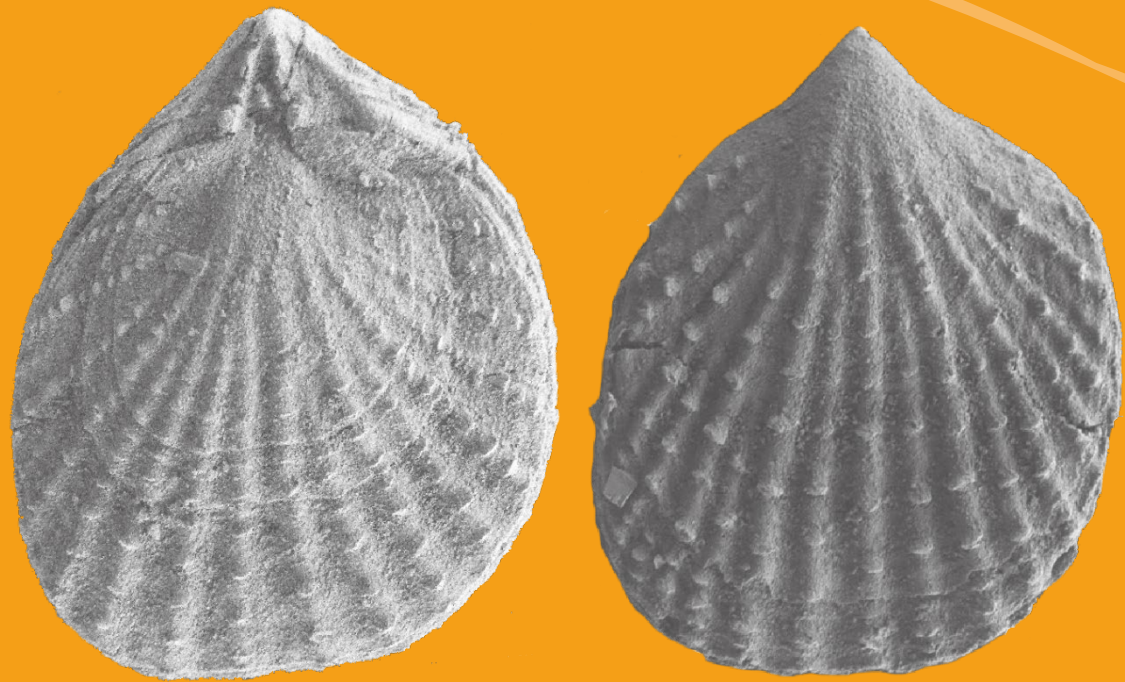


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Cover photo: SEM images of the brachiopod *Rugia stenius*. See this volume pp. 49–118: Surlyk, F.: Maastrichtian brachiopods from the chalk of Denmark.

Fauna of the Sæterdal Formation (Cambrian Series 2, Stage 4) of North Greenland (Laurentia)

JOHN S. PEEL



Geological Society of Denmark
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The fauna preserved in decalcified sandstones of the Sæterdal Formation (Cambrian Stage 4) of southern Peary Land, North Greenland (Laurentia) is dominated by the trilobites *Kootenia marcoui* and *Bonnina brennus*, which also occur in the equivalent dark carbonates and mudstones of the Henson Gletscher Formation to the west. They are associated with *Olenellus* and small ptychoparioid trilobites. Brachiopods compared to *Nisusia ancauchensis*, originally described from the Precordillera terrane in Argentina, show variation in shell morphology and the form of the pseudodeltidium. They occur together with *Kutorgina* cf. *cingulata*, which is conspicuous in the overlying Paralledal Formation, rare *Matutella* sp. and an indeterminate hyolithid.

Keywords: Trilobites, brachiopods, Cambrian Stage 4, North Greenland, Laurentia.

John S. Peel, [john.peel@pal.uu.se], Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE-75236 Uppsala, Sweden.

The Sæterdal Formation (Cambrian Series 2, Stage 4) of Peary Land, North Greenland, crops out in a narrow belt along the northern side of Wandel Dal from ‘Midsommersøer’ via Sæterdal to Paralleldal in the east (Fig. 1C; Ineson & Peel 1997). In the type area of Sæterdal the formation consists of about 130 m of recessive pale buff sandstones (Fig. 1A) lying between pale dolostones of the Aftenstjernesø and Paralleldal formations in steep cliffs above the dark, recessive mudstones and sandstones of the Buen Formation (Cambrian Stages 3–4), heralding the establishment of the Cambrian–Silurian carbonate platform that dominates southern Peary Land and much of northern Greenland to the west (Higgins et al. 1991a, b). The Wandel Dal outcrops of the formation are sub-parallel to strike but the pale sandstones of the formation interdigitate with dark mudstones and carbonates of the Henson Gletscher Formation in the ‘Midsommersøer’–Fimbuldal area, in which they form a prominent middle member (Fig. 1B), to the west. From a regional perspective, the Sæterdal Formation consists of a wedge of sandstones, probably transported seawards during severe storms and interrupting the deposition of the outer shelf–slope carbonates and mudstones that comprise the Henson Gletscher Formation (Higgins et al. 1991a, b). The Sæterdal Formation thins out 18 km to the east of the type section, where the Paralleldal

Formation directly overlies the Aftenstjernesø Formation (Ineson & Peel 1997).

The Sæterdal Formation is poorly fossiliferous but trilobites (Fig. 2) and brachiopods (Figs 3–6) may be locally abundant in the Sæterdal area where the moulds of the decalcified fossils display a distinctive orange brown colouration. Trilobites, including *Olenellus* Hall, 1861, indicate an early Cambrian age (Cambrian Series 2, Stage 4), with *Bonnina brennus* (Walcott, 1916) and *Kootenia marcoui* (Whitfield, 1884) documented by Blaker & Peel (1997) also in the Henson Gletscher Formation in outcrops to the west. Oryctocephalid trilobites definitive of the latest Cambrian Stage 4, *Ovatoryctocara granulata* assemblage (Blaker & Peel 1997; Geyer & Peel 2011; Peel et al. 2016) are not recorded from the Sæterdal Formation, likely indicating that the latter formation is slightly older than the *Ovatoryctocara granulata* assemblage of the Henson Gletscher Formation. However, this assemblage occurs in dark carbonates and mudstones in the Henson Gletscher Formation quite unlike the sandstones of the Sæterdal Formation, suggesting that the difference may be related to sedimentary facies. Similarly, the brachiopod fauna of the Sæterdal Formation lacks the organophosphatic linguliformean brachiopods that dominate the *Ovatoryctocara granulata* assemblage of the Henson Gletscher Formation in western Peary Land (Peel et al. 2016).

The present paper revisits the fauna of the Sæterdal Formation, additionally describing brachiopods, mainly *Nisusia* Walcott, 1905 and *Kutorgina* Billings, 1861, and a rare hyolithid. *Kutorgina* is abundant in the Paralleldal Formation some 20 km to the east (Popov et al. 1997) but was also described from the Bastion Formation of North-East Greenland by Poulsen (1932) and

Skovsted & Holmer (2005) and from the Wulff River Formation of Inglefield Land, North-West Greenland (Poulsen 1958). The fauna as a whole is similar in general composition and preservation to that of the lower Cambrian lower Parker Shale of Vermont documented by Shaw (1954, 1955).

Of particular interest is the occurrence in the Sæter-

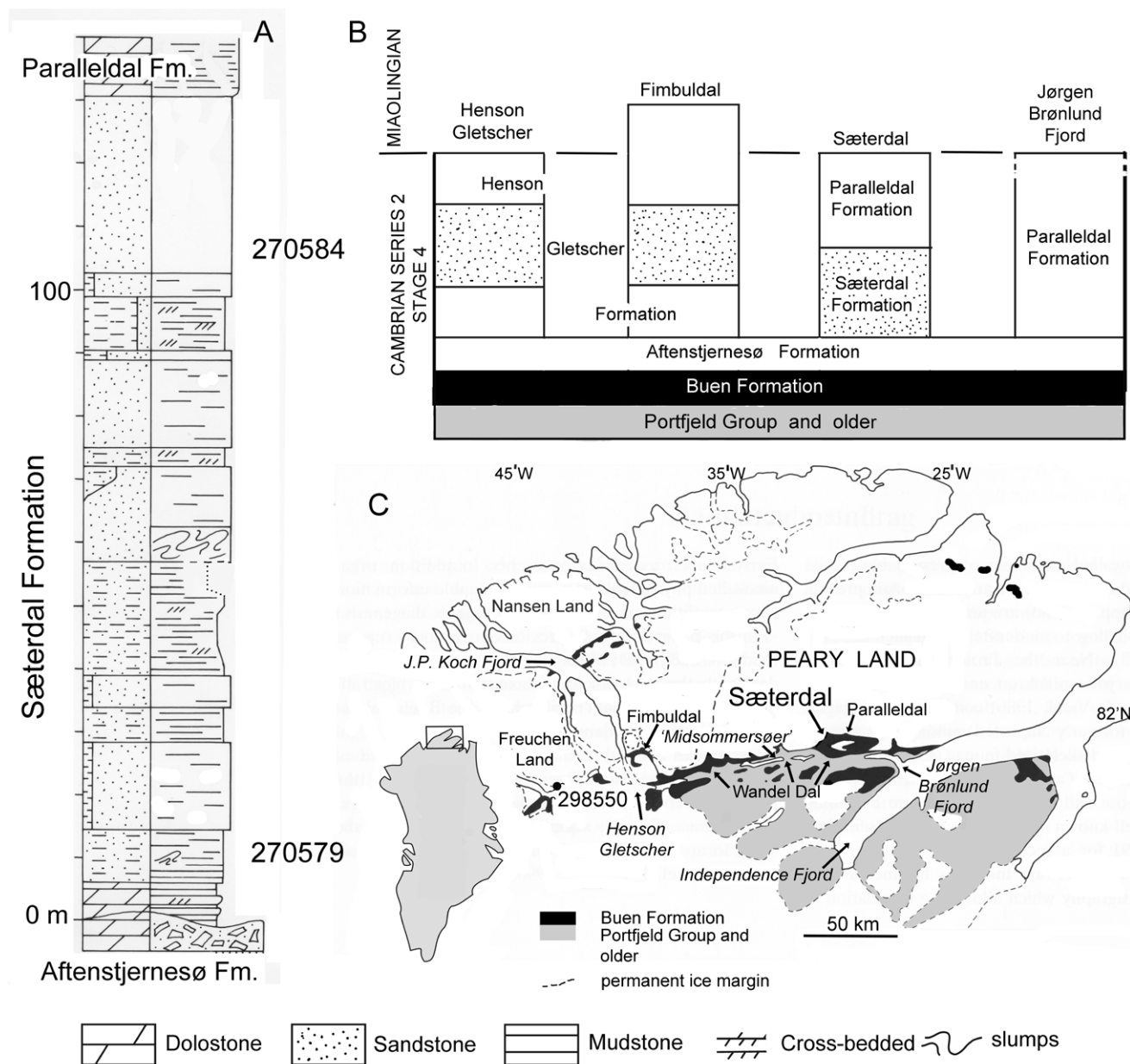


Fig. 1. **A:** type section of the Sæterdal Formation measured by J.R. Ineson in 1979 (Ineson & Peel 1997, fig. 69) showing the equivalent location of *in situ* faunas (GGU numbers) collected during 1978, about 2 km to the south-west of the type section, and described herein. **B:** distribution of sandstone-dominated intervals (stippled) in the Sæterdal and Henson Gletscher formations of southern Peary Land. **C,** locality map with a regional datum provided by the dark siliciclastic sediments of the Buen Formation (black). Carbonate rich sediments and pale sandstones of Cambrian Series 2, Stage 4 (see B) form a narrow outcrop immediately to the north of the outcrop belt of the Buen Formation. 'Midsommersøer' consists of Øvre Midsommersø in the west and Nedre Midsommersø in the east. Derivation of GGU sample 298550 from the Henson Gletscher Formation in southern Freuchen Land.

dal Formation of *Nisusia* cf. *ancauchensis* (Figs 3, 4), a species originally described by Benedetto & Foglia (2012) from the uppermost beds of the Ancaucha olistolith near Jáchal City, San Juan province, Argentina (Cambrian Stage 4). Assignment of the North Greenland material to *Nisusia* cf. *ancauchensis* supports the recognition of the Precordillera terrane of Argentina as a microcontinent derived from Laurentia (Keller et al. 1998; Bordonaro et al. 2013; Pratt & Bordonaro 2014). A single specimen of *Nisusia* from the uppermost Henson Gletscher Formation (Cambrian Stage 4, *Ovatoryctocara granulata* assemblage) of southern Freuchen Land is included for comparative purposes.

Material

All material from the Sæterdal Formation was collected on the north-western side of Sæterdal, Peary Land, North Greenland (82°17'09"N, 32°45'W). The locality is situated about 2 km south-west of the type section of the formation (Ineson & Peel 1997, fig. 68A).

GGU samples 270579 and 270584 were collected by J.S. Peel on 4th August 1978 at about 10 m above the base (GGU sample 270579) and about 25 m below the top (GGU sample 270584) of the formation (Fig. 1A). Other GGU samples 270563–270590 were collected by J.S. Peel on 3rd–5th August 1978. Each of these samples is derived from an individual talus block from the outcrop of the formation at an altitude of about 425 m a.s.l.

GGU sample 298550 was collected by J.S. Peel on 15th July 1985 from the uppermost Henson Gletscher Formation in southern Freuchen Land (82°09'N, 42°25'W), about 45 km west of Henson Gletscher (Geyer & Peel 2011, fig. 1D, locality 1; see also Streng et al. 2016; Oh et al. 2024).

Following mechanical preparation, specimens from the Sæterdal Formation were coated with colloidal carbon black in aqueous suspension, dried and then whitened prior to photography with ammonium chloride sublimate from a hot glass tube. The specimen from GGU sample 298550 is silicified and was extracted from the host limestone with weak acetic acid prior to scanning electron microscopy. All images were assembled in Adobe Photoshop 7 and CS4.

Systematic palaeontology

Repositories and abbreviations. GGU prefix indicates a sample made as a participant in the North Greenland Project (1978–1985), a regional mapping programme

of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now the Geological Survey of Denmark and Greenland, Copenhagen, Denmark (GEUS). Type and figured specimens are deposited in the type collection of the Natural History Museum of Denmark, Copenhagen (MGUH prefix) and the Museum of Evolution, Uppsala University (PMU prefix).

Phylum Arthropoda Siebold, 1848

Class Trilobita Walch, 1771

Order Redlichida Richter, 1932

Suborder Olenellina Walcott, 1890

Superfamily Olenelloidea Walcott, 1890

Family Olenellidae Walcott, 1890

Genus *Olenellus* Hall, 1861

Type species. *Olenus thompsoni* Hall, 1859 from the lower Cambrian of Vermont, U.S.A.

***Olenellus* cf. *howelli* Meek in White, 1874**

Fig. 2G, I

1997 *Olenellus* cf. *O. gilberti*; Blaker & Peel, p. 60, fig. 55.10, 55.12, 55.13.

Figured material. Cephalae; MGUH 23229 from GGU sample 270584 and MGUH 34845 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. GGU samples 270565, 270568, 270582, 270584, 270587, 270589, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Olenellid cephalae from the Sæterdal Formation are indifferently preserved due to their occurrence in coarse sandstone; other skeletal elements are not known. Blaker & Peel (1997) compared this species to *Olenellus gilberti* Meek in White, 1874, which was described with a detailed morphological analysis by Webster (2015), following earlier descriptions by Palmer (1957, 1998).

Specimens of *Olenellus gilberti* illustrated by Webster (2015) display a well-marked anterior deflection of the border between the intergenal angle and the genal angle whereas the posterior border continues as a uniform curve out to the genal angles in the Sæterdal material (Fig. 2G). In this feature it more closely

resembles *Olenellus howelli* (Meek in White, 1874) and *Olenellus fowleri* Palmer, 1998 as illustrated by Palmer (1998, fig. 9.5) from the Pioche Formation of Nevada. However, the palpebral lobes of *Olenellus howelli* differ in extending to the posterior furrow, while *Olenellus fowleri* has a well developed plectrum joining the glabella to the anterior border. Genal spines in the Sæterdal material are slender and about 40% of the length of the cranidium, although not preserved in either of the illustrated specimens.

Order Corynexochida Kobayashi, 1935

Family Dorypygidae Kobayashi, 1935

Genus *Bonnia* Walcott, 1916

Type species. *Bathyrurus parvulus* Billings, 1861 from the lower Cambrian of Labrador.

Bonnia brennus (Walcott, 1916)

Figs 2C, J, L–O, R

- 1916 *Corynexochus brennus* Walcott, p. 314, pl. 57, figs 3–3b.
- 1948 *Bonnia brennus*; Rasetti, p. 16, pl. 3, figs 16–25 (includes synonymy).
- 1997 *Bonnia brennus*; Blaker & Peel, p. 87, figs 50, 51.1–5, 51.8, 51.10.
- 2016 *Bonnia* cf. *brennus*; Peel et al., figs 3U, V, 4G, N.

Figured material. Cranidia: MGUH 23361 and MGUH 23362 from GGU sample 270563. Pygidia: MGUH 23368 from GGU sample 270579, MGUH 34843 from GGU sample 270563. Hypostome: MGUH 34842 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. GGU samples 270565 and 270587, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. A full description of *Bonnia brennus* was given by Blaker & Peel (1997) on the basis of material from the Henson Gletscher and Sæterdal formations in North Greenland. Disarticulated cranidia and pygidia are common in the Sæterdal Formation. A single hypostome (Fig. 2C) is proportionately slightly wider than specimens illustrated by Blaker & Peel (1997, figs 50.7, 50.8, 50.12) and Peel et al. (2016, fig. 4N) from the Henson Gletscher Formation. It is distinguished from hypostomes of the co-occurring *Kootenia marcoui* (Whitfield, 1884) by its angular anterior margin and well developed antero-lateral wings.

Genus *Kootenia* Walcott, 1889

Type species. *Baythyriscus (Kootenia) dawsoni* Walcott, 1889 from the middle Cambrian (Miaolingian Series) of British Columbia, Canada.

Kootenia marcoui (Whitfield, 1884)

Fig. 2E, F, H, K

- 1884 *Dikellocephalus? marcoui* Whitfield, p. 150, pl. 14, fig. 7.
- 1997 *Kootenia marcoui*; Blaker & Peel, p. 90–95, figs 52, 53, 54.1–6, 54.10, 54.11 (includes synonymy).

Figured material. Cranidium: MGUH 23378 from GGU collection 270590. Pygidia: MGUH 23399 from GGU collection 270590 and MGUH 23401 from GGU collection 270564, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. Abundant in most samples from the Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. *Kootenia marcoui* is distinguished from other lower Cambrian species of the genus in North Greenland by its seven pairs of pygidial spines (Blaker & Peel 1997). Disarticulated cranidia and pygidia of *Kootenia marcoui* are common in the samples from the Henson Gletscher Formation in western Peary Land and in the Sæterdal Formation.

Family Zacanthoididae Swinnerton, 1915

Genus *Zacanthopsis* Resser, 1938

Type species. *Olenoides levis* Walcott, 1886 from the lower Cambrian of Pioche, Nevada, U.S.A.

Zacanthopsis sp.

Fig. 2D

Figured material. MGUH 34844 from GGU sample 270587, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Within the limits imposed by its poor preservation, this single internal mould of a cranidium can be compared with *Zacanthopsis blakeri* Geyer & Peel, 2011 from the Henson Gletscher Formation of western Peary Land, originally referred to *Zacanthopsis levi* (Walcott, 1886) by Blaker & Peel (1997). Unfortunately, most of the broad convex anterior border has been worn away.

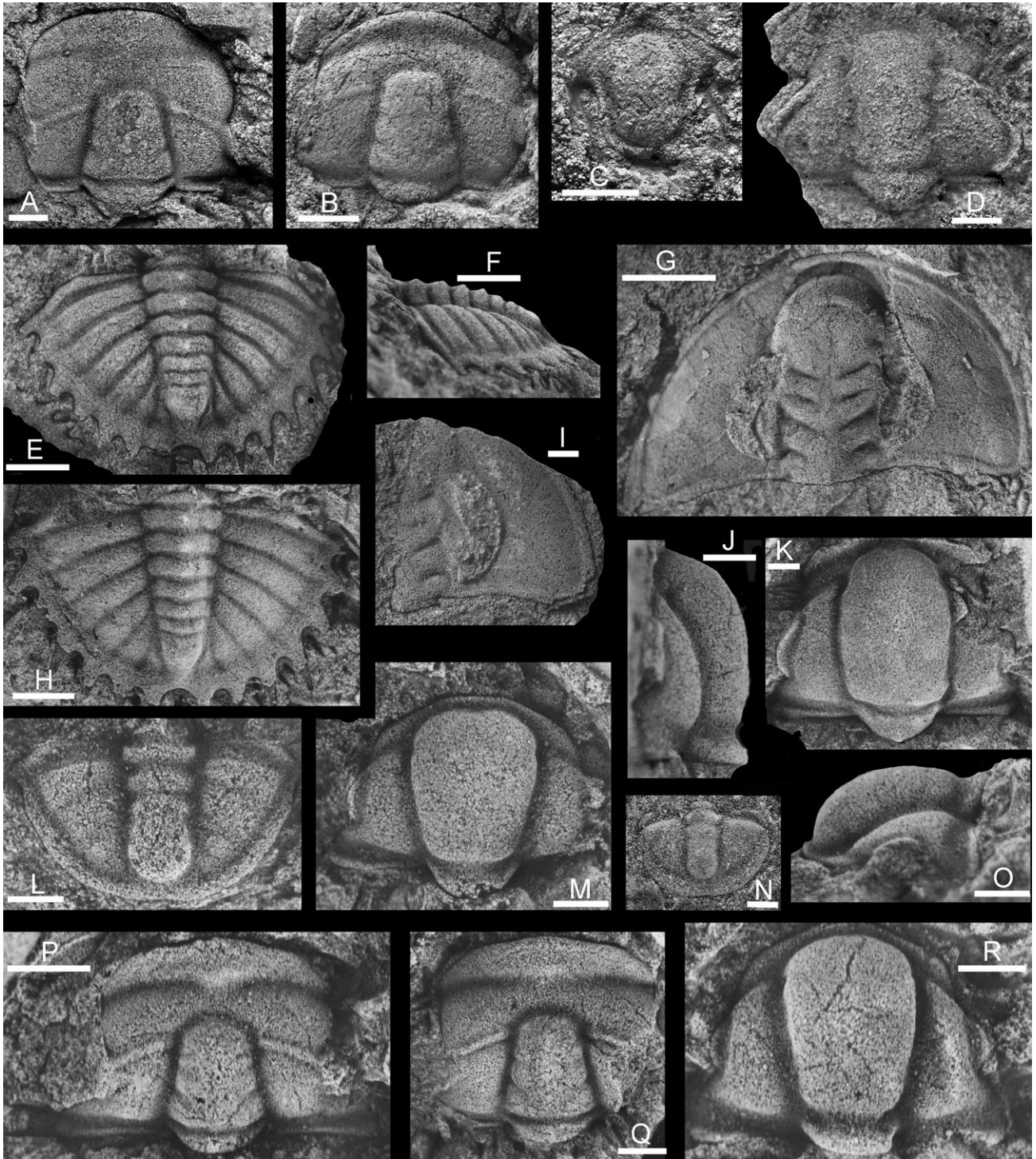


Fig. 2. Trilobites from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland; internal moulds. **A:** Undetermined ptychopariid, MGUH 34840 from GGU sample 270563, cranidium. **B:** *Anebocephalus?* sp., MGUH 34841 from GGU sample 270563, cranidium. **C, J, L–O, R:** *Bonnia brennus* (Walcott, 1916). **C:** MGUH 34842 from GGU sample 270563, hypostome. **J, R:** MGUH 23362 from GGU sample 270563, cranidium in lateral (J) and dorsal (R) views. **L:** MGUH 23368 from GGU sample 270579, pygidium. **M, O:** MGUH 23361 from GGU sample 270563, cranidium in dorsal (M) and lateral (O) views. **N:** MGUH 34843 from GGU sample 270563 pygidium. **D:** *Zacanthopsis* sp., MGUH 34844 from GGU sample 270587, cranidium with broken anterior. **E, F, K, H:** *Kootenia marcoui* (Whitfield, 1884). **E, F:** MGUH 23401 from GGU sample 270564, pygidium in dorsal (E) and lateral (F) views. **K:** MGUH 23378 from GGU sample 270564, cranidium. **H:** MGUH 23399 from GGU sample 270590, pygidium. **G, I:** *Olenellus* cf. *howelli* Meek in White, 1874. **G:** MGUH 23229 from GGU sample 270584, cranidium. **I:** MGUH 34845 from GGU sample 270563, broken cranidium. **P, Q:** *Harklessaspis?* sp. **P:** MGUH 23581 from GGU sample 270568, cranidium. **Q:** MGUH 23582 from GGU sample 270563, cranidium. Scale bars: 1 mm (J); 2 mm (A–D, G, I, K–O, Q, R); 3 mm (H); 4 mm (E, F, P)

Order Ptychopariida Swinnerton, 1915

Remarks. In available material, small ptychopariidans are known only from isolated cephalons, with the result that generic assignments are tenuous.

