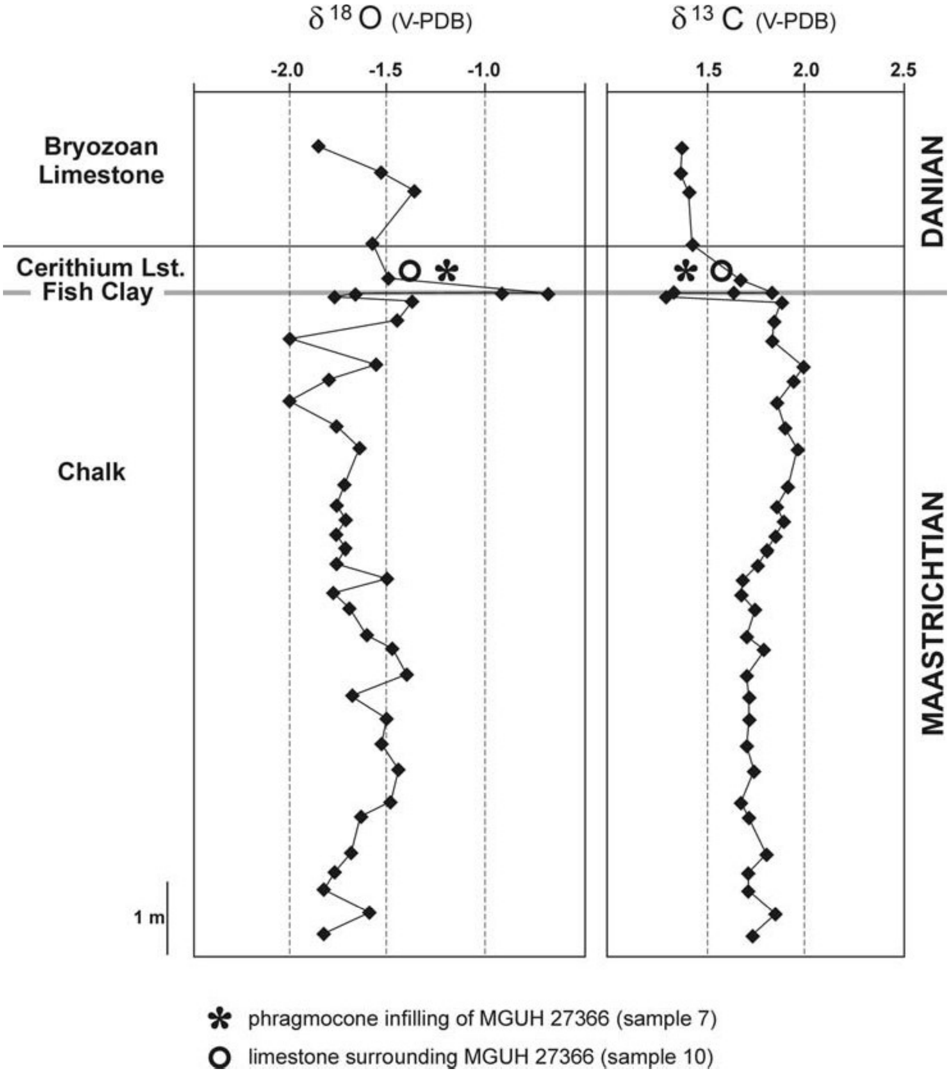

Fig. 9. δ^{18}O and δ^{13}C values for the infilling of the phragmocone of MGUH 27366 and for the limestone outside the specimen, compared with fine-fraction δ^{18}O and δ^{13}C curve for the Stevns Klint succession (modified from Hart *et al.* 2004, fig. 4).

(2004) do not differ significantly, except for a positive anomaly at the K–Pg boundary itself (Fig. 9). In contrast, the δ^{13}C value for the ammonite infilling matches the values for the Danian segment of the curve much better than the more positive Maastrichtian values (Fig. 9). This is additional support for the interpretation of MGUH 27366 as an indigenous Danian ammonite, although it is based on the single measurement only.

