

The last Mesozoic brachiopods

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A rich brachiopod fauna has been found in the topmost Maastrichtian chalk immediately below the Cretaceous–Paleogene (K–Pg) boundary clay at Stevns Klint, Denmark – the UNESCO World Heritage Site for the boundary. The brachiopods were obtained from the washing residue of a 25 kg bulk sample, Holtug-1. They represent the latest known Mesozoic brachiopod fauna, which lived in the Late Cretaceous Chalk Sea of northern Europe immediately before the cataclysmic boundary incident. The fauna comprises 28 mainly micromorphic species represented by 1967 individuals. This is more than the faunas obtained from the otherwise most benthos-rich parts of the Upper Cretaceous Chalk Group in terms of both number of species (richness) and individuals and includes the full range of morphological adaptations to life on the fine-grained seafloor recognised in the literature. The sample shows the highest richness compared to stratigraphically lower samples from Stevns Klint and is higher than in all other Danish sections where the K–Pg boundary is exposed. It is also higher than the richest samples from the densely sampled older Maastrichtian successions at Møns Klint, Denmark and at Hemmoor, northern Germany. The Chalk Sea was a unique macro-habitat for about 34 million years and the last Mesozoic brachiopods from Holtug-1 thus represent a climax in the long evolution of the very specialized brachiopod fauna of the chalk.

Keywords: Brachiopoda, Mesozoic, Maastrichtian, chalk, richness, Denmark

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The end-Mesozoic, Maastrichtian chalk of NW Europe contains a rich brachiopod fauna dominated by micromorphic species. Washing of 10–20 kg bulk samples of chalk from 42 Maastrichtian sections in Denmark have thus yielded at least 44 species represented by about 35,000 individuals (Surlyk 2025b). A 25 kg sample, Holtug-1 collected in the abandoned quarry Holtug, immediately below the Cretaceous–Paleogene (K–Pg) boundary at Stevns Klint marked by the black boundary clay, the Fiskeler Member, has yielded a rich brachiopod fauna. The aims of the study are:

- To examine the richness (number of species) and abundance (number of individuals) of this, the latest Mesozoic brachiopod fauna.
- To test if there are any changes in richness and abundance in the brachiopod fauna at the end of the Mesozoic Era.
- To investigate whether there are signs of selective decreases or other changes in the number of ecological, mode-of-life groups or higher taxonomic categories such as genera or families.

- To compare the Holtug-1 brachiopod fauna with faunas from other K–Pg localities in Denmark and to interpret similarities and differences in terms of richness and abundance.
- To compare this fauna with the otherwise richest fauna known from densely spaced sample series in a slightly shallowing up lower Maastrichtian succession at Møns Klint, Denmark and from a long mid-Maastrichtian sample series at Hemmoor, northern Germany.
- To compare the fauna from Holtug-1 with some of the richest brachiopod faunas described in the literature.

Geological setting and stratigraphy

The 14.5 km long coastal cliff Stevns Klint, Denmark is situated on the northern flank of the Ringkøbing-Fyn High which constitutes the southern margin of the Danish Basin (Fig. 1). The locality was designated a UNESCO World Heritage Site in 2014, illustrating

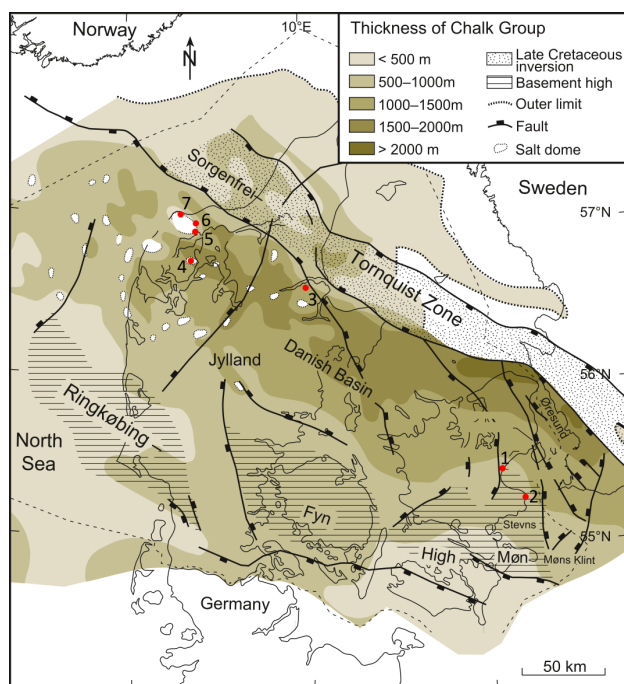


Fig. 1. Map showing the position of the localities with K-Pg boundaries exposed. 2 shows the position of the locality the Holtug-1 sample at Stevns Klint. 1: Karlstrup; 2: Holtug; 3: Dania; 4: Erslev; 5: Hov; 6: Kjølbjergård/Nye Kløv; 7: Bjerre.

the mass extinction at the Cretaceous–Palaeogene boundary (Damholt & Surlyk 2012). Stevns Klint was selected based on careful analyses of boundary sections worldwide demonstrating that it is the finest place to study the boundary, the boundary clay and the mass extinction event.

The succession exposed along the cliff belongs to the Møns Klint Formation (Fig. 2) (Surlyk *et al.* 2013). It comprises from below about 30 m of the relatively deep-water, poorly fossiliferous chalk of the Sigerslev Member, the lower part of which is gently mound-bedded (Surlyk *et al.* 2006; Anderskov *et al.* 2007). This passes gradually into the evenly bedded upper part of the member, which is interpreted as representing the deepest water chalk exposed in Denmark. The member is topped by a double incipient hardground representing a major fall in sea level. The hardground pair is overlain by up to 6 m of the mound-bedded, bryozoan-rich Højerup Member (Figs 2, 3). The top of this unit is wavy, reflecting the morphology of the mounds and thus the seafloor topography. The small basins between the mound crests are draped by a mainly 5–10 cm thick clay bed, the lowermost Danian Fiskeler Member. The base of the clay defines the Cretaceous–Palaeogene (K–Pg, Maastrichtian–Danian) boundary. It contains the famous iridium anomaly which heralded the lively and quite intense discussion of the cause of the mass extinction at the boundary (Alvarez *et al.* 1980, 1984).