Genus *Anebocephalus* Sundberg & Webster, 2022

Type species. *Anebocephalus silverpeakensis* Sundberg & Webster, 2022 from the Harkless Formation, Cambrian Series 2, (mid-Dyeran Regional Stage), Nevada, U.S.A.

Anebocephalus? sp.

Fig. 2B

Figured material. MGUH 34841 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. The anterior margin of this internal mould of a cranidium (Fig. 2B) is more convexly curved in dorsal view than in *Eoptychoparia pearylandica* Geyer & Peel, 2011 from the Henson Gletscher Formation (Cambrian Stage 4), but the specimens illustrated by Geyer & Peel (2011, fig. 21) show variation both in the curvature and the width of the brim. The posterolateral extensions of the fixigenae are not exposed. The transverse width of the fixigenae at the anterior margin of the eye is slightly greater than the corresponding width of the glabella. *Eoptychoparia pearylandica* was referred to *Anebocephalus* by Sundberg & Webster (2022).

Cranidia of *Onchocephalus? freucheni* Geyer & Peel, 2011, also from the Henson Gletscher Formation (Cambrian Stage 4), differ in terms of a more parallel-sided glabella and a straight anterior border furrow. *Onchocephalus? freucheni* was referred to the new genus *Coenoides* by Sundberg & Webster (2022), with type species *Coenoides scholteni* Sundberg & Webster (2022) from the upper Harkless Formation, Nevada.

Genus *Harklessaspis* Sundberg & Webster, 2022

Type species. *Harklessaspis parvigranulosus* Sundberg & Webster, 2022, from the Harkless Formation, Cambrian Series 2 (Dyeran Regional Stage), Nevada, U.S.A.

Harklessaspis? sp.

Fig. 2P, Q

1997 Ptychoparioid genus and species undetermined B, Blaker & Peel, p. 132, fig. 51.6?, 51.9, 51.11.

1997 Ptychoparioid genus and species undetermined C, Blaker & Peel, p.133, fig. 51.7.

Figured material. Cranidia; MGUH 23581 from GGU sample 270568; MGUH 23582 from GGU collection 270563. Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Blaker & Peel (1997) placed the two illustrated specimens (Fig. 2P, Q) in separate species, but they are united here, given their relatively poor preservation and the variation in the shape of the front border illustrated by Sundberg & Webster (2022) in the type species. The degree of expression of the median expansion within the anterior border varies, but the border furrow itself is characteristically deep to either side.

Undetermined ptychopariid

Fig. 2A

Figured material. Cranidium: MGUH 34840 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. The glabella of this internal mould is proportionately shorter than in *Harklessaspis?* sp., while the brim is wider anteriorly and less sharply defined.

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams *et al.*, 1996

Class Kutorginata Williams *et al.*, 1996

Order Kutorginida Kuhn, 1949

Superfamily Nisusioidea Walcott & Schuchert *in* Walcott, 1908

Family Nisusiidae Walcott & Schuchert *in* Walcott, 1908

Genus *Nisusia* Walcott, 1905

Type species. *Orthisina festinata* Billings, 1861, Potsdam Group, Cambrian Series 2; Vermont, U.S.A.

Remarks. Bell (1941) divided nisusiids into two groups on the basis of their shape and the location of the ventral umbo. Mao *et al.* (2017) listed 39 species of *Nisusia* from the Cambrian but Holmer *et al.* (2019) considered only half of these in their cladistic analysis. Holmer *et al.* (2019) recognised two clades of nisusiids, with most species referred to a group in which the umbo is elevated above the rest of the ventral valve (cf. Figs 3I, 4D), which is shallowly concave behind the umbo

in lateral profile. The second group included mainly non-spinose species with biconvex shells. They suggested that *Laurentia* was the main place for *Nisusiid* dispersal during Cambrian Series 2 with possible records existing from Cambrian Stage 3 (Saxen 2017), although *Nisusia alaica* (Popov & Tikhonov, 1990) was described from Cambrian Stage 3 in the Kyrgyz Republic. Cambrian Stage 4 representatives include the type species *Nisusia festinata* (Billings, 1861), originally described from Vermont (Billings 1861, p. 10, figs 11, 12), and *Nisusia ancauchensis* Benedetto & Foglia, 2012, described from the Precordillera terrane in Argentina (Benedetto & Foglia 2012, fig. 4.1–4.5).

Oh et al. (2022) analysed the phylogeny and distribution of *Nisusia*, adding a few more species to the data base of Holmer et al. (2019) and recognising two clades descended from a paraphyletic basal group. Spinose taxa occur in all three groups. *Nisusia festinata* and *Nisusia ancauchensis* were placed in separate clades and considered to be derived from a basal group with strong and long spines. Such coarse spines are known in *Nisusia alaica* and *Nisusia metula* Brock et al., 1998, the latter from Cambrian Series 3 (Miaolingian) in New South Wales. A silicified juvenile specimen referred to *Nisusia* sp. undet. from the uppermost Henson Gletscher Formation (Cambrian Series 2, Stage 4, *Ovatoryctocara* assemblage; Fig. 4K–N) in southern Freuchen Land, about 45 km west of Henson Gletscher, also displays coarse spines that are much more prominent than those preserved in specimens of *Nisusia* from the Sæterdal Formation (Figs 3A–Q, 4A–J).

***Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012**
Figs 3A–I, K–Q, 4A–J

Figured material. MGUH 34846, MGUH 34848–34853, MGUH 34857 and MGUH 34858 from GGU sample 270563; MGUH 34847 and MGUH 34856 from GGU 270587; MGUH 34855 from GGU sample 270566. Sæterdal Formation, Cambrian Series 3, Stage 4.

Description. All specimens from the Sæterdal Formation occur in decalcified sandstone as external moulds (Fig. 3N, O) and composite moulds with variable preservation of the strongly costellate outer surface and growth lines. Herein, the relief of described morphological features relates to their form on the specimens as illustrated. Conjoined valves have not been observed. Maximum observed width is about 15 mm, length 11 mm, measured on a ventral valve. Greatest width is slightly anterior of the hinge line.

The highest point of the ventral valve lies at the pointed umbo, which may extend posteriorly to overhang the apsacline to catacline interarea (Figs 3K, L, 4C–D) or rise abruptly from the valve surface (Fig. 3I,

P). The foramen is apparently located at the apex of the umbo (Fig. 4B, C, E). In lateral profile the ventral valve is initially flattened, sometimes shallowly concave (Figs 3H, 4H) behind the umbo before increasing in convexity towards the anterior margin (Figs 3C, 4D). The ventral surface may show a median sinus posteriorly (Fig. 4E) but its anterior margin is almost planar (Fig. 3D) or even with a shallow fold (Fig. 3P). The junction between the ventral surface and interarea is angular, usually with a prominent rounded cord along the crest (Figs 3B, G, M, 4E, J). The pseudodeltidium varies from transversely narrow (Fig. 3B) with grooved margins near the apex (Figs 3G, 4I) to wide with diffuse margins (Fig. 4B, C); it may be depressed medially (Fig. 3B) or uniformly convex (Fig. 3G, H). The depth of the open delthyrium is about half the height of the interarea (Fig. 3M, arrow). Grooves delimiting the margins of the adapical portion of the pseudodeltidium may curve onto the valve surface (Figs 3G, 4I). In one specimen (Fig. 3F) the grooves persist almost to half the length, suggesting an association with muscle scars. Radial dorsal ornamentation initially consists of 7–10 costellae close to the umbo, with only two or three on the projecting apex (Fig. 3K, L). About 30 radial elements are present at the anterior margin due to progressive interdigitation of additional costellae (Fig. 3A). Comarginal ornamentation consists of obscure fine growth lines and more prominent cords. Tubercles (fine spine bases) occur at the intersection of the cords and costellae (arrows in Figs 3A, D, 4E) and are seen as pits in the external mould (arrows in Figs 3N, O).

The dorsal valve is poorly known, with a rounded apex. Its radial ornamentation is crossed by comarginal growth lines but may be subdued except near the anterior margin (Figs 3Q, 4F), as in one ventral valve (Fig. 3P). However, ornamentation is uniformly developed, with spines, in an external mould (arrow in Fig. 3O).

Remarks. Specimens from the Sæterdal material show variation in terms of shell shape and the nature of the pseudodeltidium. End members in this continuum (Figs 3A–D, 4A–E) could easily be assigned to different species, but on account of the small sample size, ontogenetic variation and the lack of information concerning the dorsal interarea, they are collectively compared to *Nisusia ancauchensis* Benedetto & Foglia, 2012, while recognising similarities with some of the varied material assigned by Walcott (1912) to the type species *Nisusia festinata*. However, unlike the Sæterdal specimens, some material from Vermont assigned to *Nisusia festinata* by Walcott (1912) and Shaw (1955) has the hinge line extended into alae and forming the greatest width of the shell.

Material assigned to *Nisusia ancauchensis* was based on a few specimens described by Benedetto & Foglia

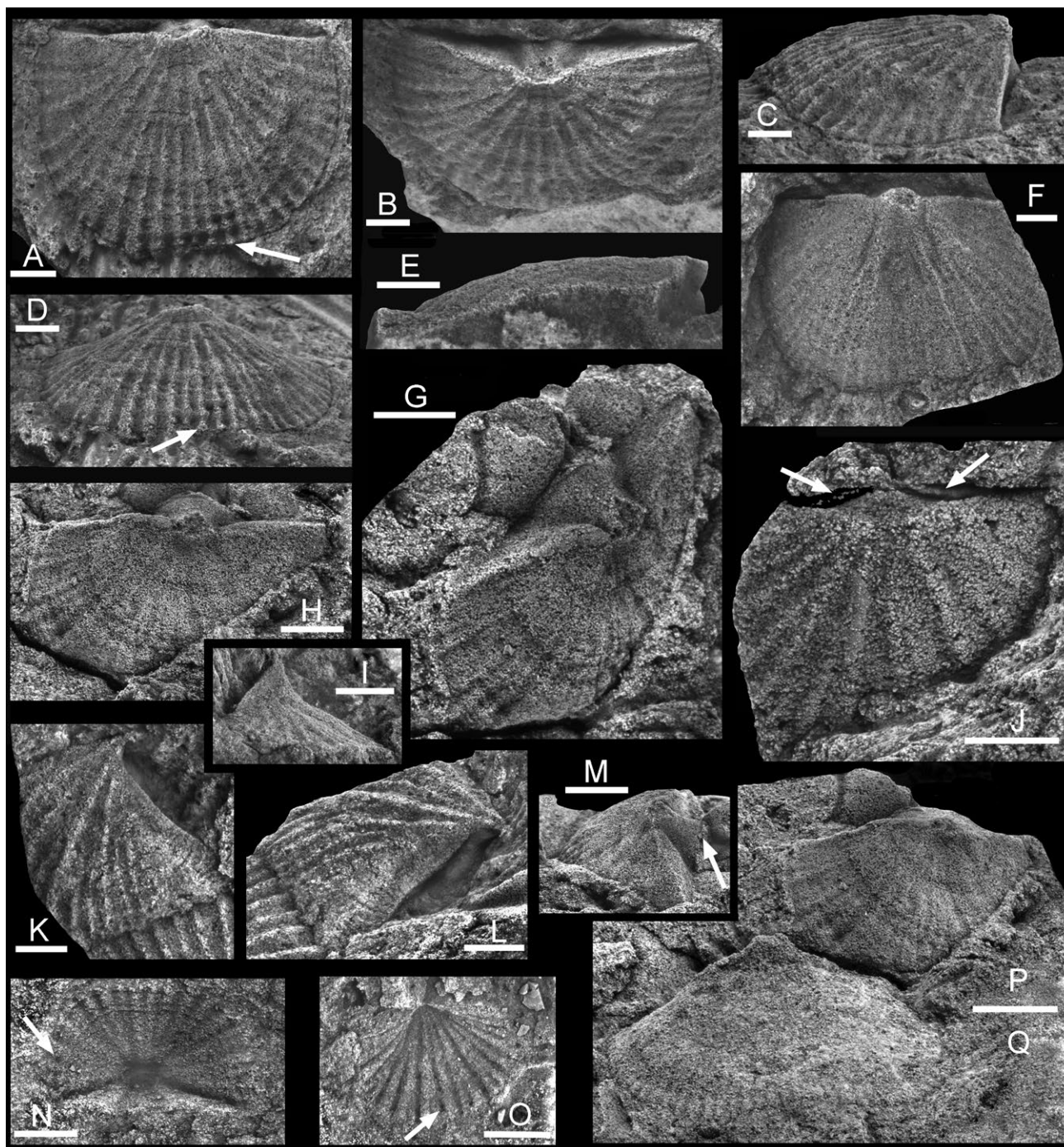


Fig. 3. Brachiopods from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland. **A–I, K–Q:** *Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012. **A–D:** MGUH 34846 from GGU sample 270563, ventral (A), postero-ventral (B), lateral (C) and oblique anterior (D) views of ventral valve, with arrows indicating spine bases. **E, F:** MGUH 34847 from GGU sample 270587, lateral (E) and ventral (F) views of ventral valve, with apex broken away. **G, H, M, P:** MGUH 34848 from GGU sample 270563, oblique postero-ventral (G), ventral (H, P) and postero-lateral (M) views of ventral valve with arrow in M indicating delthyrium. **I:** MGUH 34849 from GGU sample 270563, ventro-lateral view of ventral valve. **K, L:** MGUH 34850 from GGU sample 270563, oblique views of central valve. **N:** MGUH 34851 from GGU sample 270563, external mould of ventral valve with hole produced by spine (arrow). **O:** MGUH 34852 from GGU sample 270563, external mould of dorsal valve, with holes produced by spines (arrow). **Q:** MGUH 34853 from GGU sample 270563, antero-ventral view of ventral valve on same slab as P. **J:** *Nisusia* sp., MGUH 34854 from GGU 270563, dorsal view of dorsal valve with cardinal ridges arrowed. Scale bars: 2 mm (A–N); 3 mm (O, P).

(2012) from the uppermost beds of the Ancaucha olistolith at Quebrada Ancaucha, about 30 km west of Jáchal City, San Juan province, Argentina (Cambrian Stage 4). Benedetto & Foglia (2012) commented that the pseudodeltidium of *Nisusia ancauchensis* was greatly enlarged, twice as wide as long, and unbounded by lateral furrows. This is seen in a ventral valve from GGU sample 270566 where the dark pits in the posterior view relate to shadow under the apsacline interarea rather than to sockets (Fig. 4B, C). Other similar specimens from GGU sample 270587 (Fig. 4E, I) show that the adapical part of the pseudodeltidium is parallel-sided before expansion. In an additional specimen it is bounded by a groove that deepens adapically (Fig. 3G, H, M) and terminates at an open delthyrium (arrow in Fig. 3M), although this groove is much narrower than that seen in *Nisusia alaica* (Popov & Tikhonov (1990, pl. 3, figs 21a, 23). More frequently, the pseudodeltidium expands slowly and uniformly, occupying about a quarter to a fifth of the width of the interarea (Fig. 3B) in a manner reminiscent of *Nisusia festinata* as illustrated by Billings (1861) and Walcott (1912).

A prominent, cord-like elevation along the angulation between the interarea and the valve surface in the holotype ventral valve of *Nisusia ancauchensis* (Benedetto & Foglia, 2012, fig. 4.1–4.4) is also seen specimens from Sæterdal (Figs 3B, G, 4E, I) but it is lacking in *Nisusia festinata*.

Apart from its longer and coarser spines, the silicified specimen of *Nisusia* sp. undet. from the Henson Gletscher Formation in southern Freuchen Land (Fig. 4K–N), displays a pseudodeltidium that is similar to some specimens of *Nisusia* cf. *ancauchensis* from the Sæterdal Formation (Figs 3G, 4E).

Nisusia sp.

Fig. 3J

Figured material. MGUH 34854 from GGU sample 270563, Sæterdal Formation.

Remarks. A single internal mould of a shallowly convex dorsal valve attributed to *Nisusia* preserves about 15 coarse costellae with rare branching that in their coarseness resemble *Eoconcha* Cooper, 1951. Traces of ridges

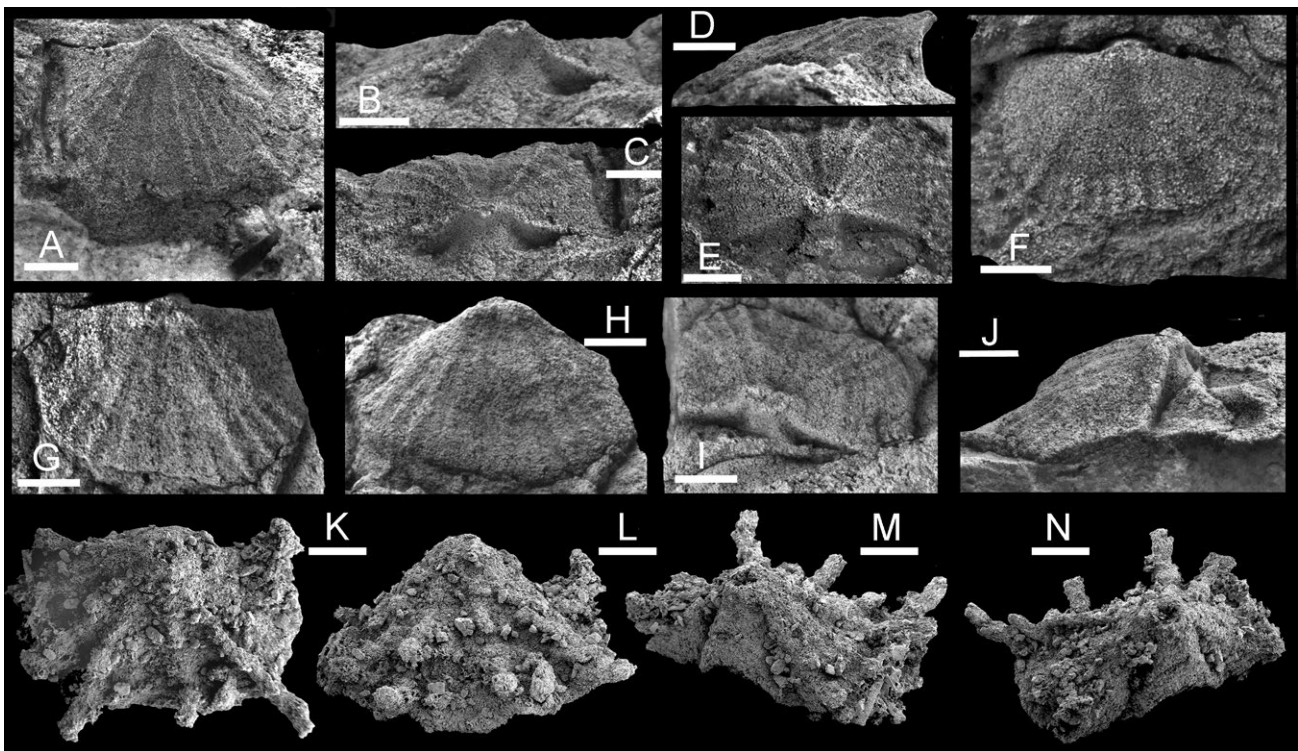


Fig. 4. *Nisusia* Walcott, 1905, Cambrian Stage 4, North Greenland. **A–J:** *Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012 from the Sæterdal Formation (Cambrian Stage 4), Sæterdal. **A–D:** MGUH 34855 from GGU sample 270566, ventral valve in ventral (A), postero-ventral (B, C) and lateral (D) views. **E:** MGUH 34856 from GGU sample 270587, ventral valve in postero-ventral view. **F:** MGUH 34857 from GGU sample 270563, dorsal valve. **G–J:** MGUH 34858 from GGU sample 270563, ventral valve in ventral (G), antero-ventral (H), postero-ventral (I) and postero-lateral (J) views. **K–N:** *Nisusia* sp. undet., uppermost Henson Gletscher Formation (Cambrian Stage 4), southern Freuchen Land. PMU 38495 from GGU sample 298550, silicified ventral valve in ventral (K), anterior (L) and posterior (M, N) views. Scale bars: 1 mm (K–N); 2 mm (A–J).

corresponding to linear cardinal sockets (Popov & Tikhonov 1990, fig. 3b) extend laterally from the apical area (Fig. 3O, arrows), which is slightly depressed as a result of thickening by a notothyrial plate on the shell interior.

Superfamily Kutorginoidea Schuchert, 1893

Family Kutorginidae Schuchert, 1893

Genus *Kutorgina* Billings, 1861

Type species. *Kutorgina cingulata* Billings, 1861, Cambrian Series 2, L'Anse au Loup (Belle Isle), Labrador, Canada.

Kutorgina cf. *cingulata* Billings, 1861

Fig. 5A–C, F–I

Figured material. MGUH 34860–MGUH 34862 and MGUH 34864 from GGU sample 270563; MGUH 34863 from GGU sample 270566; MGUH 34859 from GGU sample 270587. Sæterdal Formation, Cambrian Series 3, Stage 4.

Remarks. Specimens of *Kutorgina* cf. *cingulata* Billings, 1861 from the Sæterdal Formation contrast markedly in terms of preservation with the silicified material described from the Paralleldal Formation by Popov et al. (1997). While the pronounced comarginal rugae are conspicuous in external and composite moulds (Fig. 5A–C), they are only weakly visible on internal moulds (Fig. 5F, G). Similar preservation was illustrated by Shaw (1955) in specimens from the lower Parker Shale of Vermont.

Order Chileata Williams *et al.*, 1996

Superfamily Matutelloidea Andreeva, 1962

Family Matutellidae Andreeva, 1962

Genus *Matutella* Cooper, 1951

Type species. *Matutella clarkei* Cooper, 1951 from the Shady Formation, Cambrian Series 2, Austinville, Virginia, U.S.A.