MGUH 27366 as an indigenous Danian ammonite

In summary, the specimen MGUH 27366 is complete and bears no physical traces of reworking. Its infilling is indistinguishable from the surrounding Danian matrix, yields a 'Danian' isotopic signal, and contains a calcareous dinocyst, typical of Danian strata in the area. All this suggests that MGUH 27366 is an indigenous Danian ammonite.

The ammonite specimens embedded in the topmost Maastrichtian chalk at Stevns Klint are always completely filled with sediment. An interpretation of MGUH 27366 as a reworked Cretaceous fossil would imply the following series of events: 1) filling of the specimen with Maastrichtian chalk; 2) ammonite reworking into the Danian and removal (at least partial) of the original infilling from its interior; 3) refilling of the ammonite conch with a new, Danian sediment. This complicated scenario is rather improbable. Cephalopod shells or moulds with many generations of internal sediment do occur in the fossil record (e.g. Kennedy & Garrison 1975, fig. 8; Henderson & McNamara 1985, figs 1, 9). However, the origin of such multiple infills seems to be typically related to (multiple) mechanical or biologically mediated punctures in the outer wall of the cephalopod conchs (Henderson & McNamara 1985). This mechanism can be excluded for MGUH 27366 as the only damages of its surface are those related to handling of the specimen (see above).

Evidence from calcitic macrofossils

The postulated indigenous nature of MGUH 27366 does not imply that the remaining ammonites from the Cerithium Limestone belong to the same category. More general clues for reconstruction of the taphonomic conditions across the K–Pg boundary at Stevns Klint are thus needed to interpret their origin. These clues are provided by fossils of biota with calcitic skeletons: brachiopods (mostly micromorphic), bryozoans and calcitic bivalves. Representatives of these three groups occur in masses in the topmost Maastrichtian chalk at Stevns Klint (e.g. Rosenkrantz 1939; Rasmussen 1971; Surlyk 1972, 1997; Bromley 1979; Heinberg 1999). In contrast, they are either absent or very rare in the Cerithium Limestone and its time-equivalents in Jylland (Jessen & Ødum 1923; Johansen 1987; Håkansson & Thomsen 1999).

Table 1

Sample	Weight (kg)	Calcitic bivalves	Ammonites
No. 2. Rødvig	12	1 *'Ostrea'*	–
No. 5. Rødvig	?	1 *Spondylus*	–
No. 6. Rødvig	7	1 *Syncyclonema nilsoni*	–
No. 10. Klintegård	2.6	–	1 *Baculites**
No. 11. Klintegård	1.6	–	1 *Baculites*
No. 16. Holtug	?	–	1 *Baculites* *
No. 17. Holtug	0.3	1 *Pycnodonte*	–
No. 22. Barmhjertigheden	6	-	1 *Baculites*
No. 38. Knøsen	2.5	1 *'Ostrea'*	–
No. 39. Knøsen	2.5	1 *'Pecten'*	–
No. 47. Eskesti north	3	1 *Syncyclonema nilsoni*	1 *Hoploscaphites**
No. 52. Mandehoved south	2	-	1 *Baculites**
No. 59. Eskesti	4.5	-	1 *Baculites*
No. 60. Mandehoved north	13	-	1 *Baculites** 1 *Hoploscaphites**
No. 63. Holtug	8	1 *Lima*	–
Total:	Over 65	8 specimens	9 specimens

*specimens included in this study

Particularly worthwhile to emphasise is the total absence of brachiopods in the Cerithium Limestone which contrasts to their mass occurrence in the Maastrichtian chalk below (e.g. Rosenkrantz 1939; Rasmussen 1971; Surlyk 1972). According to Surlyk (1972), hundreds of brachiopod specimens may be found in washing residues from 10 kg samples of the topmost Maastrichtian chalk at Stevns Klint.

In contrast to brachiopods, bryozoans do occur sporadically in the Cerithium Limestone and in their time-equivalents in Jylland, but generally represent different taxa than those from the topmost Maastrichtian chalk (Håkansson & Thomsen 1999).