Methods

The material described in this study was obtained by washing of a 25 kg bulk sample, Holtug-1, involving repeated heating and deep-freezing of the chalk in a supersaturated Glauber's Salt solution (see Surlyk 1972, 2025b). The sample was collected in the abandoned Holtug quarry immediately below the K–Pg boundary (Fig. 3). The washing residue was sieved through a stack of 2 mm, 1 mm and 0.5 mm sieves and yielded a rich fauna of very well-preserved small fossils, with juvenile specimens being strongly represented (Fig. 4). All figured specimens are stored in the collection of Østsjællands Museer/Museums of East Zealand OESM 14158–14183.

The brachiopod fauna

The Holtug-1 sample has yielded 28 brachiopod species, represented by 1967 individuals (Tables 1, 2). In addition, two specimens of the largest Maastrichtian brachiopod *Neolithyrina obesa* Sahni, 1925 were found immediately below the K–Pg boundary in the nearby Sigerslev chalk quarry (Surlyk 2025b).

Chrono-stratigraphy		Lithostratigraphy		Biostratigraphy			
				Forami-nifers (Rasmussen <i>et al.</i> 2005; Stenestad 1979)	Nannofossils (Perch-Nielsen 1979a, b)	 (Thomsen 1995)	
Palaeogene	Danian	Chalk Group	Stevns Klint Fm	Korsnæb Mb	P1c	D4	3
					P1b	D3	
				Rødvig Fm	Cerithium Limestone Mb	P1a	D2
			Fiskeler Mb		Pα		
						P0	D1
			Cretaceous	Maastrichtian	Chalk Group	Møns Klint Fm	Højerup Mb
Sigerslev Mb	<i>Pseudotextularia elegans</i>						

Fig. 2. Stratigraphic scheme covering the Maastrichtian–Danian succession exposed at Stevns Klint. Modified after Surlyk *et al.* (2006) and Rosenkrantz *et al.* (2021).



Fig. 3. The southern wall of the abandoned Holtug quarry showing the K-Pg boundary succession. The sample Holtug-1 was collected in the horizontal terrace adjacent to this quarry wall. Note that the hardground (HG) is horizontal in reality. H: uppermost Maastrichtian Højerup Member; F: basal Danian Fiskeler Member; C: lower Danian Cerithium Limestone Member; HG: lower Danian erosional hardground; K: lower Danian Korsnæb Member.

The richness (number of species) in Holtug-1 is much higher than the relatively benthos-poor chalk from the upper Sigerslev Member at Stevns Klint which is interpreted as representing the deepest water chalk in Denmark and higher than samples from the relatively shallow water, benthos-rich lower Maastrichtian chalk of Denmark at Møns Klint (Surlyk 1972, 2005b). However, it is emphasized that deposition of all chinks exposed in Denmark took place in relatively deep water well below the photic zone.

The K-Pg boundary clay is or has been exposed in at least eight localities in Denmark, including Stevns Klint, Karlstrup, Dania, Erslev, Vokslev, Nye Kløv, Kjølbygård and Bjerre (Fig. 1). The topmost Maastrichtian chalk exposed at Stevns, the Højerup Member represents the shallowest, but still sub-photoc water depth, and is the most benthos-rich part of the

Chalk Group in Denmark. Karlstrup is located off the north-eastern end of the Ringkøbing-Fyn High and exposes somewhat deeper water facies and has a much lower content of brachiopods both in terms of richness and number of individuals (Table 3). The rest of the boundary localities are situated in the northern part of the Danish Basin characterized by relatively deep-water chalk, and the top Maastrichtian brachiopod faunas are rather poor in terms of both richness and abundance. The uppermost Maastrichtian sample, immediately below the boundary clay in the most densely sampled locality, Nye Kløv has yielded 14 species represented by only about 30 specimens (Surlyk & Johansen 1984; Johansen 1987, figs 6, 7). This stands in strong contrast to the Holtug-1 fauna which has yielded 28 species represented by as many as 1967 individuals.

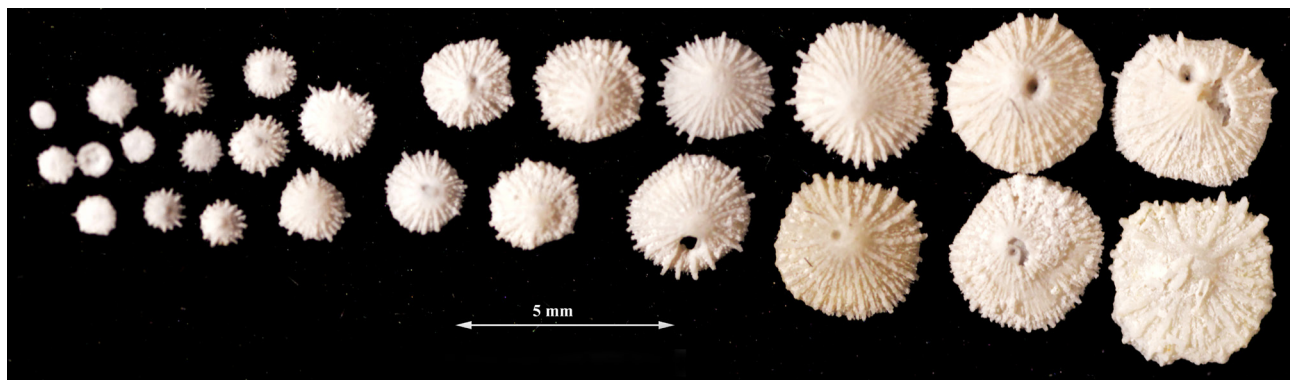


Fig. 4. *Isocrania sendeni* Simon, 2007 obtained from Holtug-1. The figure shows the presence of all growth stages of the species from sub-millimetre sized juveniles to adults. Valves of *I. sendeni* are commonly bored by gastropods as shown by several of these specimens.