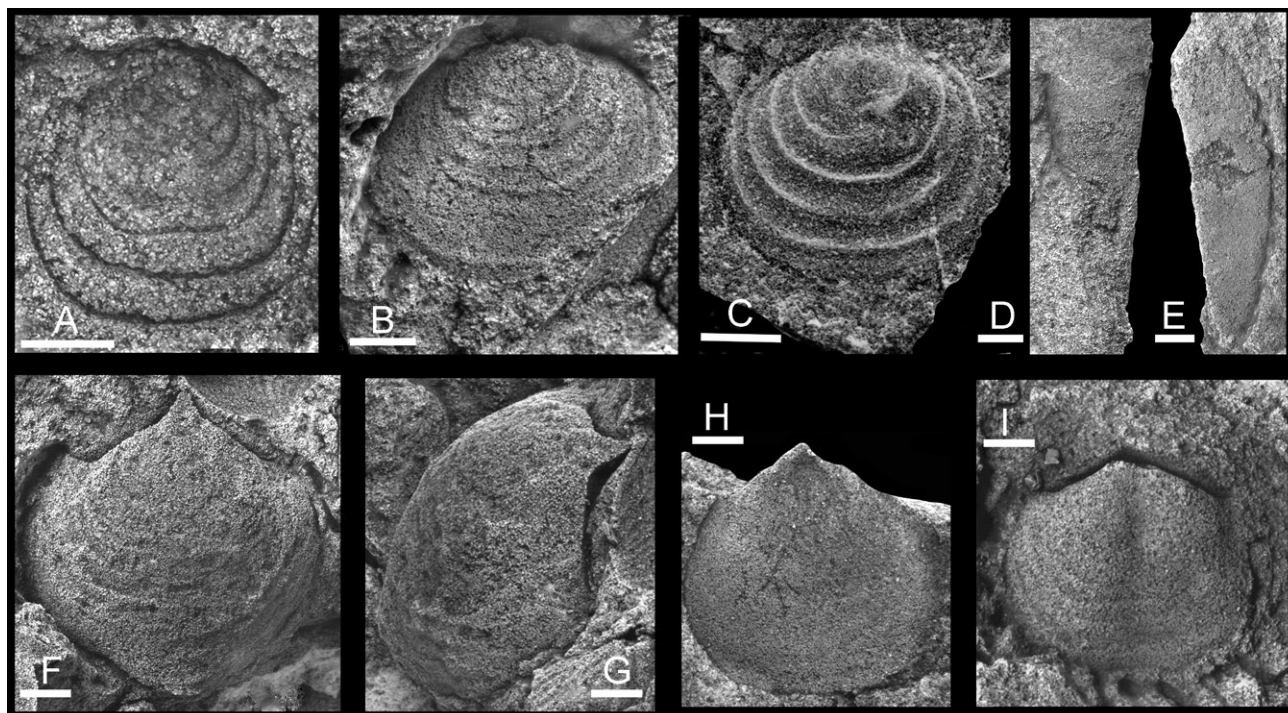


Fig. 5. *Kutorgina* cf. *cingulata* (Billings, 1861) and hyolithid from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland. GGU sample 270563 unless stated. **A–C, F–I:** *Kutorgina* cf. *cingulata* (Billings, 1861). **A:** MGUH 34859 from GGU sample 270587, composite mould of juvenile dorsal valve. **B:** MGUH 34860, composite mould of juvenile dorsal valve. **C:** MGUH 34861, digitally reversed external mould of juvenile dorsal valve. **F, G:** MGUH 34862, internal mould of ventral valve. **H:** MGUH 34863 from GGU sample 270566, internal mould. **I:** MGUH 34864, internal mould of dorsal valve. **D, E:** Hyolithid sp. indet. MGUH 34865 from GGU sample 270566, internal mould in dorsal (D) and lateral (E) views. Scale bars: 2 mm.

Matutella sp.

Fig. 6

Figured material. MGUH 34866 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. This is known from a single, poorly preserved, incomplete internal mould of a dorsal valve. Traces of coarse costellae are retained lateral to the prominent dorsal fold. Preservation is too poor to permit meaningful comparison with material described by Cooper (1951), Andreeva (1962) and Aksarina & Pelman (1975).

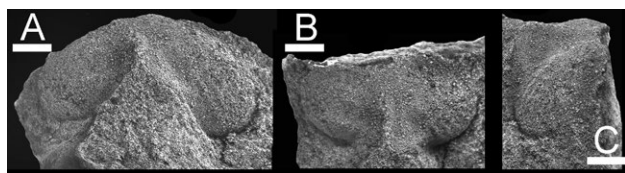


Fig. 6. *Matutella* sp., MGUH 34866 from GGU sample 270563, internal mould of dorsal valve in oblique anterior (A), dorsal (B) and lateral (C) views. Sæterdal Formation, Cambrian Series 2, Stage 4. Scale bars: 3 mm.

Phylum uncertain

Class Hyolitha Marek, 1963

Order Hyolithida Syssoiev, 1957

Hyolithid sp. indet.

Fig. 5D, E

Figured material. MGUH 34865 from GGU sample 270566, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. A single, poorly preserved conch has a transversely uniformly convex dorsum and rounded angular transitions to the flattened basal surface. The conch is curved slightly towards the dorsum; the presence of a ligula is not confirmed.

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A cluster of the brachiopod *Magas chitoniformis* (von Schlotheim, 1813) represents settling of a single spatfall on a soft-bodied substrate, probably a sponge: instantaneous burial by a chalk ooze debris flow (Maastrichtian, Denmark)

FINN SURLYK



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A well-defined monospecific cluster of the brachiopod *Magas chitoniformis* (von Schlotheim, 1813) was found in uppermost Maastrichtian chalk at Stevns Klint, Denmark. It comprises a sheet-like accumulation of 53 well-preserved adult specimens with an average length of 7.0 mm. The stratigraphical level is the ‘Sponge Bed’ named so by fossil collectors because of the wealth of imprints or skeletal elements of large sponges, commonly showing 3D-preservation. The unimodal size-frequency distribution of the brachiopod shells indicate that they represent a single successful spatfall most likely on a soft-bodied sponge. There are no signs of transport or winnowing of the chalk and the cluster is interpreted as formed by instantaneous burial of the sponge and its epifauna by a chalk ooze debris flow. The triggering mechanism was probably a major earthquake caused by movement on a nearby syn depositional fault. Another cluster dominated by *Magas chitoniformis* was found in the Nørre Flødal quarry in northern Jylland in an upper Maastrichtian chalk rich in imprints after sponges. A similar burial mechanism is envisaged based the position of the locality in the tectonically very active Sorgenfrei-Tornquist Zone. The clusters are excellent examples on brachiopod attachments to a soft-bodied organism, which has left no direct trace in the sediment.

Keywords: Terebratulida, Cretaceous, Stevns Klint, epifauna.

Finn Surlyk [finns@ign.ku.dk] Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark.

Most brachiopods are attached to a substrate by means of a muscular pedicle. The pedicle can have many different functions and is much more than just a holdfast. Surlyk (1972) thus interpreted the pedicle of the Maastrichtian generalist species *Terebratulina chrysalis* (von Schlotheim, 1813) as root-like by analogy with the modern relative *Terebratulina retusa*. Richardson (1997) highlighted the great variability of brachiopod pedicles in terms of morphology and function. Fossil pedunculate brachiopods are only rarely found preserved in life position as the fleshy pedicle

rapidly decays after death of the brachiopod. However, several specimens of the micromorphic brachiopods, *Aemula* n. sp. were found in life position on the test of an irregular echinoid (Surlyk 1974). *Aemula* n. sp. and its host lived on the quiet Maastrichtian chalk ooze at Hemmoor in northern Germany. This fortuitous preservation was probably caused by rapid burial of the echinoid by a predator whereby the minute specimens of *Aemula* were covered in chalk while still attached.

An almost identical find in the upper Maastrichtian of Belgium of several specimens of the closely related

pedunculate *Aemula inusitata* Steinich, 1968 was reported as preserved in life position also in this case on the test of the echinoid *Echinocorys* (Jagt & Simon 2004). These two finds indicate that the mm-sized *Aemula* possessed a short pedicle and lived with the dorsal valve closely pressed against the substrate. Sudden burial of the substrate – in these cases an echinoid test – resulted in preservation in life position.

A number of examples have been described where an assemblage of mainly monospecific brachiopods was preserved in a cluster without any signs of concentration caused by currents or other means of transport. An assemblage of the rhynchonellid brachiopod *Owenirhynchia triangularis* (Wahlenberg, 1821) was interpreted as representing a result of a densely clustered attachment strategy (Asgaard & Bromley 1990). This interpretation was supported by the abundant occurrence of the boring *Podichnus* isp. on the shells. The boring was formed by the brachiopod pedicle being split into holdfast papillae, which could penetrate the carbonate shells (Bromley & Surlyk 1973). *O. triangularis* was an important member of the early Campanian rocky shore fauna at Ivö Klack, southern Sweden (Surlyk & Sørensen 2010; Schröder *et al.* 2019).

A remarkable example of an immense, high-density monospecific Early Silurian assemblage of the brachiopod *Stricklandia lens lens* (Sowerby, 1839) was described and interpreted by Johnson & Baarli (2022) as resulting from an extensive spatfall settling on a barren shell

pavement, covering a large area during a short interval of time. Clusters of Devonian, Carboniferous and modern discinid brachiopod shells were interpreted as original life assemblages by Mergl (2010). The living, modern clusters of *Discradisca lamellosa* (Broderip, 1833) and *Discinisca laevis* (Sowerby, 1822) comprised up to 25 individuals which were attached to each other with a short pedicle illustrated by some quite remarkable photographs (Mergl 2010, fig. 5). The clustering was interpreted as a protection against grazing. Fine examples of brachiopod clusters, notably *Lepidocyclus capax* (Conrad, 1842) and *Rhychotrema dentatum* (Hall, 1847) clearly preserved in life position were described from the Upper Ordovician of Indiana and Ohio by Richards (1972). Small clusters of densely packed brachiopods *Tetrarhynchia tetrahedra* (Sowerby, 1812) and *Lobothyris punctata* (Sowerby, 1812) were interpreted as genuine life assemblages by Hallam (1961). The clusters exhibited a wide size range and thus no evidence for current sorting and with only few signs of physical disturbance of the shells. Hallam (1961) suggested that at least three successive annual spatfalls were represented based on a size-frequency analysis.

The aim of this study is to describe and interpret a monospecific cluster of at least 53 specimens of the articulate brachiopod *Magas chitoniformis* (von Schlotheim, 1813) found in very fine-grained chalk in the uppermost Maastrichtian at Stevns Klint, Denmark.

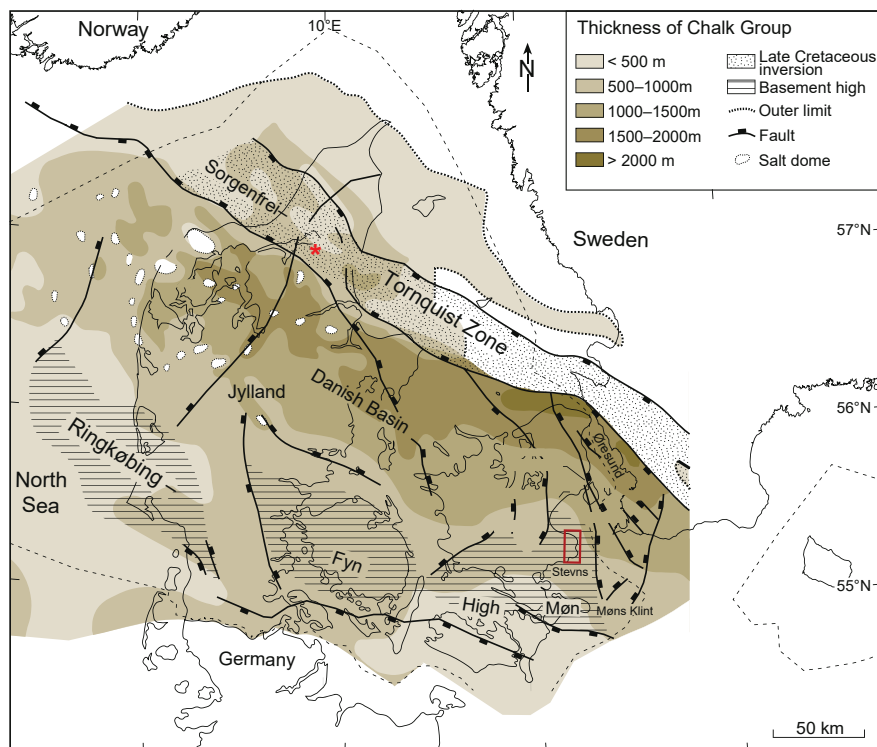


Fig. 1. Geological map, showing the outline of the Danish Basin and its southern and northern limits, the Ringkøbing-Fyn High and the Sorgenfrei-Tornquist Zone, respectively. Red rectangle marks the position of the coastal cliff, Stevns Klint. The position of the locality Nørre Flødal, northern Jylland is shown with an asterisk. Modified after Surlyk *et al.* (2013).

Geological setting and stratigraphy

The Upper Cretaceous Chalk Group of northern Europe is a major contourite complex formed at a time when the European craton was flooded by the relatively deep Chalk Sea. Reflection seismic data show that the chalk of the Danish Basin was deposited in a system of large valleys and ridges, moats and drifts sculptured by bottom currents (Lykke-Andersen & Surlyk 2004; Esmerode *et al.* 2007; Surlyk & Lykke-Andersen 2007).

The 14.5 km long coastal cliff, Stevns Klint in eastern Denmark shows excellent exposures of upper upper Maastrichtian chalk topped by an unbroken

Cretaceous–Palaeogene boundary succession overlain by mounded bryozoan limestone (Surlyk *et al.* 2006). Stevns Klint was nominated a UNESCO World Heritage Site in 2014 based on an application written by Damholt and Surlyk (2012). The chalk was deposited close to the southern margin of the Danish Basin, which is limited to the south by the Ringkøbing-Fyn High (Fig. 1).

The brachiopod cluster forming the subject of this study was found in the Sigerslev quarry also known as Stevns Kridtbrud (Stevns chalk quarry), immediately adjacent to the cliff. The quarry exposes about 30 m of the Sigerslev and Højerup Members, Møns Klint Formation (Fig. 2). The lowest part of the Sigerslev Member was deposited in a complex of low mounds (Anderskov *et al.* 2007). Mound growth was governed by currents flowing towards the WNW, the same direction as the interpreted Late Cretaceous current direction in the present Kattegat sea farther north in the Danish Basin (Surlyk & Lykke-Andersen 2007). Upwards, the mounded chalk give way to evenly bedded chalk, which is topped by a few metres of bryozoan-rich chalk of the Højerup Member. This unit overlain by the K–Pg boundary clay, the lowermost Danian Cerithium Limestone Member, the lowermost Danian Fiskeler Member, passing gradationally upwards into the Cerithium Limestone Member (together forming the Rødvig Formation). The Cerithium Limestone is topped by an erosional hardground surface overlain by lower Danian bryozoan limestone of the lower Danian Korsnæb Member of the lower Danian Stevns Klint Formation (Fig. 2; Surlyk *et al.* 2006).

Chrono-stratigraphy			Litho-stratigraphy	
LOWER PALAEOGENE	Danian	lower	Stevns Klint Fm	
			Rødvig Fm	Cerithium Limestone Mb
				Fiskeler Mb
	Maastrichtian	upper	Møns Klint Fm	Højerup Mb
				 Sigerslev Mb
				Rørdal Mb
				Hvidskud Mb
				Boesdal Mb
		lower	Mande-hoved Fm	
UPPER CRETACEOUS	Maastrichtian	lower	Mande-hoved Fm	

Fig. 2. Lithostratigraphic scheme covering the succession exposed at Stevns Klint. After Surlyk *et al.* (2013).

The *Magas chitoniformis* cluster from Stevns Klint

A cluster of the pedunculate brachiopod *Magas chitoniformis* (von Schlotheim, 1813; Fig. 4; Geomuseum Faxe, with registration number OESM-4620) was found by Peter Bennicke in the lower part of the Maastrichtian chalk of the Sigerslev Member exposed in the Sigerslev chalk quarry (Fig. 3). It was found in the so-called Sponge Bed, rich in large skeletons and imprints after sponges together with regular echinoids with all spines lying immediately adjacent to the tests (Figs 5, 6; Peter Bennicke and Sten L. Jakobsen, pers. comm. 2024). The bed has a high content of celestite, a mineral that has also been recorded in Maastrichtian chalk in the nearby fully cored Stevns-1 borehole. The celestite nodules were interpreted as formed by very early replacement of lithistid demosponges in localized reducing environmental conditions (Madsen & Stemmerik 2009). This took place during rapid burial of the sponges and the subsequent decomposition of the or-

ganic tissue by sulfide-oxidizing and sulfate-reducing bacteria forming local anoxic microenvironments. A similar interpretation is proposed for the Sponge Bed in the Sigerslev quarry both for the content of celestite

and for the unusual 3D preservation of large sponges.

The well-defined *M. chitoniformis* cluster covers an area of about 14 x 11 cm set in a very pure chalk (Fig. 4). The chalk is structureless and non-bedded but the

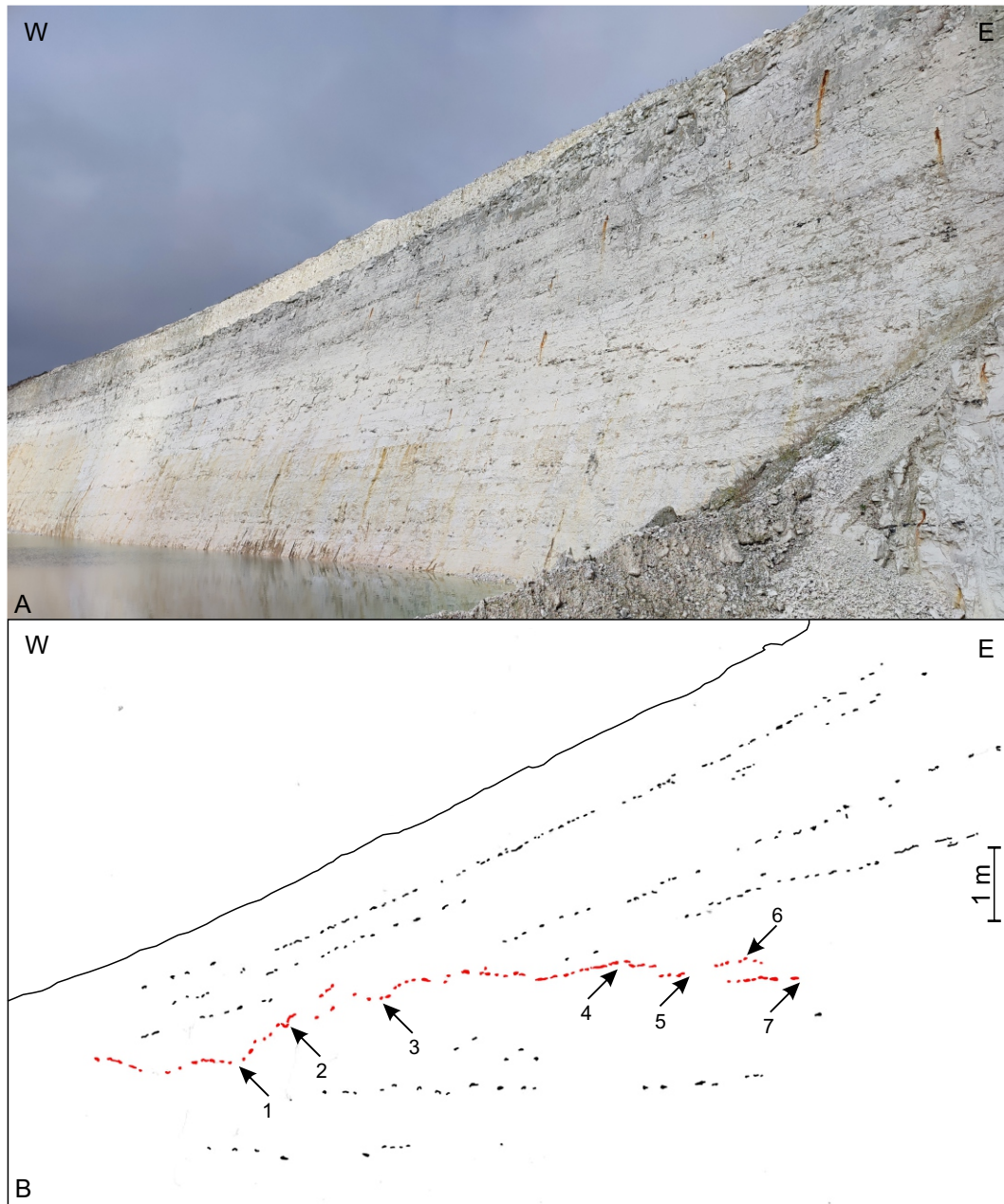


Fig. 3. A: Photograph of E–W wall in the Sigerslev quarry, Stevns Klint. The lower part of the section shows fossiliferous mound-bedded chalk, which upwards give way to horizontally-bedded, poorly fossiliferous chalk. The Sponge Bed is exposed in the adjacent N–S wall at the same level as the mounded chalk. The K–Pg boundary is situated immediately above the top of the exposed section. The mounded topography is outlined by layers of flint nodules. The mounds are mainly regular with evenly sloping flanks, but the eastern flank of the mound shown in the photograph is deformed and irregularly down stepping interpreting as reflecting redeposition of chalk and instant burial of the benthic fauna by debris flows. The western mound flank is strongly deformed with concave-up erosional surfaces interpreted as small slump scars. Photograph by Jesper Milàn. **B:** Drawing of photograph in A, highlighting the irregular, eastern mound flank interpreted as representing snouts of debris flows (flint nodules marked in red) (arrows 5, 6 and 7), and the possible slump scar at the western flank (arrows 1, 2, 3, 4).



Fig. 4. Cluster of the pedunculate brachiopod *Magas chitoniformis*. Housed at Geomuseum Faxe (OESM-4620). The 53 visible brachiopods are well preserved without any traces of wear or predation and belong to a single spatfall (Fig. 5). The few cracks are caused by later compaction of the very pure, soft chalk. Photograph by Sten L. Jakobsen.

thin slab contains only one layer of the brachiopod and is accordingly interpreted to parallel the original sediment-water interface. The cluster is monospecific and comprises at least 53 specimens. They are all well preserved without any signs of wear by transport or indications of predations such as gastropod borings, which are otherwise well known in brachiopods from the chalk (Surlyk 1972, 1973). The fragmentation, cracks and fissures seen in some of the shells are caused by late compaction of the surrounding chalk at contacts between more or less empty shells. These features and the lack of scatter of the specimens indicate rapid burial in the surrounding chalk.

The size-frequency distribution of the total assemblage (Fig. 7) is interesting and unusual for the brachiopod populations in the chalk which almost always have strongly right-skewed size-frequency distributions with a strong dominance of mm-sized juveniles (Surlyk, 1972). The size-frequency distribution of the cluster differs fundamentally from this pattern, not only in being unimodal with a *single* year class represented, but the specimens are all adults in contrast to virtually all assemblages known from the chalk (Fig. 7). Almost all specimens in the cluster fall in the 0.25–10.0 mm length class with an average length of 7.0 mm. The size-frequency distribution thus shows that the cluster represents a single spatfall. The larvae were successfully attached to a soft substrate of which there is no direct trace. This soft substrate was in all likelihood a sponge, reflected by the abundance of body fossils and imprints after sponges in the aptly

named Sponge Bed. Other fossils from the Sponge Bed also show remarkable preservation, e.g. a slab containing abundant siliceous sponge fragments also contains a specimen of a regular echinoid, with all the delicate spines preserved immediately adjacent to the test (Fig. 5). It is referred to the species *Phymosoma ravni*, which is described in detail in Schlüter *et al.* (2012).

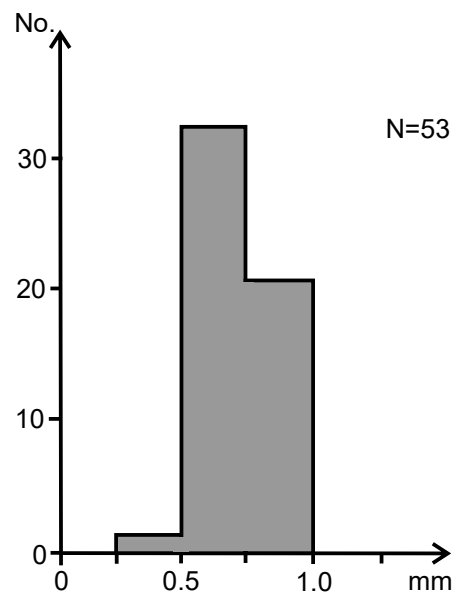


Fig. 5. Unimodal size-frequency distribution of the *Magas chitoniformis* specimens in the cluster shown in Figure 4, indicating that the cluster represent a single spatfall.