The calcitic bivalves also occur in both units, being, however, much commoner in the Maastrichtian chalk than in the Cerithium Limestone (Heinberg 1999). In fact only eight calcitic bivalves, the latter including two specimens of *Syncyclonema nilsoni*, one *Spondylus* sp., one *'Pecten'* sp., one *Lima* sp., one *Pycnodonte* sp., and two *'Ostrea'* sp. (Table 1) were found during processing of 64 bulk samples of the Cerithium Limestone from various localities during search for minute aragonitic bivalves (Heinberg 1999, 2005). Nine fragmentary ammonites, six of which are discussed in the present paper, were recorded among the associated non-bivalve fossils (Table 1). Thus the ammonites and calcitic bivalves seem to occur in equal numbers in the Cerithium Limestone.

Syncyclonema nilsoni is the commonest species among the calcitic bivalve assemblage from the topmost Maastrichtian indurated chalk (Heinberg 1999). This species should dominate in the calcitic bivalve assemblage of the Cerithium Limestone, if this was composed of specimens derived from the Maastrichtian chalk. This is not the case as there are only two individuals of *S. nilsoni* among the eight specimens of calcitic bivalves recovered from the bulk samples.

In the case of any significant reworking of Maastrichtian fossils into the Cerithium Limestone basins, the latter should be littered with remains of Maastrichtian calcitic brachiopods, bryozoans and calcitic bivalves. This is clearly not the case as the brachiopods do not occur in the Cerithium Limestone at all, and the remaining two groups are underrepresented there in comparison with their record in the topmost Maastrichtian chalk. Moreover, the rare Danian representatives of these groups seem to be dominated by other taxa than those from the Maastrichtian chalk.

These observations point against significant redeposition of the Maastrichtian macrofossils into the Cerithium Limestone. This seems hold true also for coccoliths (Perch-Nielsen *et al.* 1982). In consequence, not only the best-preserved specimen (MGUH 27366) but also the remaining ammonite fossils from the Cerithium Limestone are interpreted herein as indigenous Danian individuals. In other words, they are regarded to be representatives of the ammonite taxa which survived (for a short time) the K–Pg crisis.

Discussion and conclusions

Admittedly, none of the presented arguments for ammonite survival into the Danian is unequivocal. Most conservatively, it may be argued that only an ammonite individual with articulated aptychi, found in a Danian-age deposit, would provide a truly decisive argument in support of the survival hypothesis (Machalski 2002). However, the arguments assembled to date strongly point to short-term ammonite survival across the K–Pg boundary in Denmark. These cephalopods may have survive up to 0.2 Ma after the K–Pg event as this is the estimated age of the hardground truncating the Cerithium Limestone basins (Smit 2002).

It is worth noting that ammonite survival into the Danian has also been proposed for a baculitid/scaphitid faunule from the lowermost Danian unit IVf-7 of the Meerssen Member (Maastricht Formation) in the Netherlands (Smit & Brinkhuis 1996; Jagt 2002; Jagt *et al.* 2003; Smit 2002). Numerous baculitid specimens from this unit are preserved with their apertures intact, which makes it unlikely that these were redeposited (Jagt 2002; Jagt *et al.* 2003). An analysis of the calcareous nannoplankton and of the stable isotope composition of the sediment infills of some specimens of *Hoploscaphites constrictus* from unit IVf-7 (kindly loaned by John W.M. Jagt, Natuurhistorisch Museum Maastricht) is under way by the first author.

If ammonites actually did survive into the Danian, as suggested by data from Denmark and the Netherlands, they add to a growing list of possible short-term K–Pg survivors, identified worldwide, mostly amongst marine microfossils (e.g. Perch-Nielsen *et al.* 1982; Keller *et al.* 1993; MacLeod *et al.* 1997) but also 'non-avian' dinosaurs (Fassett *et al.* 2002). Their existence indicates that the K–Pg extinction was expanded in time. It also poses the question why short-time survivors failed to recover after surviving such extreme environmental conditions as postulated for the K–Pg boundary. Reference is made to Jablonski (2002) for a general treatment of phenomenon of the mass extinction survival without recovery.

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