Table 1. Brachiopod species in Holtug-1

<i>Ancistrocrania tubulosa</i> (Nielsen, 1909)	1 ind.	<i>Dalligas nobilis</i> Steinich 1968	11 ind.
<i>Novocrania?</i> sp.	1 ind.	<i>Ruegenella humboldtii</i> (von Hagenow, 1842)	5 ind.
<i>Isocrania sendeni</i> Simon 2007	175 ind.	<i>Dracius carnifex</i> Steinich, 1967	7 ind.
<i>Cretirhynchia</i> sp.	71 ind.	<i>Argyrotheca hirundo</i> (von Hagenow, 1842)	9 ind.
[<i>Homaletarhynchia limbata</i> (von Schlotheim, 1813)		<i>Bronnothyris stevensis</i> (Nielsen, 1928)	294 ind.
<i>Cretirhynchia retracta</i> (Roemer, 1841)]		<i>Bronnothyris bronnii</i> (Roemer, 1841)	11 ind.
<i>Thecidea papillata</i> (von Schlotheim, 1813)	13 ind.	<i>Bronnothyris coniuncta</i> Steinich, 1965	6 ind.
<i>Thecidea recurvirostra</i> (Defrance, 1828)	29 ind.	<i>Bronnothyris</i> aff. <i>coniuncta</i> Steinich, 1965	7 ind.
<i>Carneithyris subcardinalis</i> (Sahni, 1825)	56 ind.	<i>Bronnothyris?</i> cf. <i>vonkoeneni</i> (Nielsen, 1928)	4 ind.
<i>Terebratulina chrysalis</i> (von Schlotheim, 1813)	165 ind.	<i>Aemula inusitata</i> Steinich, 1968	93 ind.
<i>Terebratulina longicollis</i> Steinich, 1965	219 ind.	<i>Aemula</i> sp.	27 ind.
<i>Terebratulina faujasii</i> (Roemer, 1841)	281 ind.	<i>Scumulus inopinatus</i> Steinich, 1968	98 ind.
<i>Gyrosoria gracilis</i> (von Schlotheim, 1813)	48 ind.	<i>Leptothyrellopsis polonicus</i> Bitner & Pisera, 1979	182 ind.
<i>Gisilina jasmundi</i> Steinich, 1965	6 ind.	<i>Magas chitoniformis</i> (von Schlotheim, 1813)	3 ind.
<i>Meonia semiglobularis</i> (Posselt, 1841)	107 ind.	28 sp.	1967 ind.
<i>Rugia stenius</i> Surlyk 2025	38 ind.		

Novocrania? sp. is a dorsal valve of a juvenile craniid brachiopod, which may be related to the genus *Novocrania*. *Cretirhynchia retracta* (Roemer, 1841) and *Homaletarhynchia limbata* (von Schlotheim, 1813) are only represented by juveniles and are listed as *Cretirhynchia* sp. Most or almost all probably belong to *C. retracta* as this is by far the most common rhynchonellid brachiopod in the Maastrichtian chalk of Denmark. *Aemula* sp. is a new species, which will be described elsewhere. It was first illustrated in Surlyk (1974). The material of *Bronnothyris* aff. *coniuncta* is too sparse to justify erection of a new species. It is characterised by the ribs which extend beyond the anterior commissure. *Bronnothyris?* cf. *vonkoeneni* (Nielsen, 1928) is only represented by the illustrated shell and a few large fragments. The genus name is followed by a ? because only one complete specimen was obtained from the sample and opening of the shell to check if it belongs to *Argyrotheca* or *Bronnothyris* must wait finds of more specimens. It appears to be closely related to other species of *Bronnothyris* – the difference between the two genera is small and is in our opinion a case of oversplitting. The specimen illustrated by Nielsen (1928) has a more extended hinge margin, but the outline of the shell is on the other hand described as hemispherical just like the specimen shown here. The species was recorded from all of the Danian and also from the Selandian Lellinge Greensand Formation (Nielsen 1928).

The term ‘individual’ is used for the number of complete shells plus the largest number of either ventral or dorsal valves, giving a minimum number of individuals (Surlyk 1972). The term ‘specimen’ is used as a general term for any identifiable shell, valve or large fragment. As an example, the 175 individuals of *Isocrania sendeni* Simon, 1967 recorded in Holtug-1, are based on 336 specimens.

The brachiopod fauna of Holtug-1 is strongly dominated by micromorphic species (Figs 4–8). Medium and large-sized species are almost only represented by mm-sized juvenile specimens of *Cretirhynchia retracta* (Roemer, 1841), *Homaletarhynchia limbata* (von Schlotheim, 1813), and *Carneithyris subcardinalis* (Sahni, 1925), by a few adults of *Ruegenella humboldtii* (von Hagenow, 1842), and by the three hemispherical species *Gyrosoria gracilis* (von Schlotheim, 1813), *Magas chitoniformis* (von Schlotheim, 1813) and *Thecidea papillata* (von Schlotheim, 1813). The fauna fits well into Assemblage 1, the ‘standard’ brachiopod fauna

of the Maastrichtian chalk as identified in Hemmoor, northern Germany (Surlyk & Schröder 2026). This assemblage is characterized by high species richness and abundance dominated by micromorphic species plus the medium-sized *Terebratulina chrysalis* (von Schlotheim, 1813). The presence in Holtug-1 of the medium-sized hemispherical species *Gyrosoria gracilis* and *Magas chitoniformis* shows that it is transitional to assemblage 3 which is characterized by hemispherical species.

Out of the 44 brachiopod species described from the Maastrichtian chalk of Denmark, 12 species became extinct well below the K–Pg boundary, mainly in the early Maastrichtian (Surlyk 1984, 2025b). A total of 32 species have been recorded from the topmost Maastrichtian *stevensis*-*chitoniformis* brachiopod Zone at Stevns Klint (Surlyk 2025b). The presence of one of these is uncertain and the actual number is thus most likely 31 species. Of these, 13 are very rare, leaving only 18 species which are relatively common to very

Table 2. Brachiopod species from Holtug-1 ranked after number of individuals

<i>B. stevensis</i>	298	<i>C. subcardinalis</i>	56	<i>D. carnifex</i>	7
<i>T. faujasii</i>	281	<i>G. gracilis</i>	48	<i>G. jasmundi</i>	6
<i>T. longicollis</i>	219	<i>R. stenius</i>	38	<i>B. coniuncta</i>	6
<i>L. polonicus</i>	182	<i>T. recurvirostra</i>	29	<i>R. humboldtii</i>	5
<i>I. sendeni</i>	175	<i>Aemula</i> sp.	27	<i>B.?</i> cf. <i>vonkoeneni</i>	4
<i>T. chrysalis</i>	165	<i>T. papillata</i>	13	<i>M. chitoniformis</i>	3
<i>M. semiglobularis</i>	107	<i>D. nobilis</i>	11	<i>A. tubulosa</i>	1
<i>S. inopinatus</i>	98	<i>B. bronnii</i>	11	<i>Novocrania?</i> sp.	
<i>A. inusitata</i>	93	<i>A. hirundo</i>	9		
<i>Cretirhynchia</i> sp.	71	<i>B. aff. coniuncta</i>	7	Total	28 sp., 1967 ind.