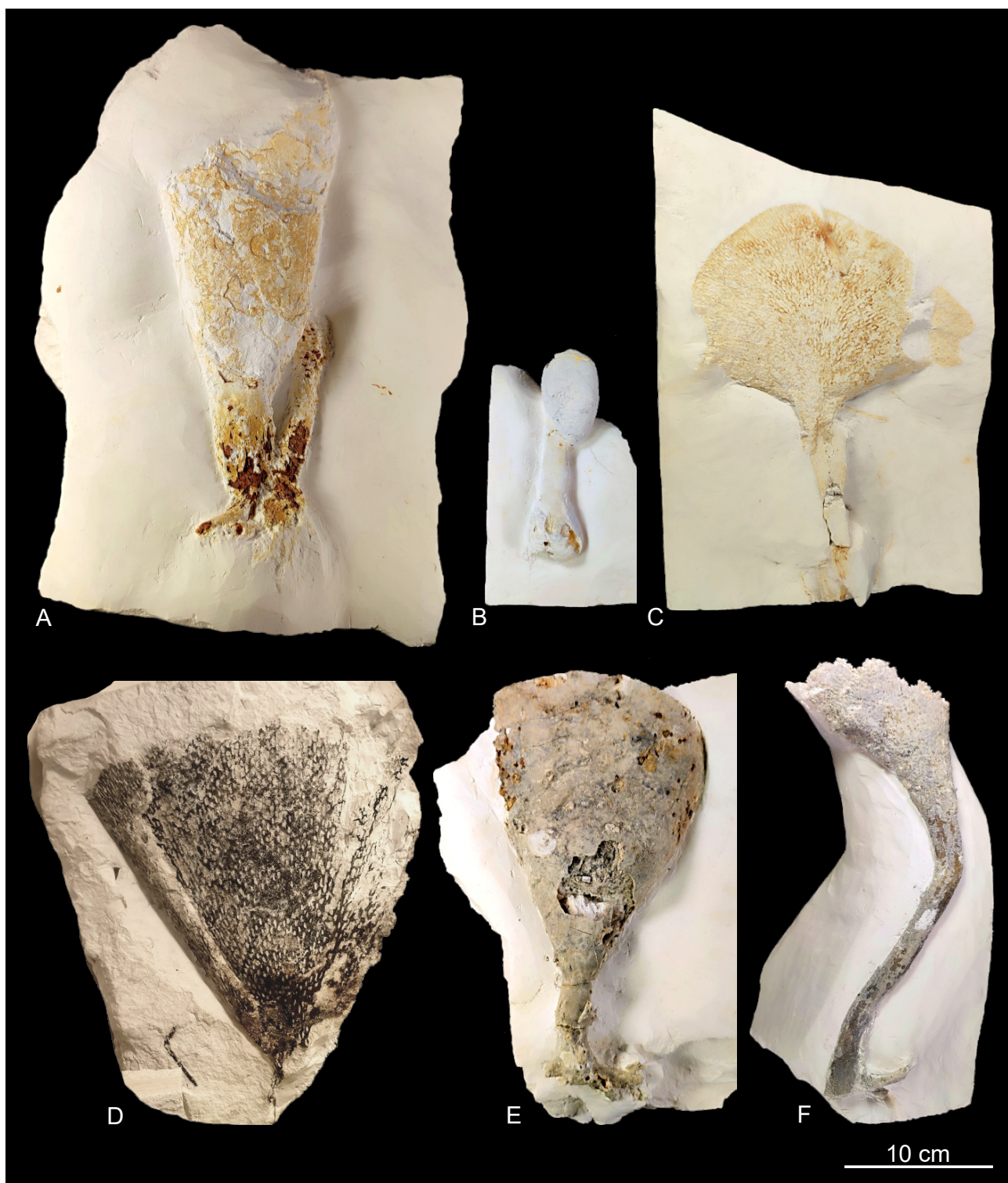


Fig. 6. Sponges preserved in 3D in the Sponge Bed. Sigerslev Member at Sigerslev quarry, Stevns Klint. **A–E:** Sponges very similar to *Ventriculites* (Hexactinellida, Lychniscosida), which is very common in the Upper Cretaceous. **E:** This sponge has the outer dense cortex layer preserved. **A, B, F:** These have pieces of a pyritified stalk preserved. **A:** This sponge has a possible *Ventriculites* attached to it. **B:** This stalk has a soft sponge with a short stalk attached to it, which may be similar to *Hyalonema* (Hexactinellida, Amphidiscophorida).

According to their outer shape and surface channels, the sponges are very similar to *Ventriculites* (Hexactinellida, Lychniscosida), a genus very common in the Upper Cretaceous (Figs 4A–E). One has the outer dense cortex layer preserved (Fig. 4E), some are pieces of a pyritified stalk (Figs 4A, B, F), one with a possible *Ventriculites* attached (Fig. 4A), another stalk has attached to it a soft sponge with a short stalk, that may be similar to *Hyalonema* (Hexactinellida, Amphidiscophorida). *Hyalonema* is an extant genus, which is occasionally found in the Upper Cretaceous (Mehl & Hauschke 1995; Dorte Janussen, pers. comm. 2024).

Attachment of brachiopods to sponges is a well-known phenomenon. Palaeozoic sclerobionts on sponges include bryozoans, brachiopods, acrothoracic

barnacles, tabulate and rugose corals and other sponges, whereas Mesozoic sclerobionts comprise brachiopods, bivalves, serpulids, bryozoans and several other groups (e.g. Palmer & Fürsich 1981; Luci *et al.* 2023). The preferred and most commonly used substrate of modern terebratulid brachiopods from Antarctica and New Zealand are erect bryozoans, but sponges, rocks and echinoid spines have also been used as suitable substrates (Lee 1990; Barnes & Peck 1996).

A second example of a brachiopod cluster was found by the author back in the 1960s in a very pure lower upper Maastrichtian chalk at Nørre Flødal, northern Jylland, Denmark (marked with an asterisk in Fig. 1). The cluster was interpreted as follows: “The chalk contains abundant imprints after sponges and it

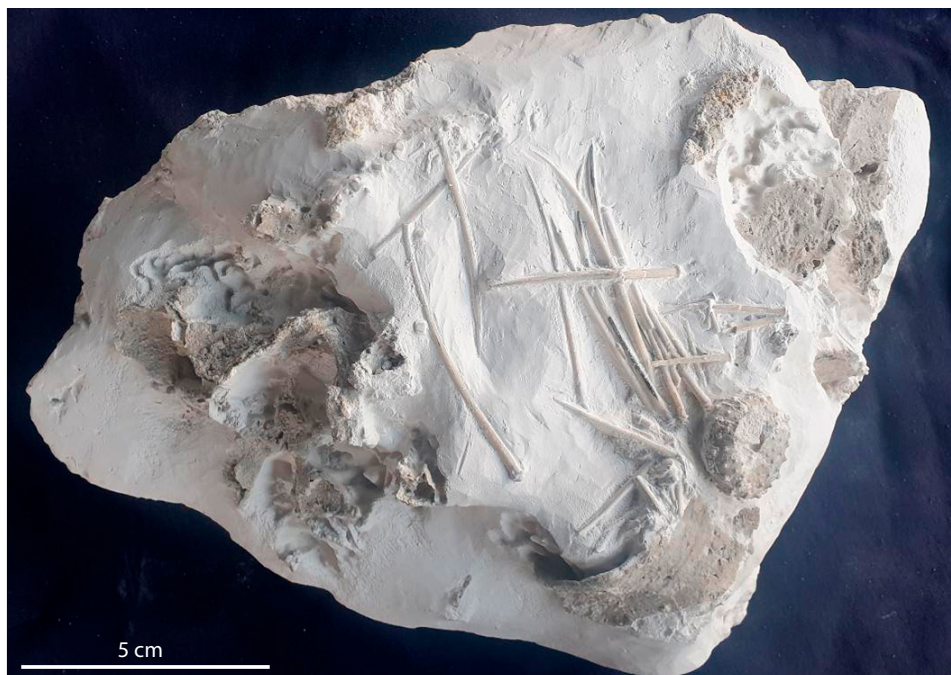


Fig. 7. Slab of pure chalk with abundant siliceous sponge fragments and a well-preserved specimen of the regular echinoid *Phymosoma ravni* with all its long, delicate spines preserved immediately adjacent to the test, indicating instantaneous burial probably by a chalk ooze debris flow. Sponge Bed, upper upper Maastrichtian, Sigerslev Member at Sigerslev quarry, Stevns Klint. Leg. Peter Benicke. Photograph by Sten L. Jakobsen.

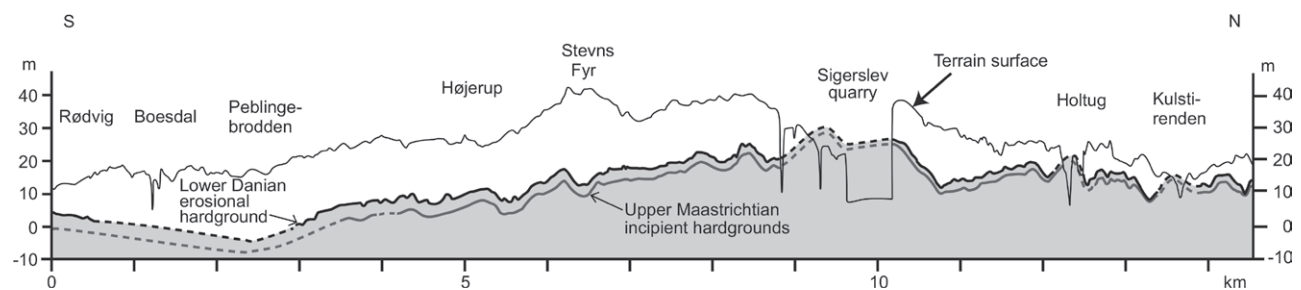


Fig. 8. Vertically exaggerated profile of Stevns Klint, showing the position of the Maastrichtian–Danian boundary which in this scale coincides with the ‘lower Danian erosional hardground’. The position of the Sigerslev quarry is indicated and the *Magas chitoniformis* cluster was found where the boundary forms a small terrace below the letters ‘arry’ in ‘quarry’. The instantaneous burial of the Sponge Bed and the *Magas chitoniformis* cluster is interpreted as caused by a debris flow on the slope of a small mound (Fig. 3) or by a debris flow sourced from the top of the large contourite ridge immediately to the south of the quarry at 9.4 km on the horizontal axis. The crest is about 30 m higher than the valley at 2.4 km, illustrating the remarkable sea-floor relief in the area formed by persistent WNW-flowing bottom currents in the latest Maastrichtian. From Lykke-Andersen & Surlyk (2004, fig. 13).

is considered most likely that the brachiopods were attached to a sponge and fell into a well-defined cluster by the death of the sponge. There are no indications of the brachiopods having been subjected to any significant transport" (Surlyk 1969, p. 283, Pl. 23, translated from Danish). This cluster is dominated by adult specimens of *Magas chitoniformis* but also contains a few specimens of *Gyrosoria gracilis* (von Schlotheim, 1813). Again, the notion of abundant imprints after soft sponges found together with a cluster of adult brachiopods is strongly suggestive of the substrate for the brachiopod spatfall being a soft-bodied sponge which was turned over and buried in the soft chalk, resulting in the death of both sponge and brachiopods.

Discussion

The examples presented here thus show that larger brachiopod species which normally require a large hard substrate could find appropriate substrates at times when the chalky sea floor was rich in soft sponges. The excellent preservation of the brachiopods in both samples apart from compaction fractures shows that the sponge and the attached fauna were instantaneously burrowed. The normal sedimentation rate is far too slow to account for rapid burial as it amounts to a few cm/ka. The large size of the extremely well-preserved sponges in the present examples supports the interpretation of instantaneous burial in soft chalk (Figs 4, 6, 7).

A causal agent overturning and burying the sponge could be by swimming animals, such as rays, which commonly seek their food in the upper sediment layers and are known to excavate bowl-shaped depressions, *Piscichnus waitemata* (e.g. Martinelli *et al.* 2001). But this interpretation does not fully explain the abundance of well-preserved sponge body fossils and imprints. Sediment gravity flows are the most likely agent responsible for the burial of the diverse fauna. Muddy turbidity currents or debris flows sourced from chalk ooze close to the sediment-water interface are close to impossible to identify directly in the monotonous chalk and would not leave any traces especially after subsequent bioturbation. A debris flow of chalk ooze from the uppermost, unlithified sea floor is thus considered the most likely cause for the instantaneous burial of the brachiopod assemblage and its soft-bodied substrate. A trigger mechanism could be strong earthquakes caused by syndepositional faulting. Syndepositional faults identified on reflection seismic data are common in the chalk offshore Stevns Klint (Esmerode *et al.* 2007; see also Erlström *et al.* 2018, fig. 1). The N–S-trending Stevns Fault is thus

situated a few kilometres east of the locality. Major earthquakes caused by movements on the faults are thus suggested as a triggering mechanism for debris flows composed of chalk ooze which would result in burial and sudden death of much of the benthic fauna. The source area of such debris flow could be the slopes of the small mounds on the seafloor adjacent to the Sponge Bed. The slope angles of the mounds were 10–15° (Anderskov *et al.* 2007). The mound topographies are normally regular and outlined by layers of flint nodules and flint layers. In contrast, the eastern flank of a nearby mound at the same level as the Sponge Bed shows step-wise terracing and a few over-steepened layers suggestive of slumping (Fig. 3). It is, however, remarkable and probably significant that the Sponge Bed is situated a short distance to the north of the crest of a major sea floor contourite ridge formed by WNW-flowing bottom currents (Fig. 8). The ridge had a relief of as much as 30 m above the deepest valley in the chalk exposed at Stevns Klint and 10–20 m above the surrounding sea floor (Lykke-Andersen & Surlyk 2004; Surlyk *et al.* 2006; Anderskov *et al.* 2007). This ridge was an obvious potential source for generating large-volume debris flows composed of chalk ooze, which would travel a short distance of about 500 m down the northern slope to come to a rest on a slope terrace (Fig. 8; Surlyk *et al.* 2006, fig. 13). Such a debris flow comprising completely unconsolidated chalk ooze would not leave any trace in the form of sedimentary structures; the main evidence being the rich instantaneously buried fauna, comprising large 3D preserved sponges and a wealth of other unusually well-preserved faunal elements (Figs 4, 6, 7). So, both short-travelled debris flows down the flanks of the small mounds (Fig. 3) and debris flows from the crest of the large ridge (Fig. 8) are likely agents in the instantaneous burial of large, delicate fossils, such as sponges.

Conclusions

A monospecific cluster comprising at least 53 adult specimens of the brachiopod *Magas chitoniformis* is described from the uppermost Maastrichtian chalk at Stevns Klint, Denmark. The cluster was found at a level called the Sponge Bed by fossil collectors, due to the abundant occurrence of commonly large body fossils and imprints of sponges, some of which were soft bodied. The size-frequency distribution of the brachiopod assemblage is unimodal, comprising fully grown individuals with an average length of 7 mm. This population structure is fundamentally different from that seen in the other brachiopod species in the

chalk, which are almost all strongly right-skewed with a dominance of juvenile individuals (Surlyk 1972).

The brachiopods are well preserved without any signs of transport or predation. They are interpreted as representing a single spatfall attached to a soft substrate, which was buried instantaneously by chalk ooze causing the death of the sponge and its epifauna. The causal mechanism for the burial is interpreted as a debris flow triggered by a strong earthquake and sourced either from immediately adjacent low chalk mounds or from the nearby crest of a major contourite sea-floor ridge. The earthquake was probably caused by movements on syn-depositional faults located offshore Stevns Klint. This is an excellent example of the substrate preference of a pedunculate brachiopod in a case where hard substrates of a suitable size were not available and adds to earlier interpretations of modes-of-life of the diverse brachiopod fauna of the Danish Maastrichtian.

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First occurrence of a fish otolith from the Eocene Fur Formation, Denmark

ANE ELISE SCHRØDER, GIORGIO CARNEVALE & WERNER SCHWARZHANS



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Bony fishes are among the best represented macrofossils from the earliest Eocene Fur Formation of Denmark. However, until now, otoliths from this formation have never been reported. Here we describe the first otolith from the Fur Formation, which was found isolated in a carbonate concretion. The specimen exhibits the typical features of an argentinoid otolith. To date, only a single argentiniform species, based on skeletal remains, has been documented from the Fur Formation – *Surlykus longigracilis* Schrøder & Carnevale, 2023 – which also represents the most abundant teleost species. Therefore, we refer the isolated otolith to *Surlykus longigracilis*. The discovery of this otolith offers the opportunity to review the many argentiniform otolith-based taxa known from the Paleocene of Denmark. One species is now also placed within the genus *Surlykus* – *S. procerus* (Schwarzhans, 2003) and another argentiniform otolith-based taxon from the Paleocene of Denmark is described – *Pseudonansenia hauniensis* n. gen., n. sp.

Keywords: north-western Limfjord area, Ypresian, carbonate concretion, Argentiniformes, *Surlykus longigracilis*.

Ane Elise Schrøder [aes@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark; also Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy [aneelise.schroder@unito.it]. <https://orcid.org/0000-0001-9371-400X>. Giorgio Carnevale [giorgio.carnevale@unito.it], Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy <http://orcid.org/0000-0002-3433-4127>. Werner Schwarzhans [wswschwarz@aol.com], Ahrensburger Weg 103, D-22359 Hamburg, Germany; also Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. <http://orcid.org/0000-0003-4842-7989>.

<http://zoobank.org/urn:lsid:zoobank.org:pub:859388AA-E6B7-4FAB-ABF6-5E16252AE99C>

Otoliths have neither been documented nor described from the Ypresian (earliest Eocene) Fur Formation in northern Denmark. This is striking as the formation is world-renowned for its exquisitely preserved fossils, particularly the articulated skeletal remains of the ichthyofauna, especially also considering the different modes of fossil preservation related to the lithologies (e.g. Kühne 1941; Bonde 1982; Pedersen *et al.* 2012, Schrøder *et al.* 2023b). With its wealth of exquisitely preserved and abundant fossil teleosts, the Fur Formation ichthyofauna is considered as one of the earliest and best preserved immediately succeeding the K/Pg-boundary (e.g. Bonde 1979, 1982, 2008; Pedersen *et al.* 2012; Schrøder *et al.* 2022, 2023a, b; Schrøder &

Carnevale 2023). Thousands of well-preserved specimens are housed in museum collections across Denmark, e.g. Fur Museum (Museum Salling), Fossil and Mo-clay Museum (Museum Mors), and the Natural History Museum of Denmark (Copenhagen University). In addition, the collection assembled by Walter Kühne (Kühne 1941) was purchased in the 1930th by the British Museum, and is hence kept at the Natural History Museum (London).

While no otoliths have so far been reported from the early Eocene Fur Formation, there is abundant knowledge of otoliths from the middle Paleocene (Selandian) of Denmark (Koken 1885; Schwarzhans 2003). The Selandian sediments of Denmark, chiefly around

Copenhagen, are rich in otoliths and have shown a high degree of diversity. We review those findings in the light of this isolated finding of a single argentiniform otolith from the Fur Formation. The otolith from the Fur Formation is preserved as a mold with the otolith body having fallen out during recovery and the remainder having been removed during preparation.

The aim of the present paper is, therefore, to document and describe the first and thus far only known otolith from the earliest Eocene Fur Formation, and to review the middle Paleocene argentiniform otolith records from Denmark.

Geological setting

The Ypresian Fur Formation crops out in the north-western Limfjord area of Denmark (Fig. 1A). The exposed formation localities and near surface occurrences cover a large region from the western part of Himmerland to the northern part of Salling, the islands of Mors and Fur, to the area of Thy (Fig. 1B). The majority of exposures are present at Mors and Fur, i.e. old digging pits and costal outcrops. The formation comprises a 60 m thick fossil-rich, marine diatomite interbedded with more than 180 distinctive ash layers. It was deposited below storm wave base in the North Sea Basin, presumably in a local, nutrient-rich area, leading to extensive diatom blooms (see Bonde 1979; Pedersen & Surlyk 1983; Pedersen *et al.* 2012; Schröder & Carnevale 2023). The original ash sequence of the Fur Fm was subdivided into a negative and positive series, assigned official numbers from –39 to –1, and from +1 to +140 (Bøggild 1918). Additional recognised ash layers, not included in the original series, have been assigned letters together with the number of the original ash layer (Gry 1940; Pedersen & Surlyk 1983; Pedersen & Buchardt 1996; Larsen *et al.* 2003). The negative and positive sequences also reflect the two separate formation members: the lower Knudeklint Mb (–33 to –1) which is largely laminated with relatively few ash layers, and the upper Silstrup Mb (+1 to +140), which is dominated by structureless beds with numerous ash layers (Fig. 1C). Together with the overall scarce benthic fauna, laminated beds and tetany evident from the well-preserved fossil fishes, the sequences indicate a fluctuating oxygen level, varying from anoxic to slight dysoxic conditions (Pedersen 1981; Pedersen & Surlyk 1983; Heilmann-Clausen *et al.* 1985; Schröder *et al.* 2022; Schröder & Carnevale 2023). The ash layers originate from the volcanic eruptions related to the opening of the North Atlantic. Radiometric $^{39}\text{Ar}/^{40}\text{Ar}$ -dating of ash layers –17 and +19 resolved the age of the formation to ~55.6

Ma and ~54.4 Ma, respectively (e.g. Chambers *et al.* 2003; Storey *et al.* 2007; Stokke *et al.* 2020). The ash layers below –33 belongs to the lowermost part of the Haslund Mb of the Ølst Formation, i.e. the so-called Stolleklint clay unit (Fig. 1C; Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995; Heilmann-Clausen & Schmitz 2000). The Paleocene–Eocene boundary was identified in the lowermost part of the Stolleklint clay established on the onset of the Carbon Isotope Excursion (Schmitz *et al.* 2004; Stokke *et al.* 2020, 2021).

Only the Stolleklint clay unit of the lowermost Ølst Fm is exposed on the islands of Mors and Fur. The Ølst Formation, which is largely replaced by the Fur Fm in the western Limfjord area of northern Denmark, is otherwise present across most of the Danish Eocene (Heilmann-Clausen 1995; Sheldon *et al.* 2012).

Material and methods

The material of the present study contains a single otolith, FUM-N-13271. It was collected as a loose slab from the Østklinten locality (klint = cliff) at the island of Fur (Fig. 1). The stratigraphic level, i.e. which ash layer the carbonate concretion originate from, is unknown. At present, this is the only known otolith retrieved from the Fur Formation. The specimen is preserved mainly as an imprint *ex situ* in a carbonate concretion originating from the Fur Formation. Scarce original matrix of the otolith body was still present, mostly in the ventral part of the impression, when the specimen was loaned from the Fur Museum (Fig. 2). The authors were subsequently granted official permission by Fur Museum to remove the remaining matrix to get a clean imprint, in order to expose as much of the morphological details. The cleaning was performed mechanically with a fine needle (Fig. 3A).

The otolith was initially examined and photographed, using a Zeiss Stemi 508 microscope, applying the Zeiss Zen Core 3.5 software, and later using a Wild M3C for visual inspection and a Wild M400 macroscope for photographing. Individual photographs of several fields of depth intervals were captured by a Canon EOS-1000D mounted on the macroscope and connected to a computer. The individual photographs were then stacked using the HeliconFocus software of Helicon Soft (Kharkiv, Ukraine) to generate a continuously focused image. Comparative figures are drawings refigured from Schwarzhans (2003). We also conducted μXRF -analyses before removal of the remaining otolith matrix using a Bruker M4 Tornado Plus Amics (see Schröder & Carnevale 2023 for machine settings). However, the element-mapping did not yield additional morphological results.