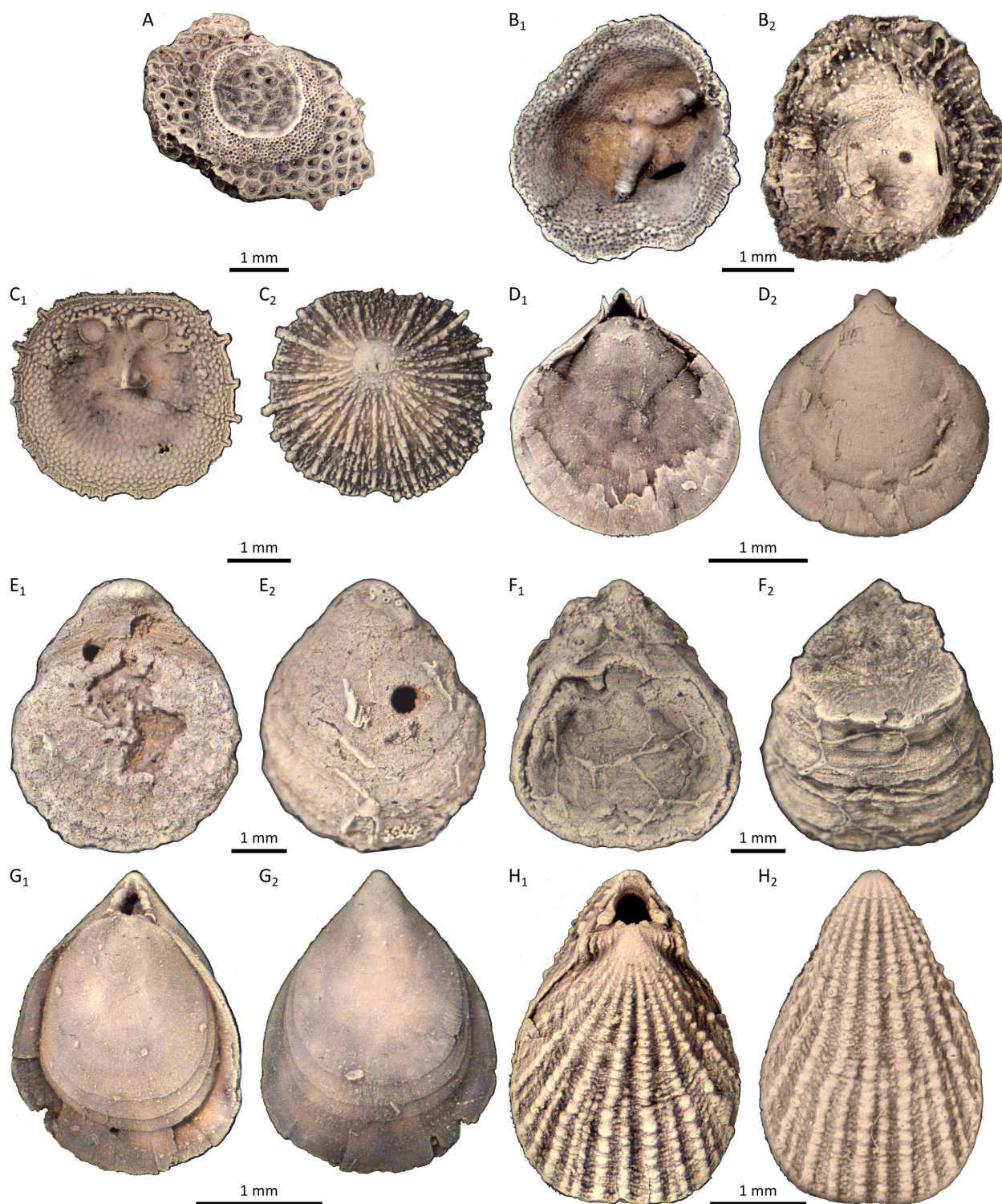


Fig. 5. A. *Ancistrocrania tubulosa* (Nielsen, 1909), ventral valve, inner side (OESM 14158). B. *Novocrania?* sp., B₁ dorsal valve inner side, B₂ dorsal valve outer side (OESM 14159). C. *Isocrania sendeni* Simon, 2007, dorsal valve, C₁ inner view, C₂ outer view (OESM 14160). D. *Cretirhynchia* sp. Juvenile specimen, representing *Cretirhynchia retracta* (Roemer, 1841) or possibly the much rarer *Homaletarhynchia limbata* (von Schlotheim, 1813), D₁ dorsal view, D₂ ventral view (OESM 14161). E. *Thecidea papillata* (von Schlotheim, 1813), E₁ dorsal view, E₂ ventral view (OESM 14162). F. *Thecidea recurvirostra* (Defrance, 1828), F₁ dorsal view, F₂ ventral view (OESM 14163). G. *Carneithyris subcardinalis* (Sahni, 1825), juvenile specimen, G₁ dorsal view, G₂ ventral view (OESM 14164). H. *Terebratulina chrysalis* (von Schlotheim, 1813), juvenile specimen. H₁ dorsal view, H₂ ventral view (OESM 14165).