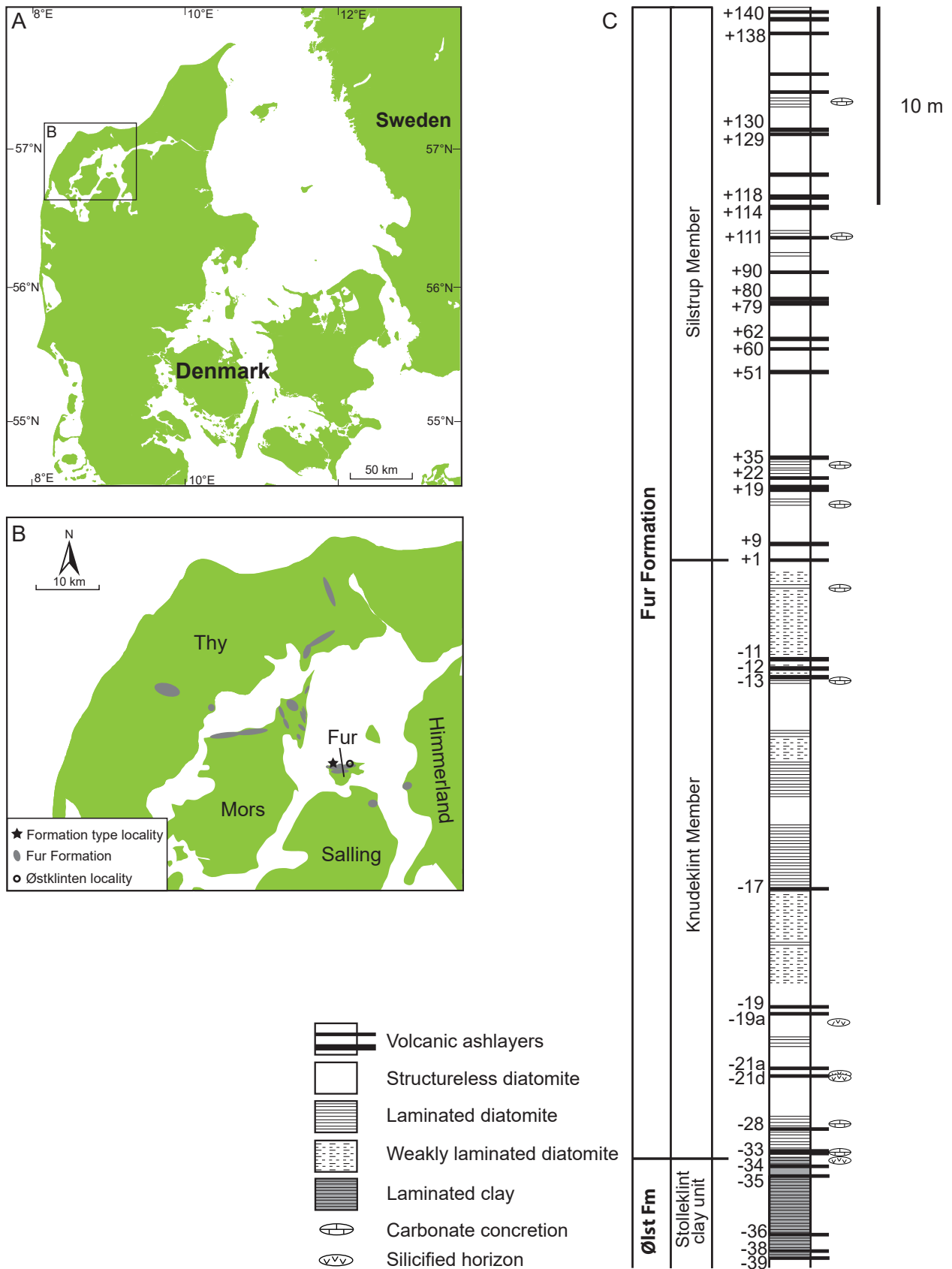


Fig. 1. **A:** map of Denmark with the western Limfjord area marked out. **B:** Fur Formation outcrop localities and near surface occurrences. The Fur Formation type locality is indicated by a black star, and the Østklinten locality by a circle. **C:** sedimentological log of the Fur Formation and lowermost part of the Ølst Formation, the Stolleklint clay, which is exposed at Mors and Fur. Levels with carbonate concreted horizons are indicated. Modified from Schröder and Carnevale (2023).

Institutional abbreviation. FUM-N, Fur Museum (Museum Salling).

Systematic palaeontology

Order Argentiniformes Bertelsen, 1958

Genus *Surlykus* Schröder & Carnevale, 2023

Type species. *Surlykus longigracilis* Schröder & Carnevale, 2023.

Otolith-based diagnosis. Argentiniform otoliths showing the following combination of characters: elongate otoliths with a moderately deep ventral rim, shallower dorsal rim, and a ratio otolith length : otolith height of 1.6 to 1.8. Rostrum strong, pointed or rounded. Postdorsal rim depressed, without prominent angle. Sulcus long, slightly supramedian, cauda length : ostium length 1.8 to 3.0. Cauda narrow, slightly bending convex along the entire length, slightly narrowed towards the tip. Ostium narrow, with flat, slightly downward bent ventral margin.

Comparison. The slight convex bending of the cauda and its narrowed tip are distinctive features that allow a clear separation from all other otoliths of argentiniform genera, with the exception of the coeval, fossil otolith-based *Protargentinolithus*. Otoliths of *Surlykus* differ from those of *Protargentinolithus* in having the ventral margin of the ostium slightly bent downward (vs. horizontal), and in being more elongate (otolith length : otolith height = 1.6–1.8 vs. 1.3–1.45).

Species. The otolith described below is attributed to *Surlykus longigracilis* based on the observation that the articulated skeletons of this species are the most common, and also the only known argentiniform species of the Fur Formation from which the otolith imprint was obtained. Furthermore, we assign *Protargentinolithus procerus* Schwarzhans, 2003 from the middle Paleocene (Selandian) of Denmark to the genus *Surlykus*.

Surlykus longigracilis Schröder & Carnevale, 2023
Figs 2, 3A

2023 (updated version published 2024)

Surlykus longigracilis, Schröder & Carnevale: figs 2–8.

Holotype. MM-13564_5, nearly complete, well-preserved articulated specimen on a single slab of carbonate concretion, bordered by five designated paratypes.

Paratypes. Five paratypes are associated with the holotype in the single slab of carbonate concretion, MM-13564, which also contains a single referred specimen (MM-13564_7; see figures 2 and 3 in Schröder & Carnevale 2023): MM-13564_1 is the largest nearly complete, well-preserved articulated paratype on the slab, 83.7 mm SL; paratype MM-13564_2 is well-preserved and almost complete, 64.4 mm SL; MM-13564_3 is a well-preserved, nearly complete paratype, however, most of the squamation and neural spines in the precaudal region are not preserved, 54.9 mm SL; MM-13564_4 is well-preserved and nearly complete, 66.0 mm SL; MM-13564_6, a well-preserved, nearly complete paratype, however, most of the squamation in the abdominal region is not preserved, 54.3 mm SL; FUM-N-10506, well-preserved head skeleton, showing exquisitely preserved details of the lateral-line canal, plus the pectoral girdle and anteriormost part of the vertebral column.

Type locality. Fur Formation, lowermost Eocene. The slab containing the holotype, five paratypes and a referred specimen originates from Ejerslev mo-clay pit, on the island of Mors, north-western Limfjord area, Denmark, from a stratigraphic level between ash layer +25 to +30, Silstrup Member.

Description of otolith FUM-N-13271. Otolith size 5.9 mm in length. Ratio otolith length : otolith height = 1.8. Ventral rim moderately deep, regularly curved and finely crenulated. Rostrum long, pointed, occupying 25% of otolith length. Dorsal rim irregularly rounded and irregularly undulating, with small, rounded postdorsal angle and long, depressed postdorsal region. Posterior tip tapering, moderately pointed.

Inner face relatively flat, with long, slightly supra-median and slightly deepened sulcus. Ratio cauda length : ostium length 1.8. Ostium narrow, with flat, slightly downward bent ventral margin, and broad opening to predorsal rim. No excisura or antirostrum discernable. Cauda narrow, slightly bending convex along entire length, slightly narrowed towards tip, terminating very close to posterior tip of otolith. Dorsal depression wide but with indistinct margins. Ventral field with very weak indication of ventral furrow at some distance from ventral rim of otolith and many fine radial furrows starting from the crenulation of the ventral rim. Outer face not known.

Comparison. The otolith allocated to *Surlykus longigracilis* differs from the Paleocene *S. procerus* (Schwarzhans, 2003; Fig. 3B) in being more slender (ratio otolith length : otolith height 1.8 vs. 1.6), a pointed and long rostrum, occupying 25% of otolith length (vs. rounded and length occupying 15% of otolith length), and a lower ratio



Fig. 2. High-resolution photograph of FUM-13271 (reversed). The otolith impression as it was found, before the scarce otolith matrix was removed.

cauda length : ostium length (1.8 vs. 3.0). The Paleocene formations of Denmark yielded a number of further argentiniform otolith-based species. *Protargentinolithus erraticus* (Roedel, 1930; Fig. 3C–E) differs from the two known *Surlykus* species in being more compressed and by having a straight ventral margin of the ostium (see above) and, occasionally, a more pronounced postdorsal angle in front of the depressed postdorsal section. *Protargentinolithus* appears to be closely related to *Surlykus*, and we therefore consider *Protargentinolithus incertae sedis* within the Argentiniformes. Furthermore, there are also two otolith-based species in the Danish Paleocene that are associated with genuine argentinids, which are placed within the genus *Argentina* – *A. tricenulata* (Stinton, 1965; Fig. 3F–I) and *A. longirostris* (Schwarzahns, 2003 (Fig. 3J–K). Otoliths of the genus *Argentina* are characterized by a prominent postdorsal angle, while this region is depressed in *Surlykus* and *Protargentinolithus*. Finally, otoliths that were originally recorded as Argentinidae *indet.* in Schwarzahns (2003) are now described as a new argentiniform genus and species – *Pseudonansenia hauniensis* – as follows.

Genus *Pseudonansenia* n. gen.

Type species. *Pseudonansenia hauniensis* n. sp.

Etymology. Based on the similarity with otoliths of the extant genus *Nansenia* Jordan & Evermann, 1898

Diagnosis. A fossil otolith-based genus of the Argentiniformes with the following combination of characters: otolith shape elongate fusiform, with obtuse mediodorsal and medioventral angles resulting in a nearly symmetrical appearance. Rostrum and posterior tip likewise symmetrical, tapering, with rounded tip. Otolith length : otolith height = 2.0. Ostium nar-

row, much shorter than cauda; cauda length : ostium length = 2.2. Cauda almost straight, slightly convex ventrally.

Discussion. *Pseudonansenia* otoliths resemble slender argentinid and microstomatid otoliths, for example those of the extant genus *Nansenia* (see Lombarte *et al.* 2006 for extant otolith) because of its slender shape. The shape of the dorsal rim with the dominant mediodorsal and the depressed postdorsal region as well as the ventrally sagging cauda does not relate to any known extant argentinid or microstomatid clade. Therefore, we consider *Pseudonansenia* as *incertae sedis* within the Argentiniformes.

Species. *Pseudonansenia* is a monospecific genus with *P. hauniensis* known from the middle Paleocene (Selandian) of Denmark.

***Pseudonansenia hauniensis* n. sp.**

Fig. 3L

2003 genus *Argentinidarum* sp., Schwarzahns: figs. 15H–J

Holotype. MGUH 26090, Sundkrogen, København, Lellinges Greensand, Selandian, middle Paleocene. Fig. 3L (refigured from Schwarzahns, 2003).

Paratypes. MGUH 26091–26092, five specimens, same data as holotype.

Etymology. Named after Hafnia, the Latin name for København.

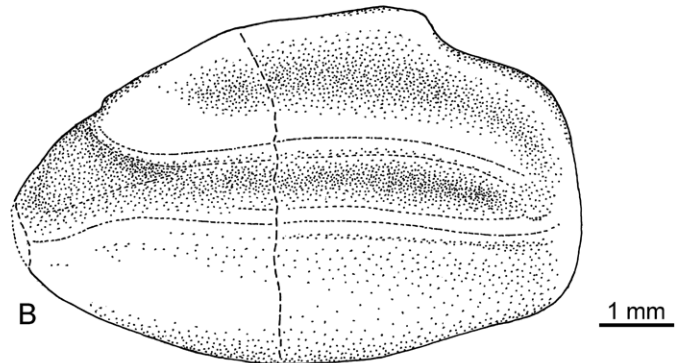
Diagnosis. See diagnosis of *Pseudonansenia* (monotypic genus).

Description. Slender, thin otoliths up to a size of about 2.4 mm in length (holotype). Otolith length : otolith height = 2.0. Dorsal rim low, anteriorly and posteriorly straight, inclined, joined at obtuse mediodorsal angle.

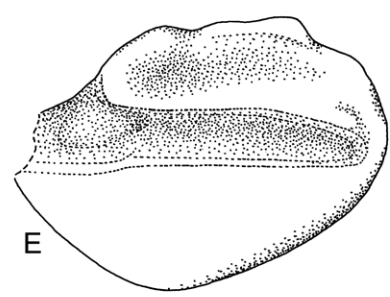
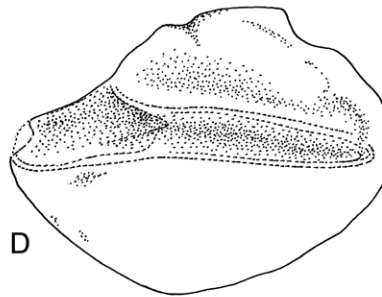
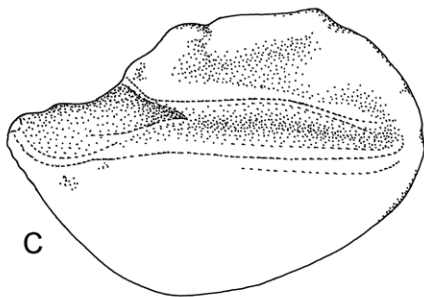
Ventral rim slightly deeper than dorsal rim, otherwise nearly symmetrical to dorsal rim with more broadly rounded medioventral angle and posteriorly faintly and irregularly undulating. Rostrum bluntly rounded,



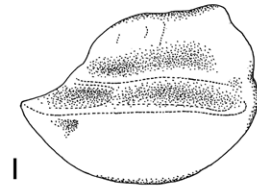
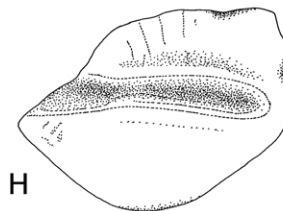
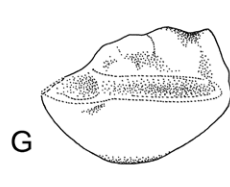
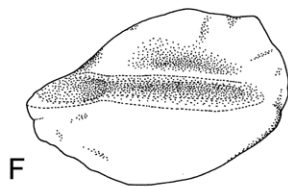
Surlykus longigracilis
Schröder & Carnevale, 2023



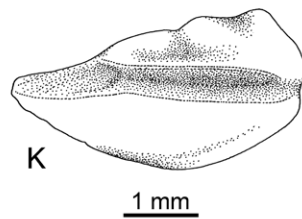
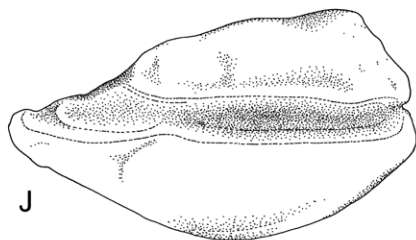
Surlykus procerus (Schwarzahns, 2003)



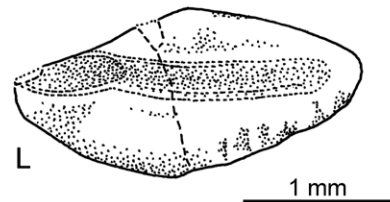
Protargentinolitus erraticus (Roedel, 1930)



Argentina tricrenulata (Stinton, 1965)



Argentina longirostris Schwarzahns, 2003



Pseudonansenia hauniensis n.gen., n.sp.

Fig. 3. Comparison panel. **A:** *Surlykus longigracilis* Schröder & Carnevale, 2023 (updated 2024), Fur Formation, high-resolution photograph of FUM-13271 (reversed). **B–L:** otolith drawings refigured from Schwarzahns (2003): **B:** *Surlykus procerus* (Schwarzahns, 2003), paratype, Selandian, Vestre Gasværk, København, MGUH 26071. **C–E:** *Protargentinolitus erraticus* (Roedel, 1930), Selandian, Sundkrogen, København, MGUH 26063–26069. **F–I:** *Argentina tricrenulata* (Stinton, 1965), Selandian, Kongedyb, off København, MGUH 26076–26079. **J–K:** *Argentina longirostris* Schwarzahns, 2003, J = paratype, MGUH 26085, K = holotype, MGUH 26084, Selandian, Sundkrogen, København. **L:** *Pseudonansenia hauniensis* n. gen. et n. sp., holotype, MGUH 26090, Selandian, Sundkrogen, København.

occupying 23% of the otolith length. No antistrotrum or excisura discernable. Posterior tip of otolith tapering, nearly symmetrical in appearance to rostrum.

Inner face nearly flat, with long, slightly supramedian and moderately deepened narrow sulcus. Ostium narrow, nearly as narrow as cauda, and much shorter; cauda length : ostium length = 2.2. Ostium widely open to anterior-dorsal rim, slightly deepened against cauda. Cauda almost straight, slightly convex towards ventral, reaching very close to posterior tip of otolith. Dorsal depression extremely faint; no ventral furrow discernable but a few radial furrows at postventral rim. Outer face nearly flat and smooth.

Discussion. The holotype is the only complete preserved specimen of the species, although broken into two parts. That was also the reason for leaving the specimen in open nomenclature in 2003. However, the otoliths of *P. hauniensis* are indeed unmistakable and now with the finding of an otolith that we link to the skeleton-based *Surlykus longigracilis*, we consider it pertinent to formally describe *P. hauniensis* and make it available for faunal and phylogenetic evaluations.

The nomenclatural acts of this paper is registered on ZooBank: <http://zoobank.org/urn:lsid:zoobank.org:act:F514C08F-EBE7-40B0-8BCF-BE23CFF30D59> (LSID of the new genus *Pseudonansenia*) and <http://zoobank.org/urn:lsid:zoobank.org:act:22B11054-36E6-415F-80F6-1D8002507F61> (LSID of the new species *Pseudonansenia hauniensis*).

Discussion

Through 2019 to 2023 several thousand fossil fish specimens from the Fur and Ølst formations were thoroughly checked for otoliths *in situ*, or possible otolith voids, by the first author. The most abundant species from the Fur Formation, *Surlykus longigracilis* Schröder and Carnevale, 2023, represents the only known argentiniform identified from the Fur Formation. Thus far, no otoliths have been found *in situ* in any of the studied articulated skeletons. The otolith impression described herein therefore represents the first to be described from the Fur Formation. It shows all the typical characteristics of an argentiniform otolith, which is the roughly pentagonal otolith shape with a deep ventral rim and a long and pointed rostrum, a supramedian sulcus divided into a long, almost straight and narrow cauda reaching very close to the posterior tip of the otolith and a shorter and narrow ostium with a nearly flat ventral margin. Since only a single argentiniform species (*Surlykus longigracilis*) is known by very abundant, articulated

skeletons from the Fur Formation, it seems reasonable to assume that the otolith impression, FUM-13271, belongs to the same species.

However, five different otolith-based argentiniform taxa are known from the middle Paleocene (Selandian; Schwarzhans 2003) and early Paleocene (Danian; Schwarzhans & Milán 2017) of Denmark. The otolith impression from the Fur Formation does not represent any of these Selandian taxa, although one of the species can be attributed to the same genus, *Surlykus procerus* (Schwarzhans 2003).

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The putative lampridiform *Iratulichthys ulrikii* gen. et sp. nov. from the Stolleklint clay unit of the Ølst Formation, Denmark

ANE ELISE SCHRØDER & GIORGIO CARNEVALE



Geological Society of Denmark
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The early Eocene Fur and Ølst formations are globally renowned for their exceptionally well-preserved ichthyofaunas. Until now, only one lampridiform genus and species, *Palaeocentrotus böggildi*, has been described from these, exclusively known from the Fur Formation. Here, we describe a new genus and species of lampridiform fish, *Iratulichthys ulrikii* gen. et sp. nov. from the earliest Eocene Ølst Formation. The single available specimen consists of moderately well-preserved and largely incomplete articulated skeletal remains, lacking most of the axial skeleton. It exhibits a unique set of morphological features that support its recognition as a new lampridiform genus, including a deep anterior concavity of the ethmoid region, orbitosphenoid lacking a ventral keel, presence of tiny, conical teeth in the lower and upper jaws, beryciform foramen piercing the anterior ceratohyal, unique predorsal formula (0/0/?+1/1/), and absence of parapophyses. Moreover, these characters, especially the presence of tiny conical teeth in the lower and upper jaws might suggest that it should be regarded as a putative stem-lampridiform. However, additional comparative information would be necessary to properly define its phylogenetic position within the lampridiform fishes.

Keywords: Lampridiformes, Ypresian, Eocene, Lampridomorpha, stem-lampridiform.

Ane Elise Schrøder [aes@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark; also Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy. <https://orcid.org/0000-0001-9371-400X>. Giorgio Carnevale [giorgio.carnevale@unito.it], Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy <https://orcid.org/0000-0002-3433-4127>.

<http://zoobank.org/urn:lsid:zoobank.org:pub:93C75928-C0CB-4E8A-9307-3729856EE9A7>

Understanding the impact of the Eocene climate in the diversification of the modern groups of teleosts may provide relevant information for investigating possible impacts of current climate changes on marine communities. The Eocene European ichthyofaunas, especially those from Denmark, England, Italy and Russia, are of global interest to understand climatic hazards today's oceans are facing. As far as concerns the Danish ichthyofaunas, the abundance of exquisitely preserved fish fossils from the earliest Eocene Ølst and Fur formations, have been largely neglected. However, over the last few years several papers on the fishes from the Ølst and Fur formations have been published, primarily dealing with

taxonomy, palaeoecological interpretations and modes of preservation (Schrøder *et al.* 2022; Schrøder and Carnevale 2023; Schrøder *et al.* 2023a; Schrøder *et al.* 2023b).