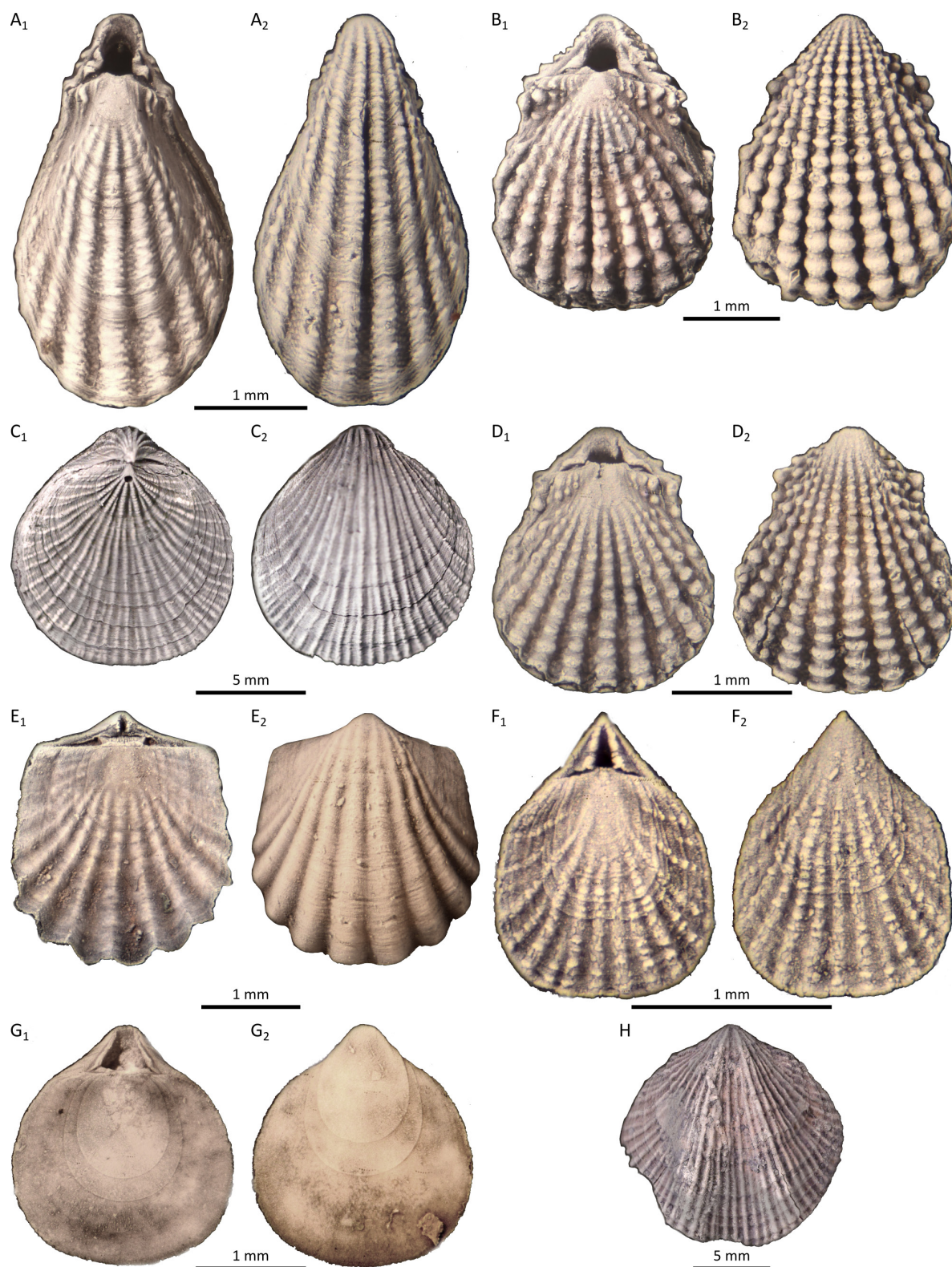


Fig. 6. A. *Terebratulina longicollis* Steinich, 1965, A₁ dorsal view, A₂ ventral view (OESM 14166). B. *Terebratulina faujasii* (Roemer, 1841), B₁ dorsal view, B₂ ventral view (OESM 14167). C. *Gyrosoria gracilis* (von Schlotheim, 1813), C₁ dorsal view, C₂ ventral view (OESM 14168). D. *Gisilina jasmundi* Steinich 1965, D₁ dorsal view, D₂ ventral view (OESM 14169). E. *Meonia semiglobularis* (Posselt, 1841), E₁ dorsal view, E₂ ventral view (OESM 14170). F. *Rugia stenius* Surlyk 2025, F₁ dorsal view, F₂ ventral view (OESM 14171). G. *Dalligas nobilis* Steinich 1968, G₁ dorsal view, G₂ ventral view (OESM 14172). H. *Ruegenella humboldtii* (von Hagenow, 1842) (OESM 14173).