Lampridiforms are a well-defined clade within the acanthomorphs. Here, we use the term Lampridiformes, rather than Lampriformes, as endorsed by Colin Patterson (see Olney *et al.* 1993), which has been widely accepted and applied in the majority of taxonomic and phylogenetic studies (e.g. Oelschläger 1983; Patterson 1993; Wiley *et al.* 1998; Sorbini & Sorbini 1999; Wiley and Johnson 2010; Betancur *et al.* 2013; Bannikov 1991, 1999, 2014; Davesne *et al.* 2014, 2016, 2017; Delbarre *et al.* 2016, Carnevale

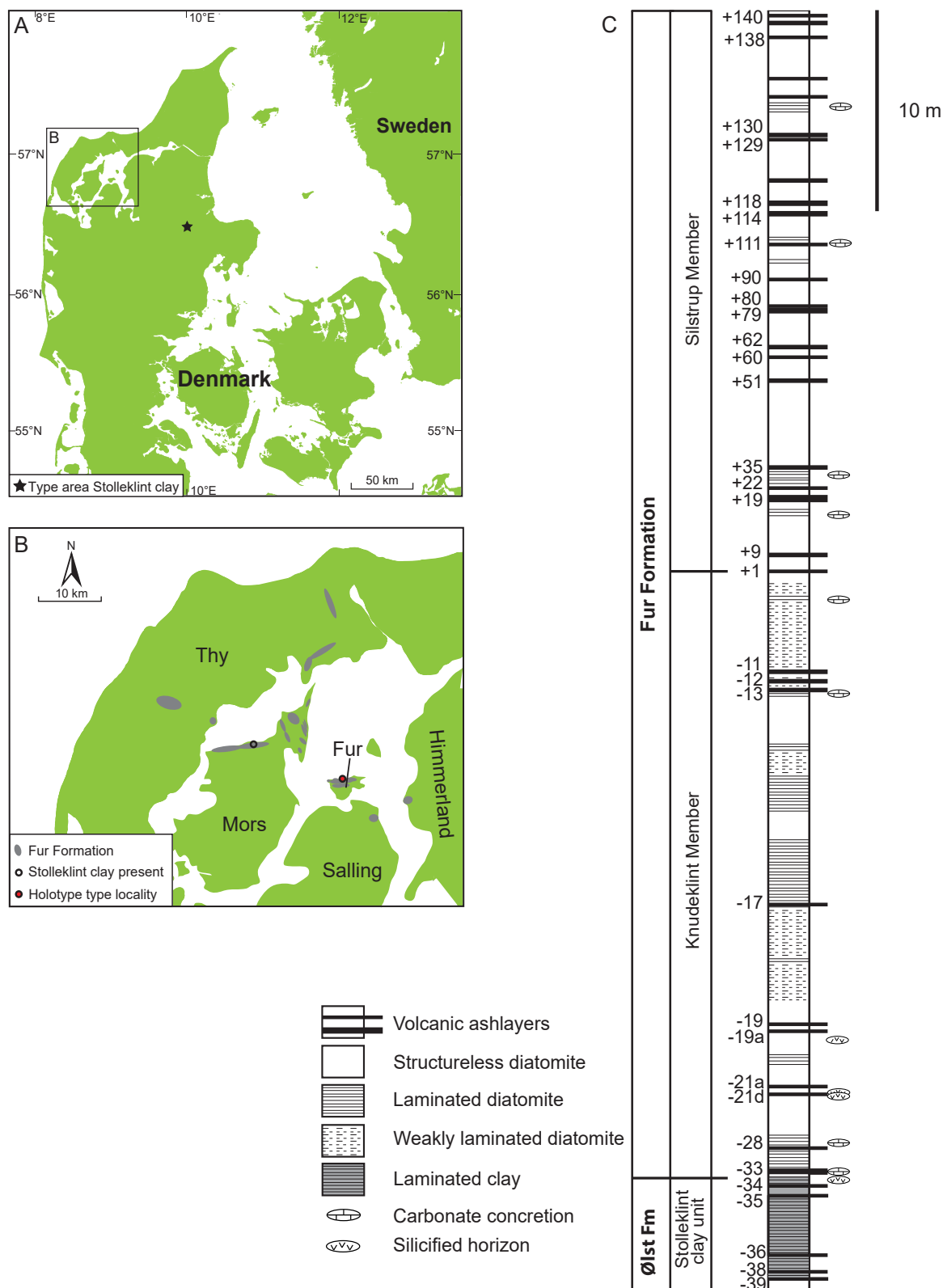


Fig. 1. A: Map of Denmark with the type area of the Stolleklint clay, located between the hills of Ølst and Hinge, marked by a star. **B:** Outcrop localities and near-surface occurrences of the Fur Formation overlying the lowermost part of the Ølst Formation, marked in grey. Circles mark locations where the underlying Stolleklint clay unit is occasionally exposed. **C:** Sedimentological log portraying the ash-series throughout the Stolleklint clay unit of the Ølst Formation, and the Fur Formation. The silicified clay slab containing the holotype specimen originates from a stratigraphic level between -39 to -34, possibly closest to -34. Modified from Schröder & Carnevale 2023.

and Bannikov 2018; Micklich & Bannikov 2022). The phylogenetic position of Lampridiformes is still debated, as molecular and morphological evidence often provide conflicting results (e.g. Davesne 2014, 2016; Brownstein & Near 2024). Molecular studies have thus placed Lampridiformes as sister group to Euacanthomorpha (e.g. Grande *et al.* 2013), as sister to the Acanthopterygii (e.g. Hughes *et al.* 2018), as sister to the Polymixiiformes (e.g. Li *et al.* 2009), as sister to the Paracanthopterygii (e.g. Betancur-R *et al.* 2013, 2017), as sister to the Polymixiiformes + Paracanthopterygii (Dettai & Lecointre 2005), and as sister to the Euacanthopterygii (Near *et al.* 2012). In addition, molecular studies based on mtDNA places Lampridiformes as sister to either Ateleopodiformes or Myctophiformes (for overviews on mitochondrial DNA-studies, see Miya *et al.* 2005, 2007; Poulsen *et al.* 2013). Conversely, the majority of the morphological studies have placed Lampridiformes as sister to all the other acanthomorphs, i.e. Euacanthomorpha (e.g. Johnson and Patterson 1993; Olney *et al.* 1993; Wiley *et al.* 2000).

Davesne *et al.* (2014) incorporated osteological datasets from both extant and fossil relatives in their phylogenetic study of Lampridiformes and found that Lampridiformes + *Pharmacichthys* Woodward, 1942 + *Aipichthyoidea* + *Pycnosteroides* Woodward, 1942 form the clade Lampridomorpha, which forms the sister group to the Euacanthomorpha, with the oldest representatives of Lampridomorpha being of Cenomanian age. This hypothesis was subsequently corroborated by Delbarre *et al.* (2016). Extant lampridiforms are strictly marine, pelagic fishes, comprising an astonishing morphological diversity considering their relatively low number, being represented by 26 extant species, arranged into six families grouped into the deep-bodied bathysomes (Veliferidae and Lamprididae) and the long-bodied taeniosomes (Lophotidae, Radiicephalidae, Regalecidae, Trachipteridae) (Olney *et al.* 1993; Davesne *et al.* 2014, 2016; Brownstein & Near 2024). At least 15 different genera of fossil Lampridiformes have been described to date (e.g. Sorbini & Sorbini 1999; Bannikov 1991, 1999, 2014; Carnevale 2004; Delbarre *et al.* 2016; Micklich & Bannikov 2022; Davesne *et al.* 2023). The oldest undisputable lampridiform *Nardovelifer altipinnis* Sorbini & Sorbini, 1999 (Campanian), was resolved as a stem-lampridiform due to the presence of a set of plesiomorphies not present in the crown group (Davesne *et al.* 2014; Delbarre *et al.* 2016; see also Brownstein & Near 2024). Morphologically, it is the most advanced Cretaceous lampridomorph taxon, with closest resemblance to extant veliferids (Sorbini & Sorbini 1999). All other Cretaceous lampridomorph taxa are morphologically similar, characterised by small, deep bodies, high and long-based dorsal fins, and moderately protrusible premaxilla (see Delbarre

et al. 2016, figure 12). *Bathysoma lutkeni* Davis, 1890, from the Paleocene of Denmark and Sweden is currently considered the oldest Cenozoic lampridiform (Patterson 1964, 1968; Davesne *et al.* 2014; Adolfssen *et al.* 2017). The latest combined morphological and molecular phylogeny supports that the origin of extant lampridiform morphotypes took place about 10 myr after the K/Pg-mass extinction event (Brownstein & Near 2024), which roughly corresponds with the age of the earliest Eocene Ølst and Fur formations of Denmark (Storey *et al.* 2007; Westerhold *et al.* 2009, Stokke *et al.* 2020) and the onset of the Paleocene-Eocene Thermal Maximum (Stokke *et al.* 2021).

To date, only a single lampridiform species, *Palæocentrotus böggildi*, Kühne, 1941, has been reported from the early Eocene of Denmark. It was the first fish from the Fur Formation to be described in detail, and to date only known from this formation (Kühne 1941; see also Patterson 1964; Bannikov 1999, 2014).

The aim of the present paper is to describe a new putative lampridiform taxon from the Stolleklint clay unit of the Ølst Formation underlying the Fur Formation in the western Limfjord region in northern Denmark.

Geological setting

The basal Eocene Ølst Formation is, contrary to the Fur Formation, present across most of the Danish Eocene, with observations from the western Limfjord area in northwestern Jutland, through eastern Jutland (Hinge, Ølst) to the Femern Bælt area (Lolland, southeastern Denmark) (e.g. Heilmann-Clausen *et al.* 1985; Sheldon *et al.* 2012). The Ølst Fm, however, is largely replaced by the Fur Formation in the northwestern Limfjord area, including on the islands of Mors and Fur (Fig. 1A–B; see also Heilmann-Clausen *et al.* 1985, figure 4 and 5). Only the lowermost part of the Ølst Formation, the Stolleklint clay unit, is exposed at these islands (Fig. 1C). This informal unit (for overviews see Heilmann-Clausen 1995 and Schröder *et al.* 2023b), comprises a non-calcareous, laminated silty clay with presence of silicified beds. The beds occur just below ash layer -33 (Fig. 1C). The Carbon Isotope Excursion (CIE) at the base of the Stolleklint clay at Fur, identifies the Paleocene–Eocene boundary (e.g. Schmitz *et al.* 2004; Stokke *et al.* 2020, Stokke *et al.* 2021). Most fossils uncovered from the Ølst Fm originate from these silicified beds exposed at Mors and Fur, between ash layers -34 to -39 (e.g. Pedersen *et al.* 2012). The type area of the Ølst Fm comprises the clay-pits situated on each side of Ølst Bakker (bakke = hill), close to the two cities Ølst and Hinge in Jutland (Fig. 1A). The Stolleklint clay reaches a thickness of approx. 15 m at the type area (Heilmann-Clausen 1995). One of the most important

localities exposing the Stolleklint clay unit is found on the island of Fur close to Stolleklint (klint = cliff), where the estimated thickness is 10 m, but difficult to determine due to the glacial reworking (Heilmann-Clausen 1995; Pedersen *et al.* 2012). The ash layers evident throughout the Ølst and Fur formations in the western Limfjord area, originate from the volcanic activity related to the opening of the Northeast Atlantic (e.g. Bøggild 1918; Pedersen & Surlyk 1983; Storey *et al.* 2007; Baumann *et al.* 2024). The ash layers were assigned official numbers by Bøggild (1918), encompassing a negative and a positive series from -39 to +140, respectively (Fig. 1C). However, as more distinctive layers are continuously identified, not included the original ash series, letters are assigned alongside the number of the original designated ash layer, e.g. 21a, 21d (e.g. Pedersen & Surlyk 1983; Pedersen & Buchardt 1996; Larsen *et al.* 2003; Pedersen *et al.* 2004).

Material and methods

The material of the present study is focused on a single, moderately well-preserved specimen, NHMD-625089, comprising the head skeleton and the posteriormost part of the body, including the pectoral and pelvic girdles and fins. The specimen is preserved in silicified, hardened clay of the Stolleklint clay unit, Haslund Member, Ølst Formation. It was collected to the left of Stolleklint on the island of Fur (Fig. 1B). The holotype, NHMD-625089 (designated herein) was declared Danekræ fossil trove in 2008 (fossil trove no. DK-551). It is therefore part of the Danekræ collection housed at the Natural History Museum of Denmark (University of Copenhagen, Denmark). However, this specimen is on permanent loan for Fur Museum, and hence kept in their collections, but not registered as a FUM-N-specimen.

The specimen was examined by both conventional methods applying a Leica M80, and by applying the μ XRF-element mapping method described by Schröder *et al.* (2023b) (see also Schröder & Carnevale 2023) using a Bruker M4 Tornado Plus Amics at the Department of Geosciences and Natural Resource Management, Copenhagen University. The benchtop device was set to a maximum acceleration of 50 kV and a current of 600 μ A. Measurements were obtained directly on the specimen with a digital caliper.

Institutional Abbreviations: NHMD, acronym for specimens housed in the collections of the Natural History Museum of Denmark; DK, acronym for specimens declared Danekræ fossil trove, and housed in the Danekræ collection of the Natural History Museum of Denmark; FUM-N, acronym for specimens

housed in the collections of Fur Museum, Museum Salling, Denmark.

Anatomical abbreviations: aa, anguloarticular; ach, anterior ceratohyal; bs, basisphenoid; dn, dentary; ect, ectopterygoid; enpt, endopterygoid; fr, frontal; hyo, hyomandibula; inth, interhyal; iop, interopercle; le, lateral ethmoid; me, mesethmoid; mtp, metapterygoid; mx, maxilla; na, nasal; ob, orbitosphenoid; op, opercle; pa, palatine; par, parietal; pas, parasphenoid; pch, posterior ceratohyal; pmx, premaxilla; pop, preopercle; pts, pterosphonoid; qu, quadrate; ra, retroarticular; sop, subopercle; soc, supraoccipital; sym, symplectic; uh, urohyal;

Morphometric abbreviations: ASL, ascending process length; HD, head depth; HL, head length; ML, mandible length; MXL, maxillary length; OD, orbit diameter (measured horizontally); PMXL, premaxillary length; POD, preorbital distance; PoOD, postorbital distance; PDD, predorsal distance; PPD, prepectoral distance; SPL1, length of first supraneural; SPL2, length of second supraneural.

Systematic palaeontology

Clade Lampridomorpha *sensu* Davesne *et al.*, 2014

Order Lampridiformes Goodrich, 1909

Genus *Iratusichthys* gen. nov.

Type species. Iratusichthys ulrikii gen. et sp. nov.

Etymology. The name is derived from the latin word 'iratus', meaning angry, and the greek word 'ichthys' (ikhthýs) meaning fish.

Stratigraphic and geographic range. Ypresian (earliest Eocene), Ølst Formation, northwestern Denmark (Fig. 1).

Diagnosis. A lampridiform genus unique in having the following combination of characters: Ethmoid region of the neurocranium with a deep anterior concavity; ventral keel of orbitosphenoid absent; premaxilla and dentary bearing numerous tiny, conical teeth arranged in multiple rows; beryciform foramen piercing the anterior ceratohyal; two straight supraneurals, the first one inserting in the first interneural space; anteriormost two dorsal fin-ptyerygiophores inserting in the third interneural space; parapophyses absent; four pectoral-fin radials; pectoral fin with 14 rays; pelvic fin with six rays; squamation represented by small and rounded cycloid scales.

Table 1. Measurements of *Iratusichthys ulrikii* gen. et sp. nov., as percentage of HL

Morphometric characters	Measurements (mm)	% of HL
HL	40.2	100.0
HD	32.0	79.6
PPD	37.0	92.0
PDD	40.6	100.9
POD	21.0	52.3
PoOD	8.9	22.0
OD	8.0	19.9
ASL	12.0	29.9
PMXL	6.2	15.3
MXL	11.2	27.8
ML	13.7	34.1
SPL1	11.7	29.1
SPL2	11.8	29.4

***Iratusichthys ulrikii* sp. nov.**

Figs 2, 3, 4, 5, 6, Table 1

Holotype. NHMD-625089. Moderately well-preserved articulated head skeleton with associated pectoral and pelvic fins and girdles, preserved on a single slab of silicified clay, 40.22 mm in HL. The specimen is exposed in left lateral view. However, some of the skeletal structures originating from the left side are exposed in lateral view, while some others originate from the right side and are exposed in medial view.

Etymology. Named in honour of the retired chief editor, Ulrik Schröder, who has a profound interest in Danish geology and is an avid amateur geologist. Ulrik has been a great inspiration to the first author. The ‘facial expression’ of the species bears an uncanny resemblance to a certain expression exhibited by Ulrik Schröder. ‘Ulriki’ is the Latinization of the masculine name Ulrik, prevalent particularly in the Nordic countries. The second ‘i’ denominates the genitive case. The complete binomen means “the angry fish of Ulrik”.

Type locality of holotype. Ølst Formation, lowermost Eocene. Collected from the Stolleklint locality on the island of Fur, northwestern Limfjord area, Denmark. The holotype, and only specimen, originates from a stratigraphic level between ash series -39 to -34 from the Stolleklint clay unit (Fig. 1).

Referred material. None

Diagnosis. As for the genus.

Description. The specimen is moderately well-preserved. Based on the relative size of the bones of the head and pectoral girdle skeleton, it is reasonable to

assume that *Iratusichthys ulrikii* gen. et sp. nov. was a deep-bodied fish. The bones of the jaws and suspensorium are slightly displaced anteroventrally due to taphonomic processes. The head is moderately elongate. The head depth is approximately 80% of HL. The snout is contained about two times in HL. The mouth is terminal. The orbit is almost circular and relatively large, its diameter is nearly 20% of HL. The mandible length is about 34% of HL. The pectoral fin inserts obliquely, approximately in the lower half of the cleithrum. The pelvic fin-origin is located just below the pectoral fin.

Neurocranium. The neurocranium is almost triangular, exhibiting a distinctive appearance with a large sagittal crest formed by the convergence of the supraoccipital and frontal crests, the latter protruding anteriorly well beyond the ethmoid region, and a deep anterior concavity located just below the anterior protruding portion of the frontal crest. The lateral surface of the supraoccipital is ornamented with ridges, which are most prominent in its anterior half. The supraoccipital largely contributes to the rear portion of the neurocranium forming a broad laminar blade with a gently curved profile that almost contacts the anterior supraneural; this laminar blade is separated from the anterior portion of the supraoccipital crest by a strong ridge that emerges obliquely from the parietal region of the skull roof and reaches the posterior vertex of the neurocranium. As described above, the supraoccipital and frontal crests articulate with each other forming a continuous structure that occupies the entire length of the skull roof. The anterior portion of the two contralateral frontals form a vault to accommodate the elongated ascending process of the premaxilla. The outline of the parietals is difficult to recognise. The lateral ethmoid is robust, nearly sigmoid in outline, and forms part of the anterior wall of the orbit. The mesethmoid is partly median and partly posterior to the lateral ethmoids and is moderately thick (Figs 2, 3A–C); it articulates dorsally with the frontals. What appears to be the orbitosphenoid forms the dorsal wall to the orbit. The parasphenoid is almost straight extending through most of the basicranial length, exhibiting a minor curvature just behind the orbit. Anteriorly, the parasphenoid articulates with the thick vomer; no vomerine teeth can be observed. The basisphenoid is short, small, thin and rod-like, and does not articulate with the parasphenoid ventrally. The bones of the otic region are difficult to recognise due to inadequate preservation in this part of the neurocranium. The nasals are short, narrow and tubular.

Infraorbital series. The bones of the infraorbital series are feebly preserved, solely represented by fragments of two infraorbitals that can be recognised immediately ventrally to the parasphenoid, and just

above the metapterygoid.

Jaws. The mouth is terminal. The upper jaws comprise the premaxilla and maxilla, while the supramaxilla is absent. The premaxilla has a large ascending process, whose length represents almost one third of the head length, also being 1.9 times the length of the alveolar process. The dorsal anterior half of the ascending process is finely sculptured. The distal portion of the alveolar portion is spatulate. There are closely spaced, small and numerous tooth sockets arranged into multiple rows along the alveolar process of the premaxilla (Figs 3D, 4A–B, 5). The maxilla is oblong with a well-developed posterior laminar portion characterised by a gently curved ventral profile, and a moderately preserved anterior articular portion exhibiting an irregular morphology. The mandible is compact and thick with an overall ovoid outline. Tiny conical teeth, apparently arranged in multiple rows, are present on the dentary (Figs 3D, 4C, 5). The anguloarticular is massive, bearing a broad articular facet for the condyle of the quadrate. The thick and compact retroarticular forms

the posteroventral corner of the mandible.

Suspensorium. The hyomandibula is slender and appears almost straight, running parallel to the anterior edge of the preopercle; the outline of the articular head is difficult to recognise. The quadrate, endopterygoid and metapterygoid are all large. The quadrate, originating from the left side, is triangular and bears a relatively small condyle that articulates with the anguloarticular. The endopterygoid is oblong and appears to be toothless. The metapterygoid is trapezoid in outline. Both the left and right ectopterygoids are present. They are stout and feebly curved. The palatine is thick, ovoid in outline and lacks an anterior process and palatine teeth.

Opercular series. The right opercular series is preserved, exposed in medial view. The preopercle is crescent-shaped with a slightly rounded, smooth posterior margin; the vertical limb appears to be more than twice as long as the horizontal one and is characterised by a thickened anterior margin. Only the smooth ventral portion of the laminar interopercle is recognisable. The opercle appears to have been

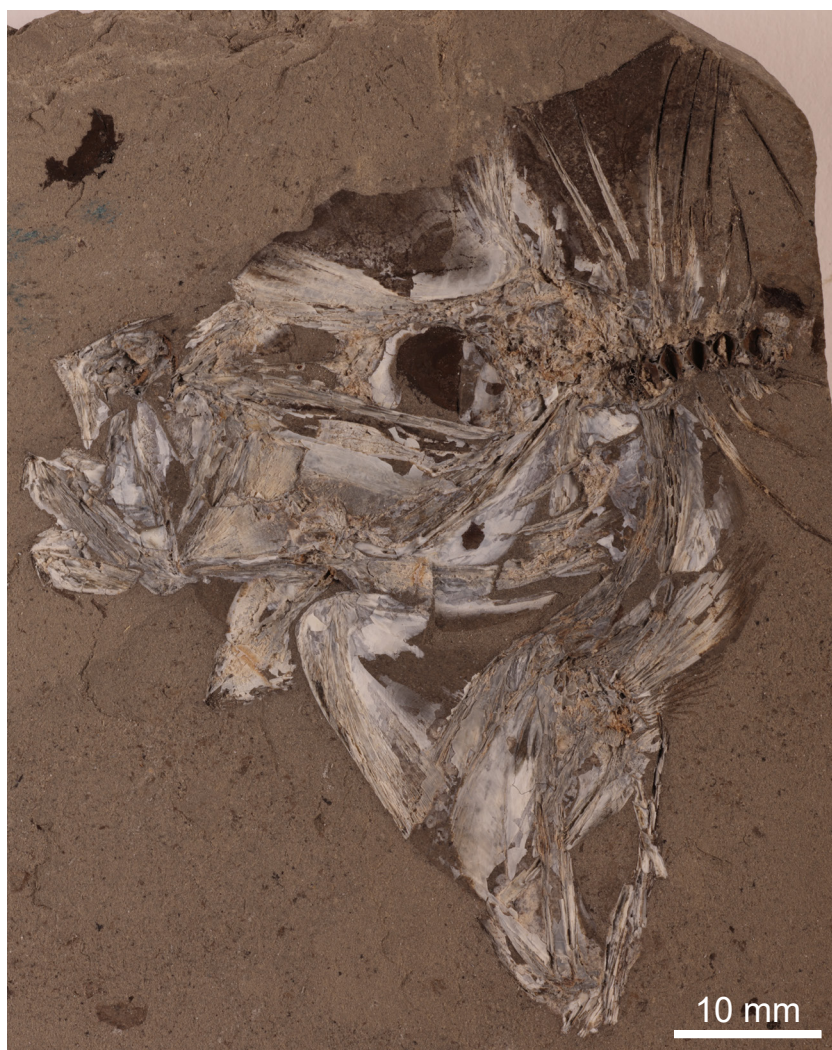


Fig. 2. High-resolution photo image of *Iratusichthys ulrikii* gen. et sp. nov., holotype NHMD-625089 (DK-551). Head skeleton and pectoral and pelvic girdles preserved on a single slab of silicified clay, collected from the Stollklint clay between ash layer -34 to -39.

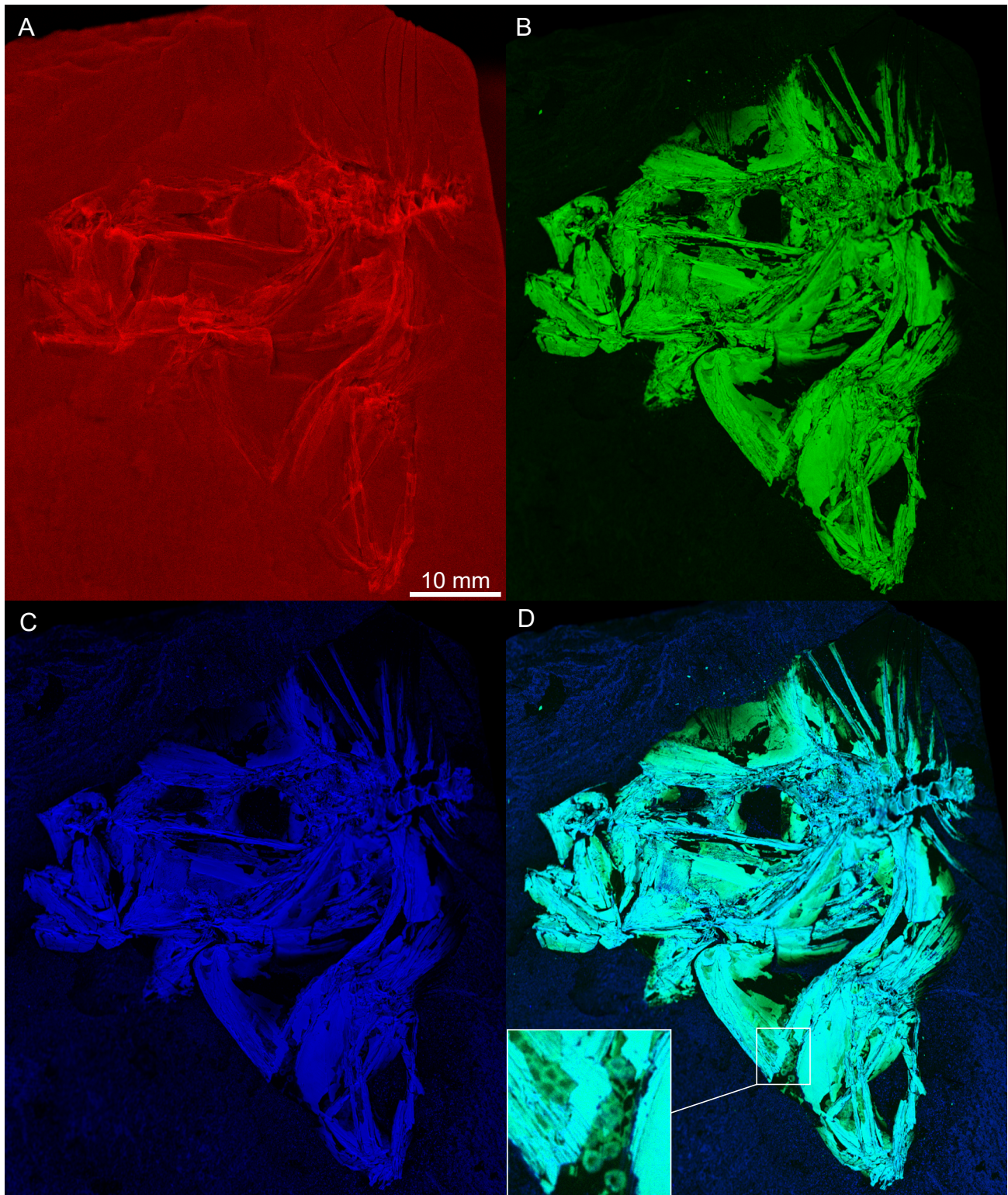


Fig. 3. μ XRF-element maps of *Iratusichthys ulrikii* gen. et sp. nov., holotype NHMD-625089 (DK-551). A: Strontium element map. Stronger ossification of the bone structures is evident with regards to the Sr-signal, i.e. more intense red colour is indicative of stronger ossification. The mesethmoid is hardly visible in the Sr map, whereas it is clearly evident in the phosphorous map. B: Phosphorous element map. Laminar portions of the bones are more easily recognisable when the same bone or part of the bone is compared to the Sr or Ca maps. C: Calcium element map, compare e.g. the mesethmoid with the Sr-map in A. D: Combined phosphorous and calcium element map with enlarged insert of the area with visible scales. The small, cycloid scales originating from the right side of the body, visible in medial view behind and posteroventral to the urohyal.

relatively large in origin, but only laminar fragments of its upper portion are preserved. The dorsal border of the opercle appears to have been almost horizontal. The laminar subopercle articulates anteriorly with the interopercle.

Hyoid apparatus and branchial skeleton. The hyoid bar is displaced from its original position and rotated clockwise so that the posterior ceratohyal is exposed anterior to the anterior ceratohyal. The dorsal margin of the anterior ceratohyal is concave and a depressed ovoid 'beryciform' foramen (see Davesne *et al.* 2014) pierces the central part (Figs 2, 6). The partially recognisable anterior end of the anterior ceratohyal seems to form a condylar structure that likely articulated with the ventral hypohyal in origin. The posterior ceratohyal is triangular and articulates dorsally with a small incompletely preserved interhyal (Fig. 6). There is no clear evidence of the hypohyals, which are likely hidden by the suspensorium

and opercular bones. There is no evidence of the branchiostegal rays in the specimen. The urohyal is massive and ventrally expanded, almost triangular in outline, with slightly curved dorsal and anterior margins (Fig. 6). Of the branchial skeleton, what appear to be slender ceratobranchials are visible in the opercular region (Figs 2, 3).

Vertebral column and intermuscular bones. Only the six anterior vertebrae are preserved in the specimen. The first and second vertebrae are compressed anteroposteriorly compared to the succeeding ones. The centra of the other vertebrae are subrectangular in outline, slightly higher than long. The neural spine of the first vertebra is broad and shortened. Both the first and second neural spines are slightly inclined forward, while those of the third to sixth vertebrae are anteroposteriorly expanded, bearing a posterior laminar outgrowth with a rounded profile. Parapophyses are absent on all preserved vertebrae

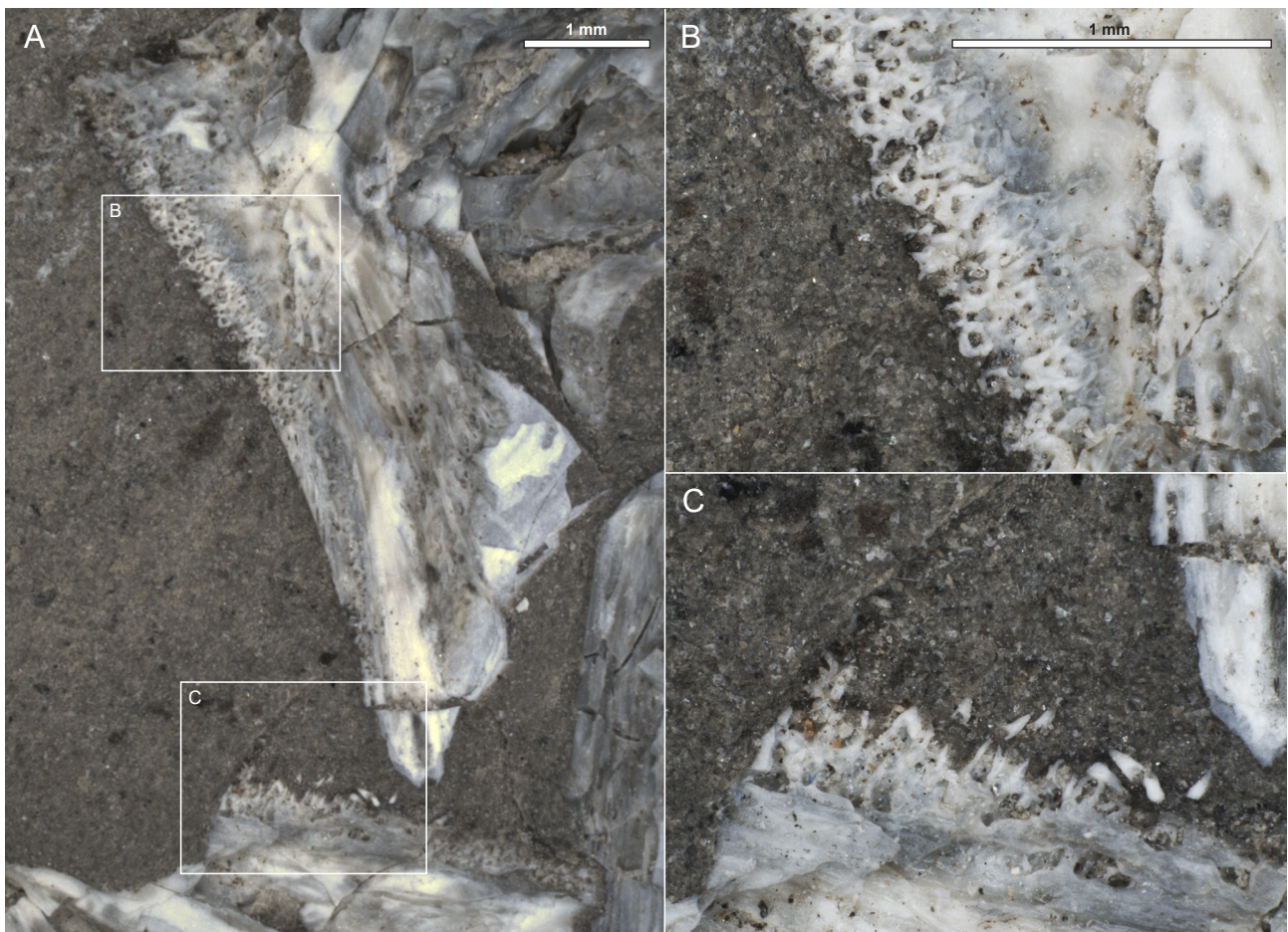


Fig. 4. *Iratusichthys ulrikii* gen. et sp. nov, holotype NHMD-625089 (DK-551). Micrographs of the tiny tooth sockets and conical teeth, arranged in multiple rows. A: Section showing the premaxilla and dentary. B: Ten times magnification of the insert of the premaxilla indicated in A, showing numerous tooth sockets arranged into multiple rows along the alveolar process of the premaxilla. C: Ten times magnification of the insert of the dentary indicated in A, showing the anterior half of the dentary with tiny conical teeth arranged in multiple rows. Several detached teeth are also visible. Scale bars = 1 mm. The scale bar in B also applies to C.

(Figs 2, 3A). The dorsal portion of three pairs of ribs is preserved, the first articulating with the third vertebra.

Median fins and supports. The dorsal fin, which is not preserved, is preceded by two slender, nearly straight and elongate supraneurals, which are almost equal in length (29% of HL). They are slightly expanded dorsally, forming the shape of a flat nail-head; the expanded parts are mostly preserved as impressions (Fig. 2, Fig. 3A, D). The supraneurals are closely spaced, but the first ends ventrally just above the boundary between the neural spines of the first and second vertebrae, possibly representing the first interneural space; the second supraneural inserts in the second interneural space. The dorsal-fin pterygiophores are mostly preserved as impressions. The first pterygiophore bears a horizontal limb that follows the dorsal profile of the nape. The first two dorsal-fin pterygiophores insert in the third interneural space, while the third pterygiophore inserts in the fourth interneural space. The fourth pterygiophore is displaced from its original position. There are no dorsal-fin spines or rays preserved. However, it is reasonable to hypothesize that the predorsal formula was /0/0/?+1/1/.

Paired fins and girdles. The posttemporal is poorly preserved, with only the dorsal, slightly curved limb being discernible. The rest of the pec-

toral girdle is displaced ventrally from its original position as indicated by the separation of the posttemporal and supracleithrum. The supracleithrum is oblong with a ventral, broad laminar expansion and a thickened anterior edge. The cleithrum is large and sigmoid-shaped; its ventral part is inflated and paddle-like and terminates ventrally abruptly into a small pungent process. The distal portion of the elongate postcleithrum is closely associated with the basipterygium. The scapula is relatively small and rounded, centrally pierced by a scapular foramen. The coracoid is narrow and terminates at the same level as the cleithrum. Four pectoral-fin radials appear to be present, of which the two posteriormost can easily be recognised; the three anterior radials articulate with the scapula and the fourth only with the coracoid. A total of 14 pectoral-fin rays are identified, of which the two dorsalmost articulate directly with the scapula.

The prominent basipterygium is dorsally inclined and attached to the pectoral girdle; the central axis of the basipterygium is almost vertical and articulates with the cleithrum, while the internal wing is associated with the ventral end of both cleithrum and coracoid. The pelvic fin appears to include at least six rays of which the outer one is thicker and apparently unsegmented; these are rotated dorsally around the articular surface of the basipterygium.

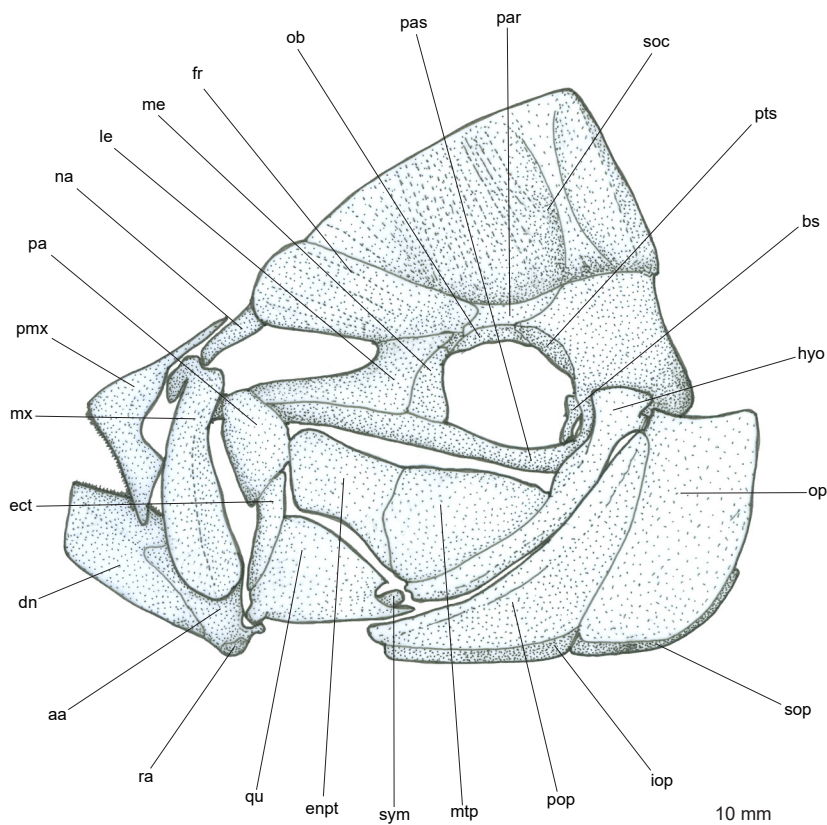


Fig. 5. *Iratusichthys ulrikii* gen. et sp. nov. Reconstruction of the head.

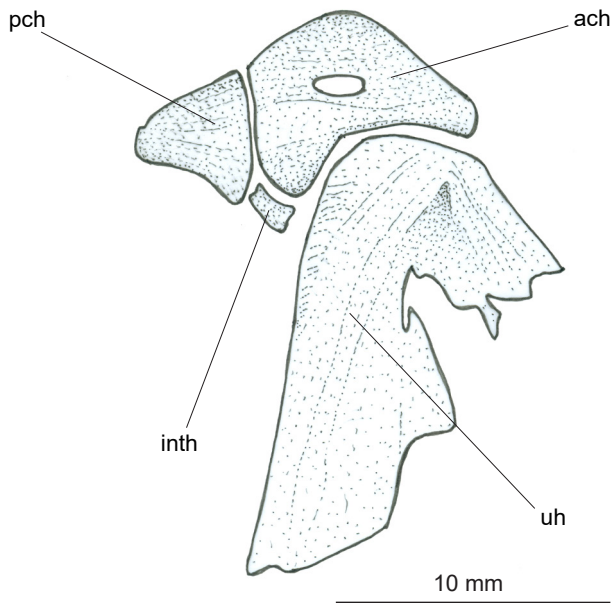


Fig. 6. *Iratusichthys ulrikii* gen. et sp. nov. Interpretive reconstruction of the hyoid apparatus.

Squamation. Small and rounded cycloid scales, originating from the right side of the body, are visible behind and posteroventral to the urohyal in medial view (Fig. 3D).

The nomenclatural acts of this paper are registered on ZooBank. LSID of the new genus *Iratusichthys*: <https://zoobank.org/NomenclaturalActs/E1EBCB81-B81B-40EF-914C-26ABC83D607B> and the LSID of the new species *Iratusichthys ulrikii*: <https://zoobank.org/NomenclaturalActs/C870AD54-3609-48E6-B652-D0AF7074FF32>

Comparative discussion

The phylogenetic relationships of lampridiform fishes have been extensively discussed in the last decades, based on morphological and molecular data (e.g. Oelschläger 1983; Olney *et al.* 1993; Wiley *et al.* 1998; Miya *et al.* 2007; Wiley and Johnson 2010; Davesne *et al.* 2014, 2016, 2017; Delbarre *et al.* 2016; Brownstein & Near 2024). Olney *et al.* (1993) proposed four main synapomorphies to support the monophyletic status of the crown Lampridiformes, including: 1) absence of the anterior palatine process (referred to as the palatine ‘prong’ by Olney *et al.* 1993); 2) mesethmoid posterior to the lateral ethmoids; 3) premaxillae with greatly elongate ascending processes associated with frontals elevated forming a vault to accommodate them; 4) first dorsal-fin pterygiophore (and, therefore, the preceding supraneurals) inserting in the preneural space. As described above, the first three

of these features can be observed in the new taxon described herein, *Iratusichthys ulrikii* gen. et sp. nov. As far as concerns the fourth of these features, as pointed out by Bannikov (1999), the pattern regarding the preneural insertion of the supraneurals and first dorsal-fin pterygiophore may diverge in certain fossil lampridiforms, including *Palæocentrotus böggildi* from earliest Eocene of Denmark (predorsal formula 0/0+2/1+1+1; Patterson 1993), and the turkmenid *Analectis pala* Daniltshenko, 1980 from the Upper Eocene and Lower Oligocene of northern Caucasus (predorsal formula 0/0+0/1; Bannikov 1999). In particular, *Analectis* Daniltshenko, 1980 is unique within lampridiforms by having three supraneurals and the first dorsal-fin pterygiophore that inserts in the second interneural space. The list of lampridiform synapomorphies was recently expanded by Davesne *et al.* (2014) by including additional features of the hyoid apparatus, intermusculars and caudal skeleton. While some of these characters refer to structures not accessible in the single available specimen described herein, at least three lampridiform synapomorphic features, absence of supramaxillae, urohyal expanded ventrally, and possession of two supraneurals, can be observed in *Iratusichthys* gen. nov., thereby reinforcing its alignment with the Lampridiformes.

Long-bodied (taeniosomous) lampridiforms have traditionally been recognised as a monophyletic assemblage (e.g. Oelschläger 1983, Olney *et al.* 1993), while the deep-bodied (bathysomous) lampridiforms are commonly not recognised as monophyletic because the Lamprididae is regarded as the sister group to the elongate families (e.g. Olney *et al.* 1993; Davesne *et al.* 2014, 2016; Delbarre *et al.* 2016). However, several studies recurrently recovered a monophyletic clade formed by lampridids plus veliferids as sister group to the taeniosomes (Grande *et al.* 2013; Wang *et al.* 2023; Brownstein & Near 2024). Therefore, due to the presence of these two contrasting phylogenetic hypotheses, it is difficult to interpret the phylogenetic relationships of fossil lampridiform taxa.

As discussed above, despite the incompleteness of the available material, *Iratusichthys ulrikii* gen. et sp. nov. should be regarded as a deep-bodied fish. In addition, *Iratusichthys ulrikii* gen. et sp. nov. has two supraneurals and a well-developed supraoccipital crest, thereby excluding any possible affinity with the long-bodied taeniosomous lampridiforms (see Olney *et al.* 1993). However, it is interesting to note that the two anterior vertebrae of *Iratusichthys ulrikii* gen. et sp. nov. are in some ways reminiscent of the first vertebra of taeniosomous lampridiforms, being characterised by an anteroposteriorly compressed centra and anteriorly inclined neural spines (see Oelschläger 1983, Olney *et al.* 1993).

Among deep-bodied bathysomous lampridi-

forms, *Iratusichthys ulrikii* gen. et sp. nov. is characterised by having a unique set of features, including numerous tiny conical teeth in both upper and lower jaws, a peculiar configuration of the ethmoid region of the neurocranium that exhibits a deep anterior concavity and lacks a ventral keel of the orbitosphenoid, and two supraneurals inserting in the first two interneural spaces followed by dorsal-fin pterygiophores inserting in the third and successive interneural spaces. Moreover, the attribution of *Iratusichthys ulrikii* gen. et sp. nov. to the Veliferidae can also be ruled out since it lacks parapophyses on the abdominal vertebrae and the dorsal-fin base is not covered by a scaly sheath (see Reagan 1907a, b; Olney *et al.* 1993; Carnevale & Bannikov 2018). Likewise, *Iratusichthys ulrikii* gen. et sp. nov. cannot be referred to Lamprididae as it exhibits a beryciform foramen piercing the anterior ceratohyal, presence of at least two infraorbitals, obliquely inserting pectoral fins, and four autogenous pectoral-fin radials (e.g. Olney *et al.* 1993; Davesne *et al.* 2023). The possession of a beryciform foramen in the anterior ceratohyal, of more than one infraorbital, and of obliquely inserting pectoral fins allows to exclude any possible alignment between *Iratusichthys ulrikii* gen. et sp. nov. and the Eocene *Whitehippus tamensis* Casier, 1966 (see Davesne *et al.* 2023). *Iratusichthys ulrikii* gen. et sp. nov. further differs from the Paleocene *Bathysoma lutkeni* by lacking a fenestration in the supraoccipital crest as well as a tubular snout resulting from the remarkable elongation of the jaw bones (Patterson 1964; Adolfssen *et al.* 2017). The Paleogene bathysomous family Turkmenidae comprises three species, including *Analectis pala*, *Danatinia casca* Daniltshenko, 1968 and *Turkmenia finitimus* Daniltshenko, 1968 which are characterised by subhorizontally inserting pectoral fins (Daniltshenko 1968, 1980; Bannikov 1999). *Iratusichthys ulrikii* gen. et sp. nov. exhibits some similarities with the turkmenids. For example, it shares the possession of two supraneurals and absence of parapophyses with *Turkmenia finitimus*; however, both the supraneurals of *Turkmenia* insert in the preneural space. Finally, as far as concerns the Paleogene bathysomous family Palaeocentrotidae, both the known species *Natgeosocus sorini* Bannikov, 2014 and *Palaeocentrotus böggildi* differ from *Iratusichthys ulrikii* gen. et sp. nov. by having heads strongly compressed antero-posteriorly, and large orbits occupying at least 30% of HL (e.g. Kühne 1941; Bannikov 2014).

One of the most salient morphological features exhibited by *Iratusichthys ulrikii* gen. et sp. nov. is the presence of tiny conical teeth in both upper and lower jaws. Extant lampridiforms as well as all the other Cenozoic taxa are characterised by toothless jaws. The Cretaceous *Nardovelifer altipinnis* recently resolved as a stem-lampridiform (e.g. Delbarre *et al.* 2016; Brownstein & Near 2024), also has small teeth

on both the premaxilla and dentary (Sorbin & Sorbini 1999). Other than in *Nardovelifer* Sorbini & Sorbini, 1999 and *Iratusichthys* gen. et sp. nov. the presence of jaw teeth has been reported in the Cretaceous lampridomorph *Aipichthys*, Steindachner, 1860 (Delbarre *et al.* 2016). Whether the presence of teeth in *Iratusichthys ulrikii* gen. et sp. nov. represents a genuine plesiomorphic condition or is an example of character reversal (i.e. taxic atavism; see Stiasny 1992) cannot be determined. The configuration of the predorsal formula of *Iratusichthys ulrikii* gen. et sp. nov. also diverges from that of all the other extant and fossil lampridiform taxa. These characters might suggest that *Iratusichthys ulrikii* gen. et sp. nov. should be tentatively regarded as a stem-lampridiform. However, additional and more complete specimens would be necessary to properly define its phylogenetic position within this lineage of basal acanthomorphs.