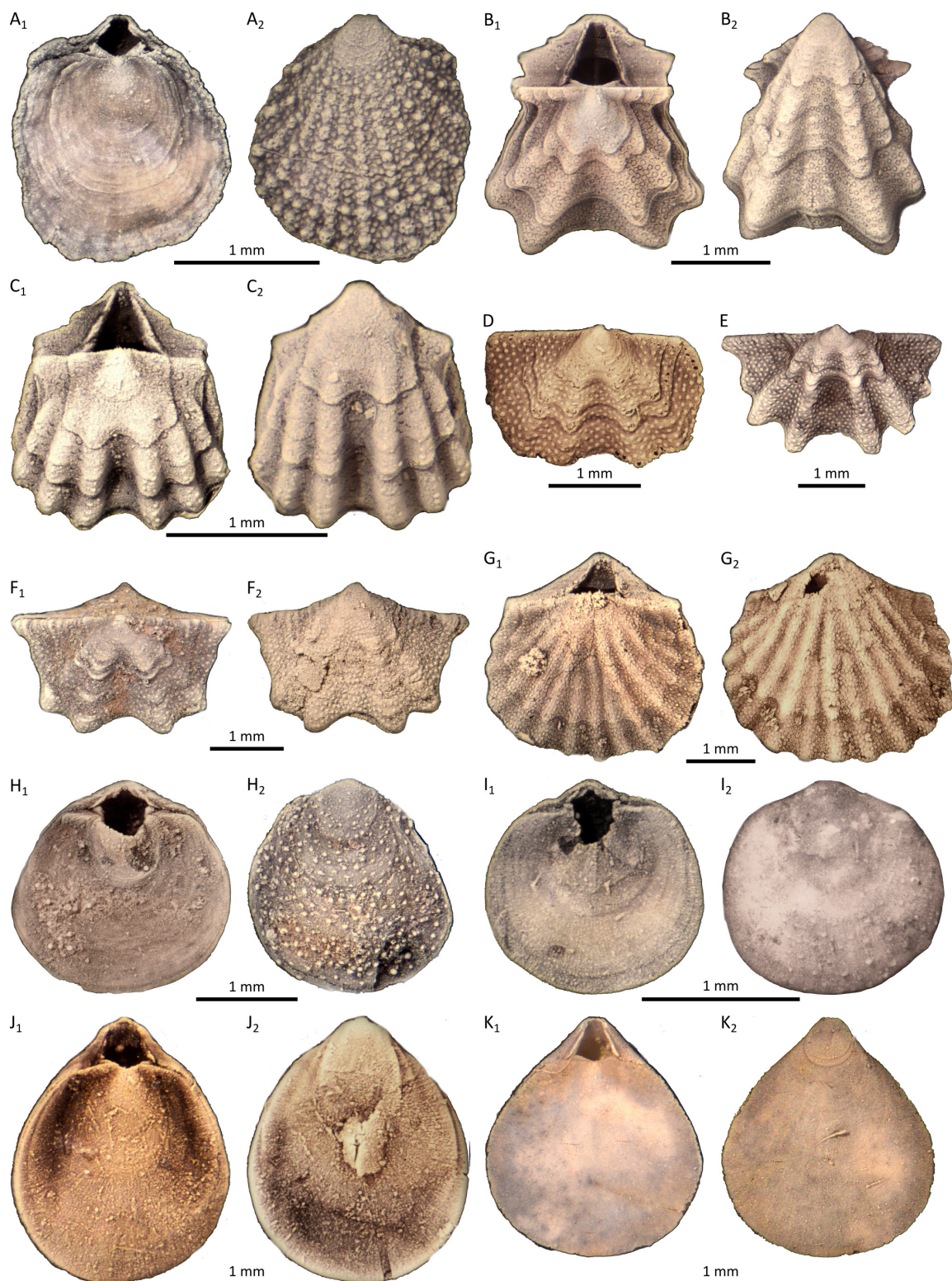


Fig. 7. A. *Dracius carnifex* Steinich 1967, A₁ dorsal view, A₂ ventral view (OESM 14174). B. *Argyrotheca hirundo* (von Hagenow, 1842), B₁ dorsal view, B₂ ventral view (OESM 14175). C. *Bronnothyris stevensis* (Nielsen, 1928), C₁ ventral view, C₂ dorsal view (OESM 14176). D. *Bronnothyris brononii* (Roemer, 1841), ventral view (OESM 14304). E. *Bronnothyris* aff. *coniuncta* (Steinich, 1965), ventral view (OESM 14178). F. *Bronnothyris coniuncta* (Steinich, 1965), F₁ dorsal view, F₂ ventral view (OESM 14177). G. *Bronnothyris*? cf. *vonkoeneni* (Nielsen, 1928), G₁ dorsal view, G₂ ventral view (OESM 14179). H. *Aemula inusitata* Steinich, 1968, H₁ dorsal view, H₂ ventral view (OESM 14180). I. *Aemula* sp., I₁ dorsal view, I₂ ventral view (OESM 14181). J. *Scumulus inopinatus* Steinich, 1968, J₁ dorsal view, J₂ ventral view (OESM 14182). K. *Leptothyrellopsis polonicus* Bitner & Pisera 1979, K₁ dorsal view, K₂ ventral view (OESM 14183).

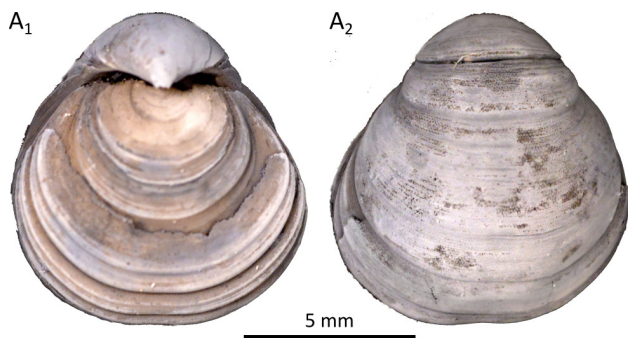


Fig. 8. *Magas chitoniformis* (von Schlotheim, 1813), A₁ dorsal view, A₂ ventral view (OESM 14184).

common at Stevns Klint. Only a few of the species collected over many years at Stevns Klint are not represented in Holtug-1. Three of these are cemented with all of the ventral valve to large hard substrates such as oyster shells and echinoid tests, 3 are exceedingly rare and 2 of those are large with large pedicle openings, suggesting attachment to large, hard substrates which are rare in the chalk and almost never represented in the sample washing residues. Thus, Holtug-1 essentially includes all those species which can be expected as occurring in the sample, where large, hard substrates are missing with very few exceptions.

The Holtug-1 fauna includes 17 micromorphic, seven larger, mainly free-living species, three species were cemented to the substrate, mainly large skeletal fragments and one, *T. chrysalis* is interpreted as a generalist possessing a root-like pedicle which enabled attachment to a great variety of substrates, including the soft chalk ooze itself (Surlyk 1972). Species which are morphologically similar to *T. chrysalis* have existed from the Jurassic until today under a variety of names, illustrating the generalist nature of this species and its adaptability to attachment to all kinds of substrates.

The associated benthic invertebrate fauna in Holtug-1 is equally rich and very well preserved although the echinoderms to a large extent are represented by isolated plates or columnae. In addition to brachiopods the fauna comprises: Foraminifers, calcareous sponges, polychaetes, cirripeds, ostracods, bryozoans, bivalves, ammonites, echinoids, crinoids, asteroids, ophiuroids, sharks and bony fish. Borings in shells are common and coprolites also occur. A fragment of finger bone of a small-bodied pterosaurs with a wingspan of less than 50 cm was found where the Holtug-1 sample was subsequently collected (Milàn *et al.* 2025) and was the basic inspiration for collecting this sample. The fauna is a good example of the main faunal elements of the Chalk Sea and essentially all the groups of this characteristic macrohabitat are represented. It is our ambition to describe this fauna in the hopefully not too distant future.

Localities exposing the K–Pg boundary in Denmark

The K–Pg boundary is or has been exposed at a number of localities in Denmark. They have all been studied for brachiopods except for Vokslev. The brachiopod faunas obtained from washed bulk samples from Karlstrup, Dania, Erslev, Nye Kløv, Kjølbjgård and Bjerre have been studied, some from closely spaced sample series (Fig. 1, Table 3).

Bjerre

A single sample was collected immediately below the boundary clay. It contained 6 species represented by 15 individuals.

Dania

A long series of 16 rather small samples collected for ostracods by N.O. Jørgensen is analysed for brachiopods. The whole section has yielded a total of 16 species represented by 302 individuals. The highest number of 120 individuals was found in a sample just below the K–Pg boundary.

Erslev

The brachiopod fauna from single sample yielded 12 species represented by 23 individuals.

Karlstrup

Five samples have been collected in mounded bryozoan-rich chalk and have yielded 19 species represented by 2048 individuals. The richest samples contained 15 species with 514 individuals and 14 species with 858 individuals. The positions of the samples are shown in Surlyk (2025b, fig. 5)

Kjølbjgård

Several samples have been analysed for brachiopods, but the boundary clay was not accessible at the time of collection and no samples were collected near the clay.

Nye Kløv

The brachiopod fauna from the chalk at this locality is known from a very dense series of samples (Surlyk & Johansen 1986; Johansen 1987, fig. 7). The whole succession has yielded a relatively large number of species totaling 27, reaching a maximum of about 20 in a sample 1 m below the boundary clay, but most species are represented by very few specimens. The number of specimens is markedly smaller than at Stevns Klint, reaching a maximum of about 50 in a sample collected about 50 cm below the boundary clay.

The stratigraphic succession of the samples shows a similar trend as at Stevns Klint with as few as 5 to 10 species and only 10–20 specimens in the lowest samples about 4–5 m below the boundary, corresponding to the equally poor fauna in the upper Sigerslev Member at Stevns Klint. Richness and abundance increase up-section to reach a maximum close to the boundary. Johansen (1987, fig. 7) did not give exact numbers for richness and abundances so the numbers quoted here are read out of the stratigraphic diagram. It is remarkable that large-sized species are represented by two species which are only represented by mm-sized juveniles and one of these, *C. subcardinalis* was found only in the two uppermost samples. Medium-sized species are represented by six species, two of which were hemispherical (*M. chitoniformis* and *G. gracilis*), probably secondarily free living or specialised to attachment to large siliceous sponges (Surlyk 1972, 2025a), and two very rare species which were cemented to large, hard substrates. The medium- and large-sized species are almost all restricted to the uppermost Maastrichtian samples. The remaining 19 species are all micromorphic. The assemblage structure in the lower part of the succession corresponds to assemblage 2 recognised at Hemmoor, comprising almost only micromorphic

species (Surlyk & Schröder 2026). It is quite similar to the fauna of the deep-water upper Sigerslev Member at Stevns Klint, whereas the assemblage in the highest samples corresponds to assemblage 1, the ‘standard’ chalk brachiopod fauna also characterising Holtug-1 and comprising micromorphic species with a few mainly uncommon medium-sized notably hemispherical species.

Hvidskud, Møns Klint and Hemmoor, Northwestern Germany

Faunas obtained from a long sample series collected in the lower Maastrichtian cliff section Hvidskud, Møns Klint (Fig. 1) are the richest and show the highest number of individuals in the Danish chalk next to Holtug-1 (Surlyk 1972). All samples contain more than 10 species reaching the highest numbers of 20, 17 and 15, respectively, in a slightly upwards shallowing part of the section topped by a thin hardground (Surlyk 1972, fig. 14). This is still far below the 28 species found in Holtug-1.

Comparison with a long sample series from the chalk at Hemmoor, northern Germany gives a similar result (Surlyk & Schröder 2026). The highest species number is 15 and this is only recorded in very few samples. Most of the Hemmoor samples contain

Table 3. Brachiopod richness and abundance at Danish K–Pg boundary sections

Bjerre. Immediately below the K-Pg boundary	6 sp.	15 ind.
Dania 2. Marl 4.5 m above floor of quarry	6 sp.	19 ind.
Dania 4. Marl. 13.5 m below the K-Pg boundary, 6 m above floor	3 sp.	10 ind.
Dania 5. 9.5 m below the K-Pg boundary. 10 m above floor	4 sp.	9 ind.
Dania 6. 8 m below the K-Pg boundary. 11.5 m above floor	4 sp.	7 ind.
Dania 7. 4.5 m below the K-Pg boundary. 15 m above floor	7 sp.	18 ind.
Dania 8. 1.75 m below the K-Pg boundary. 17.75 m above floor	7 sp.	7 ind.
Dania 9. 0.5 m below the K-Pg boundary. 19.5 m above floor	5 sp.	12 ind.
Dania 10. Boundary clay level	2 sp.	3 ind.
Dania 11. 20 m above floor	5 sp.	48 ind.
Dania 12. 21 m above floor	9 sp.	120 ind.
Erslev	12 sp.	83 ind.
Kjølbygård	10 sp.	56 ind.
The Kjølbygaard Marl is situated 11.5 m below the K-Pg boundary clay		
Kjølbygård. 1 m below the Kjølbygård Marl	6 sp.	15 ind.
Kjølbygård Marl	3 sp.	19 ind.
Kjølbygård. 1 m above the Kjølbygård Marl	6 sp.	20 ind.
Kjølbygård. 2 m above the Kjølbygård Marl	2 sp.	2 ind.
Karlstrup 1. Just above F1	10 sp.	260 ind.
Karlstrup 2. 5 kg. Betw. F2 and F3	14 sp.	858 ind.
Karlstrup 3. 5 kg. Betw. F3 and F4	15 sp.	584 ind.
Karlstrup 4. 5 kg. Betw. F4 and F5	10 sp.	132 ind.
Karlstrup. F5 Immediately below the K-Pg boundary	7 sp.	10–15 ind.
Karlstrup. Section 1, sample 1	13 sp.	89 ind.
Stevns 1. Immediately below the K-Pg boundary	13 sp.	254 ind.
Stevns 2. 1.4 m below the K-Pg boundary	13 sp.	1880 ind.
Stevns 3. 3.5 m below the K-Pg boundary	15 sp.	148 ind.
Stevns 5. 4.5 m below the K-Pg boundary	7 sp.	59 ind.
Stevns 5. 6.5 m below the K-Pg boundary	6 sp.	25 ind.
Stevns 6. Ca 30 m below the K-Pg boundary	5 sp.	10 ind.
Stevns 7. Ca 32 m below the K-Pg boundary	11 sp.	40 ind.

The samples from the Dania quarry were collected for ostracods and are much smaller than the rest of the samples, which mainly weighed 5 kg. Positions of the Karlstrup samples are shown in Surlyk (2025b, fig. 5).

10 or less species.

It is thus clear that the last Mesozoic brachiopod fauna represented by Holtug-1 is by far the richest known from a single sample of the north European chalk.

Discussion

The micromorphic brachiopod fauna characterising the Holtug-1 sample started to develop in the late Campanian to reach a climax in the Maastrichtian chalk. This is interpreted as reflecting the evolution of a rich fauna of delicate cheilostome and cyclostome bryozoans (Eckart Håkansson, pers. comm. 2026) which could serve as attachment for minute brachiopods on the very fine-grained chalk sea floor (Surlyk 1972). The brachiopods of the lower parts of the Upper Cretaceous Chalk Group are in contrast similar to the Jurassic and Early Cretaceous faunas dominated by medium to large-sized rhynchonellid, terebratulid and terebratellid species.

The presence of 17 micromorphic out of 28 brachiopod species in Holtug-1, combined with the near-absence of large-sized species, is a fine example of the evolution of this remarkable fauna. The large-sized species are only represented by juveniles of the same size as the micromorphic species. This is exemplified by the very common *Carneithyrus subcardinalis* (Sahni, 1925) and *Cretirhynchia retracta* (Roemer, 1841; Table 1).

The Chalk Sea of northern Europe was one of the longest ranging uniform macrohabitats in the geological record, lasting for about 34 million years, and covering a large area (e.g. Surlyk *et al.* 2003). This opened the possibility of evolution of the specialized micromorphic brachiopods which were able to find small skeletal fragments, notably bryozoans, in the otherwise very fine-grained chalk ooze. It is noteworthy that this evolutionary trend took place in a number of different higher order taxonomic groups. It is not a case of dwarfing as suggested by Ager (1965) for the abundant micromorphic species from the middle Danian carbonates at Faxe close to Stevns Klint. It is an example of specialization to a very fine-grained habitat type which was not normally accommodating pedunculate brachiopods.

A few species survived the mass extinction at the K-Pg boundary and rapidly gave rise to a somewhat similar fauna already in the early Danian by filling the vacant niches (e.g. Surlyk & Johansen 1984; Johansen 1987). It is interesting that several species which evolved in the latest Maastrichtian survived the boundary mass extinction. *Isocrania sendeni* (Simon, 2007) has recently been recorded from the lower and middle Danian limestones at Stevns Klint and Faxe, respectively (collection of S.L. Jakobsen). *Bronnothy-*

ris? cf. *vonkoeneni* (Nielsen, 1928) which is only represented by one shell and a few fragments in Holtug-1 is common in the Danian. Johansen (1987) recorded six species crossing the K-Pg boundary at Nye Kløv: *Isocrania costata* (probably *I. sendeni*), *Terebratulina* cf. *longicollis*, which in our opinion clearly belongs to *T. longicollis*, *Terebratulina chrysalis*, *Argyrotheca hirundo*, *Bronnothyris stevensis* and *Aemula inusitata*. It is important to note that the uppermost Maastrichtian is missing almost everywhere in the area of the North European Chalk Sea outside Denmark. So, the evolution of new species at the end of the Maastrichtian is not known from other areas.

High richness values are otherwise mainly found in Palaeozoic faunas from times when brachiopods were among the most important shelly marine benthic invertebrates. A number of studies highlighting a high richness include Curry & Williams (1985), Harper (2006), Halamski & Balinski (2013), Wright *et al.* (2022) and Gallagher & Harper (2023).

Williams & Curry (1985) described a rich fauna from the Lower Ordovician Tourmakeady Limestone in Ireland, comprising 45 species. It is the only one of the taxonomic studies listed here which gives information about sampling techniques. Many fossils in the formation had been silicified and bulk sampling followed by acid etching of over two tons of limestone “revealed an early Ordovician brachiopod fauna of unprecedented diversity, much of it previously undescribed” (Williams & Curry, 1985, p. 186). As in the other studies mentioned here, details on sample locations are lacking.

Wright *et al.* (2022) described the brachiopods from the Upper Ordovician Portrane Limestone Formation in eastern Ireland. Many of the fossils collected from that formation were extracted by dilute acetic acid. A significant fauna was thus found in a single silicified band and a total of about 70 taxa were recognised, taken to represent the formation as a whole.

Halamski & Balinski (2013) recorded 62 species represented by more than 1300 specimens from two Middle Devonian formations in the eastern Anti-Atlas of Morocco. Much of the material was assembled in connection with field mapping and the collections are therefore unlikely to represent a specific sampling protocol.

Gallagher & Harper (2023) described the rich brachiopod faunas from the Silurian (upper Llandovery – lower Wenlock) of the Pentland Hills in Scotland represented by five formations forming a regressive succession ranging from distal turbidite facies to continental deposits. A total of 53 species were recognised representing four different associations characterising different stages of the regression. However, no information on sampling techniques was provided, suggesting that the fossils were collected individually, although ‘nests’ are also men-

tioned.

Combined, these examples illustrate the brachiopod richness characterizing many Palaeozoic formations, but the faunas were rarely presented on a sample or bed-by-bed basis in relation to logged lithological sections. To a high extent such shortcomings reflect the fact that only few lithologies can be broken down in the way possible for many levels in the Chalk Group, allowing the superior resolution in analyses of the Late Cretaceous brachiopods. Obviously therefore, the high number of species reported in these studies cannot be directly compared to those of the Holtug-1 material. The studies of the Paleozoic faunas commonly included brachiopods collected over many years, and the richness may not be directly compatible with those retrieved from the chalk samples. On this background, Holtug-1 may take the prize of the highest number from a single sample. This is quite remarkable for a sample representing the last Mesozoic fauna from a time interval immediately predating the K-Pg boundary asteroid impact and postdating the onset of the Deccan volcanic province (e.g. Kale and Pande 2022).

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