As a final comment to this taxonomic discussion, it is interesting to note that some of the morphological features of *Iratusichthys ulrikii* gen. et sp. nov. are reminiscent of those observed in the species of the percomorph family Menidae, which were especially abundant in the earliest portion of the Paleogene (see, e.g. Blot 1969; Friedman & Johnson 2005). In particular, the overall configuration of the neurocranium, characterized by a frontal vault, a prominent supraoccipital crest ornamented with ridges, as well as the presence of tiny teeth in the oral jaws are in some ways similar to those of the menids. However, the fossil described herein lacks numerous characters diagnostic of the Menidae, (e.g. robust scleral ossicles; large series of narrow infraorbitals and a broad lachrymal with a large, depressed area on its lateral surface; diamond-shaped palatine prong; large metapterygoid foramen; massive postcleithrum; three supraneurals; Blot 1969; Friedman & Johnson 2005), thereby suggesting that the similar cranial features might be regarded as the result of convergent evolution.

Concluding remarks

The fossil record of lampridiform skeletal remains in Denmark is restricted to the earliest part of the Paleogene. As reported by Adolfssen *et al.* (2017), articulated skeletal remains of *Bathysoma lundensis* have been collected from the Selandian erratic boulders near Klint. *Iratusichthys ulrikii* gen. et sp. nov. is the oldest known Eocene lampridiform, dating back to about 55 Ma. *Palaeocentrotus böggildi* also known from the earliest Eocene of Denmark, is slightly younger, exclusively known from the overlying Fur Formation. In addition, incomplete material tentatively referred to the genus *Palaeocentrotus* has been reported from the middle Danian deposits, preserved in a flint nod-

ule from a loose boulder at Endelave Strand (e.g. Adolfssen *et al.* 2017). Bonde (1987) pictured a possible new turkmenid species from the Fur Formation in his popular scientific Skamol-booklet (Bonde 1987, p. 38). However, it has been impossible to locate this or other similar specimens in the museums' collections in Denmark, including in the Vertebrate Palaeontology and Danekræ collections of the Natural History Museum of Denmark (Copenhagen University), and in the collections of the Fossil- and Moclav Museum (Museum Mors) and in the Fur Museum collections (Museum Salling). The collections of the Natural History Museum, London (UK), that also house material of the ichthyofauna from the Fur Formation were also checked for possible turkmenid specimens in November 2024, but no specimens were located.

Extant bathysomous lampridiforms are characterised by epipelagic or demersal habits. According to Delbarre *et al.* (2016), some extinct deep-bodied lampridiforms (e.g. *Nardovelifer*) are reminiscent of extant veliferids and were probably characterised by a similar demersal and neritic ecological lifestyle. The Paleogene taxa, except for those from the shallow tropical biotopes of Bolca (see Marramà *et al.* 2016; Carnevale & Bannikov 2018; Friedman & Carnevale 2018), appear to be associated with open oceanic environments (Davesne *et al.* 2023). This was probably also the case for *Iratusichthys ulrikii* gen. et sp. nov. The depositional environment of the basal Ølst Formation is poorly defined, although it is assumed that the climate conditions were subtropical to tropical, the bottom waters strongly anoxic, and the palaeo-North Sea may have been restricted to form an inland sea at this time (Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995).

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Maastrichtian brachiopods from the chalk of Denmark

FINN SURLYK



Geological Society of Denmark
<https://2dgf.dk>

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A rich brachiopod fauna from the Maastrichtian chalk of Denmark is obtained from washed bulk samples from 42 localities. Two of these may, however, show uppermost Campanian chalk. A total of 44 species are recognized, represented by more than 35,000 specimens, most of them being micromorphic, millimetre-sized forms. The species are described with emphasis on their ontogenetic evolution. Their stratigraphic distribution allows recognition of 12 zones in the uppermost Campanian – Maastrichtian of the North European chalk, based on lowest and/or highest occurrence of selected species. The zonation has been applied in contemporaneous chalks of Denmark, southern Sweden, Poland, northern Germany, Belgium and eastern England.

Keywords: Brachiopoda, Maastrichtian, chalk, Denmark, taxonomy, biostratigraphy.

Finn Surlyk [finns@ign.ku.dk] Department of Geosciences and Natural Resource Management, Øster Voldgade 10, 1350 København K, Denmark.

<http://zoobank.org/urn:lsid:zoobank.org:pub:78596342-37C1-432A-A947-F4410F8749FD>

A rich brachiopod fauna dominated by micromorphic, mm-sized species is obtained from washed bulk samples of chalk from the Maastrichtian of Denmark. The study is based on an unpublished prize dissertation awarded the Gold Medal of the University of Copenhagen (Surlyk 1969). It was never published but formed the basis for an analysis of the palaeoecology, notably the morphological adaptations and population structures of the fauna (Surlyk 1972). This was supplemented by later works by myself and co-workers involving the Maastrichtian brachiopod fauna mainly from the Danish chalk (Surlyk 1970a, b, 1972, 1973, 1974, 1982, 1984; Surlyk & Birkelund 1977; Surlyk & Dieni 1988; Johansen & Surlyk 1990; Surlyk & Johansen 1984; Surlyk *et al.* 2006, 2010, 2013; Anderskov *et al.* 2007; Lauridsen & Surlyk 2008; Rasmussen & Surlyk 2012; Hansen & Surlyk 2014; Schrøder & Surlyk 2020; Thibault *et al.* 2024b).

A total of 42 localities have been sampled, ranging from long sample series from key sections to single samples mainly from small localities. Two of these sections may show chalk from the uppermost Campanian or the Campanian–Maastrichtian boundary interval. Application of the method resulted in the retrieval of 44 species represented by more than 35,000 specimens which are in general very well preserved, allowing the study of minute details and of the ontogenetic evolution of the species.

The morphological key characters and ontogenetic

evolution, occurrences and stratigraphic distribution are described for all species if at all possible. The

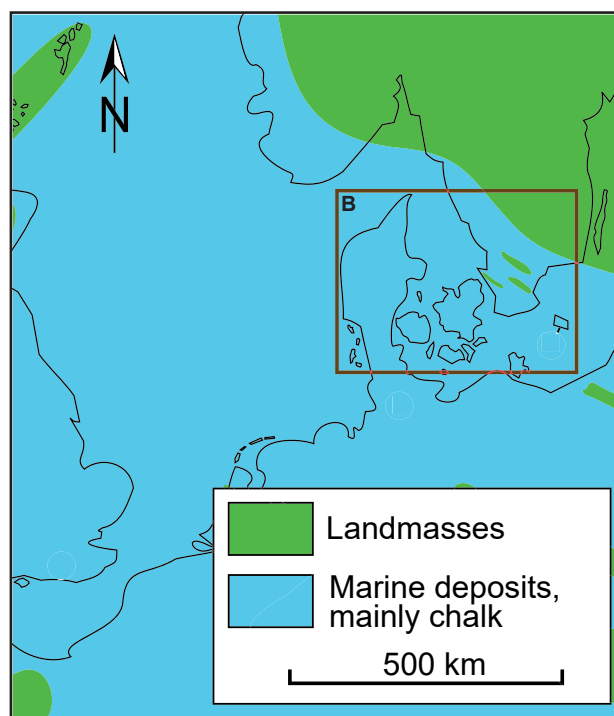


Fig. 1. Map showing the extent of the deep, epeiric Chalk Sea, which covered northern Europe in the Late Cretaceous. Modified from Surlyk *et al.* (2003).

stratigraphic distribution of selected species allowed recognition of five biozones in the lower Maastrichtian chalk of the island of Rügen, north-east Germany by Steinich (1965). The Danish Maastrichtian chalk was subdivided into a number of zones based on the combined key sections Rørdal, Møns Klint and Stevns Klint supplemented with material from all Danish chalk localities. This extended the number of Maastrichtian brachiopod zones to 10 (Surlyk 1969, 1970a, 1972, 1984), later extended downwards to 12 zones for the uppermost Campanian – Maastrichtian chalk of northern Europe. The zonal biostratigraphy was shown to be applicable in the chalk of Skåne in southern Sweden (Surlyk 1969), Poland (Bitner & Pisera 1979; Machalski & Bitner 2024), Rügen, Hemmoor and Krons Moor in northern Germany (Surlyk 1970a, 1982, 1984), Belgium (Simon 1998), and Norfolk in eastern England (Johansen & Surlyk 1990).

Geological setting

In Late Cretaceous times NW Europe was flooded by the relatively deep, epeiric Chalk Sea where thick successions of chalk were deposited (Fig. 1; e.g. Ziegler 1990; Surlyk *et al.* 2003). The study area comprises the Danish Basin which is separated from the North German Basin by the Ringkøbing-Fyn High (Fig. 2). The Danish Basin passes to the west into the North Sea Basin. Towards the north the Danish Basin is limited by the Sorgenfrei-Tornquist Zone (Fig. 2), an important long-lived tectonic structure that experienced several phases of uplift (e.g. Liboriusen *et al.* 1987; Mogensen & Korstgård 2003; Surlyk & Lykke-Andersen 2007). The greatest thicknesses of the Upper Cretaceous – Danian Chalk Group are found in a NW–SE oriented belt along the southwestern margin of the Sorgenfrei-Tornquist Zone,

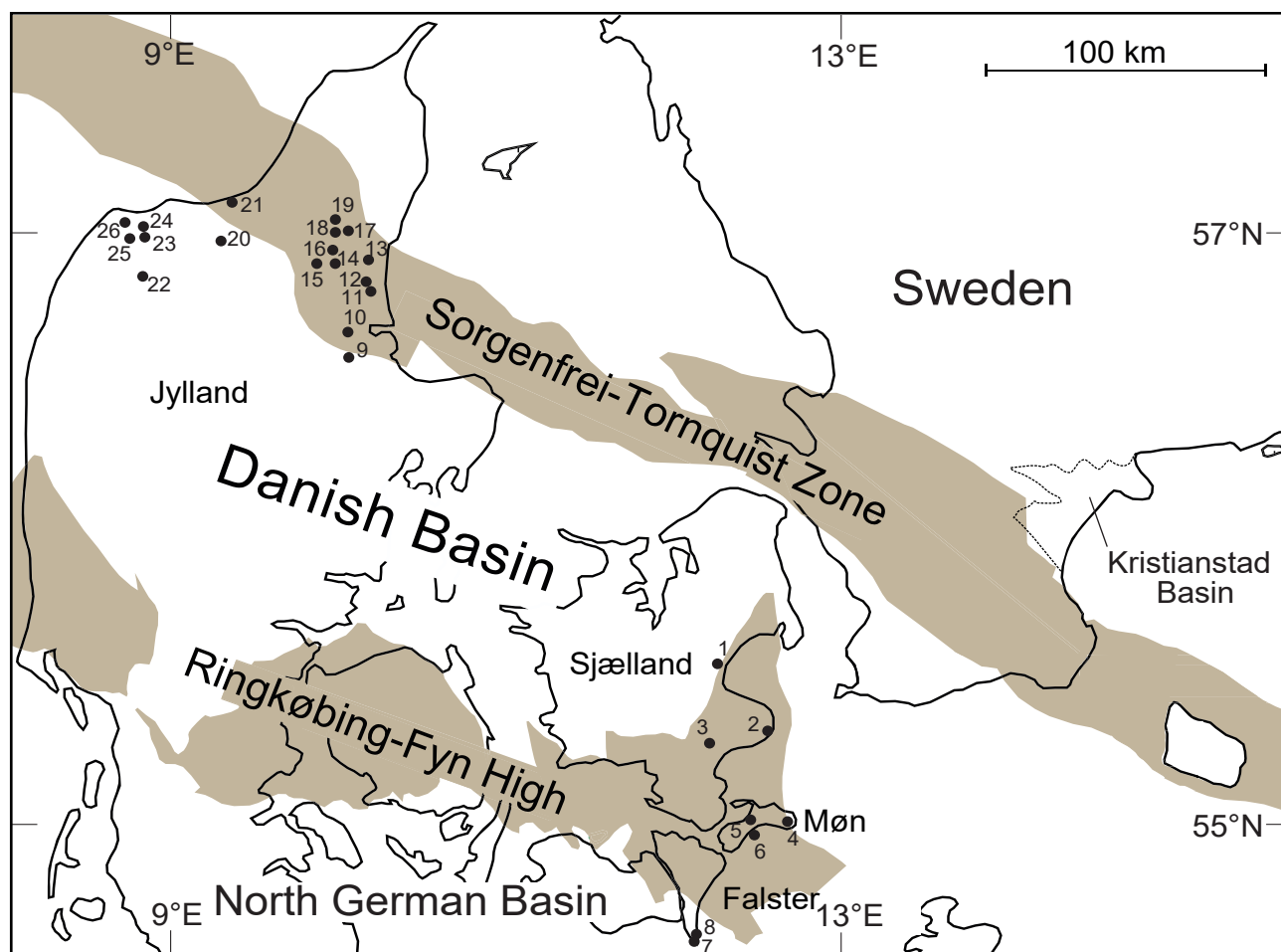


Fig. 2. Map showing the main structural features limiting the Danish Basin and the sample localities, forming the basis for this study. 1. Karlstrup, 2. Stevns Klint, 3. Kongsted, 4. Møns Klint (including 13 sampled thrust sheets), 5. Lille Bissinge, 6. Hvide Klint, 7. Gedser Fyr, 8. Gedser Odde, 9. Spentrup, 10. Dania, 11. Smidie, 12. Sønder Kongerslev, 13. Gudumholm, 14. Mjels, Ellidshøj, 15. Nørre Flødal, Linds, 16. Ferslev, 17. Rørdal, 18. Danmark, 19. Lindholm, 20. Aggersund, 21. Svinkløv, 22. Eerslev, 23. Hov, 24. Nye Kløv, Kjølbjgård, 25. Hillerslev, 26. Bjerre.

Table 1. Specimen numbers.

<i>'Lingula cretacea'</i> Lundgren, 1885 (Fig. 10). A: OESM 8898, B: OESM 4655, C: MGUH 34869.
<i>Crania craniolaris</i> Linnaeus, 1758 (Fig. 11). MGUH 34870.
<i>Crania antiqua</i> Defrance, 1818 (Fig. 12). A: OESM 13285, B: OESM 8629, C: MGUH 34871, D: OESM 4472, E, F: MGUH 34872, G: OESM 4521, H: OESM 13248.
<i>Ancistrocrania parisiensis</i> Defrance, 1818 (Fig. 13). A: OESM 4672, B: OESM 13286, C: OESM 10919, D: MGUH 34873, E: MGUH 34874.
<i>Ancistrocrania tubulosa</i> Nielsen, 1909 (Fig. 14). A: MGUH 34875, B: MGUH 34876, C: MGUH 34877, D: 34878, E: MGUH 34879, F: MGUH 350 (holotype), G: MGUH 34880.
<i>Isocrania costata</i> (Sowerby, 1823) (Fig. 15). A, B: MGUH 34881, C, D: MGUH 34882, E, F: MGUH 34883.
<i>Isocrania sendeni</i> Simon, 2007 (Fig.) 16. A, B: OESM 8628.
<i>Isocrania barbata</i> (von Hagenow, 1842) (Fig. 17). A, B: MGUH 34884.
<i>Cretirhynchia retracta</i> (Roemer, 1841) (Fig. 20). A, B, C: MGUH 34885.
<i>Cretirhynchia plicatilis</i> (J. Sowerby, 1816) (Fig. 21). A, B, C: MGUH 34886.
<i>Homaletarhynchia limbata</i> (von Schlotheim, 1813). (Fig. 22). A, B, C: MGUH 34887, D, E: OESM 4611, F, G: OESM 4616.
<i>Thecidea papillata</i> (von Schlotheim, 1813) (Fig. 24). A, B: MGUH 34889.
<i>Thecidea recurvirostra</i> (Defrance, 1828) (Fig. 25). A, B: MGUH 34890. C: MGUH 34891. D: MGUH 34892.
<i>Vermiculothecidea vermicularis</i> (von Schlotheim, 1813) (Fig. 27). A, B: MGUH 34895.
<i>Neolithyrina obesa</i> Sahni, 1925 (Fig. 28). A, B, C: MGUH 34896.
<i>Neolithyrina fittoni</i> (von Hagenow, 1842) (Fig. 29). A: OESM 10942, B, C: MGUH 34897.
<i>Carneithyrus subcardinalis</i> (Sahni, 1925) (Fig. 30). A, B, C: MGUH 34898.
<i>Terebratulina chrysalis</i> (von Schlotheim, 1813) Fig. 33). A, B: MGUH 34899.
<i>Terebratulina longicollis</i> Steinich, 1965 (Fig. 36). A, B: MGUH 34900.
<i>Terebratulina faujasii</i> (Roemer, 1841) (Fig. 41). A, B: MGUH 34904.
<i>Terebratulina subtilis</i> Steinich, 1965 (Fig. 45). A, B: MGUH 34908.
<i>Gyrosoria gracilis</i> (von Schlotheim, 1813) (Fig. 48). MGUH 34909.
<i>Gisilina gisii</i> (Roemer, 1841) (Fig. 51). A, B: MGUH 34910.
<i>Gisilina jasmundi</i> Steinich, 1965 (Fig. 54). A, B: MGUH 34912.
<i>Meonia semiglobularis</i> (Posselt, 1894) (Fig. 57). A, B: MGUH 34912.
<i>Rugia tenuicostata</i> Steinich, 1963 (Fig. 62). A, B: MGUH 34915.
<i>Rugia acutirostris</i> Steinich, 1965 (Fig. 65). A, B: MGUH 34916.
<i>Rugia stenius</i> n. sp. (Fig. 68). A: Holotype, MGUH 34917, B–C, E–F: Paratypes, MGUH 34918–34919, 34921–34922. D: Dorsal valve, internal view, showing hinge, MGUH 34920.
<i>Rugia tegulata</i> Surlyk, 1970 (Fig. 70). A: MGUH 11015, B: MGUH 11016, C, D, E: MGUH 11017.
<i>Rugia tegulata</i> Surlyk, 1970 (Fig. 71). A: MGUH 11021, B: MGUH 11022, C, D: MGUH 11023.
<i>Rugia spinosa</i> Surlyk, 1970 (Fig. 73). A, B: MGUH 11018, C: MGUH 1019, D: MGUH 11020.
<i>Dracius carnifex</i> Steinich, 1967 (Fig. 76). A, B: MGUH 34923.
<i>Kingena pentangulata</i> (Woodward, 1833) (Fig. 79). A, B: MGUH 34924.
<i>Dalligas nobilis</i> Steinich, 1968 (Fig. 83). A, B: MGUH 34925.
<i>Ruegenella humboldtii</i> (von Hagenow, 1842) (Fig. 85). A, B: MGUH 34926.
<i>Trigonosemus pulchellus</i> (Nilsson, 1827) (Fig. 89). A, B: MGUH 34928.
<i>Argyrotheca hirundo</i> (von Hagenow, 1842) (Fig. 92). A, B: MGUH 34929.
<i>Bronnothyris bronnii</i> (Roemer, 1841) (Fig. 95). A, B: MGUH 34930.
<i>Bronnothyris coniuncta</i> (Steinich, 1965) (Fig. 98). A, B: MGUH 34931.
<i>Bronnothyris stevensis</i> (Nielsen, 1928) (Fig. 101). A, B: MGUH 34932.
<i>Aemula inusitata</i> Steinich, 1968 (Fig. 104). A, B: MGUH 34933.
<i>Scumulus inopinatus</i> Steinich, 1968 (Fig. 107). A, B: MGUH 34934.
<i>Magas chitoniformis</i> (von Schlotheim, 1813) (Fig. 110). A, B: MGUH 34935.

Photographed specimens kept in the collections of the Natural History Museum of Denmark (MGUH numbers) and of Geomuseum Faxe (OESM numbers). Some specimens are kept in private collections and others in the collection of the author (University of Copenhagen) for further study in other projects.

where thicknesses of more than 2000 m are reached in some areas (Vejbæk *et al.* 2007). Onshore Denmark the Maastrichtian chalk reaches the greatest thicknesses in the Danish Basin and is thinner over the

Ringkøbing-Fyn High (Fig. 2). One of the main outcrops of Maastrichtian chalk, Møns Klint (4 in Fig. 2) is located over the eastern end of the Ringkøbing-Fyn High, where the Chalk Group is only 450–600 m

Table 2. The uppermost Campanian – Maastrichtian brachiopod zones in the chalk of northern Europe (Denmark, Sweden, Poland, Germany, Belgium, the Netherlands, England).

<i>tenuicostata</i> – <i>longicollis</i> Zone (upper upper Campanian, Flagbanke Member, Mandehoved Formation)
<i>longicollis</i> – <i>jasmundi</i> Zone (upper upper Campanian, lower Boesdal Member, Mandehoved Formation)
<i>jasmundi</i> – <i>acutirostris</i> Zone (upper upper Campanian, middle Boesdal Member, Mandehoved Formation)
<i>spinosa</i> – <i>subtilis</i> Zone (lowermost lower Maastrichtian, uppermost Boesdal Member – lowermost Hvidskud Member, Møns Klint Formation)
<i>subtilis</i> – <i>pulchellus</i> Zone (upper lower Maastrichtian, Hvidskud Member); the <i>pulchellus</i> – <i>pulchellus</i> Zone (upper lower Maastrichtian, Hvidskud Member)
<i>pulchellus</i> – <i>tenuicostata</i> Zone (upper lower Maastrichtian, Hvidskud Member)
<i>tenuicostata</i> – <i>semiglobularis</i> Zone (uppermost lower Maastrichtian, Hvidskud Member). The top of this zone roughly coincides with the lower–upper Maastrichtian boundary, but <i>Meonia semiglobularis</i> , defining the upper boundary is found a short distance below the boundary as currently defined by belemnites (Birkelund 1957; Schulz <i>et al.</i> 1984)
<i>semiglobularis</i> – <i>humboldtii</i> Zone (uppermost lower – lower upper Maastrichtian, upper Hvidskud Member – Rørdal Member, Møns Klint Formation)
<i>humboldtii</i> – <i>stevensis</i> Zone (top of the lower upper Maastrichtian – lowermost upper upper Maastrichtian, upper Rørdal Member – Sigerslev Member, Møns Klint Formation)
<i>stevensis</i> – <i>chitoniformis</i> Zone (upper upper Maastrichtian, upper Sigerslev Member, top Møns Klint Formation). The top of this zone coincides with the Maastrichtian–Danian (K–Pg) boundary

thick (Vejbæk *et al.* 2007). The UNESCO World Heritage Site for the Cretaceous–Palaeogene boundary, the long coastal cliff, Stevns Klint (Surlyk *et al.* 2006; Damholt & Surlyk 2012) is located over the north-eastern end of the high (2 in Fig. 2). Other important outcrops are located in large quarries in and around the town of Aalborg at the north-western end of the Sorgenfrei-Tornquist Zone (17 and 18 in Fig. 2).

Material and methods

This study was initiated in 1965 by collection of a series of 20 kg chalk bulk samples in the Hvidskud section at Møns Klint, which formed the basis for my MSc in 1968. Subsequently samples were collected from all known localities exposing Maastrichtian chalk in Denmark. The retrieved material, comprising about 35,000 brachiopod specimens was described in detail in an unpublished prize dissertation (Surlyk 1969). The emphasis was on taxonomy and stratigraphy, supplemented with chapters on chalk sedimentology and palaeoecology of the brachiopods and of the other main invertebrate groups represented in the chalk. The brachiopod palaeoecology was subsequently used as the theme for my PhD thesis (Surlyk 1972). The present study is an updated version of the previously unpublished taxonomic part of my 1969 dissertation extended to include craniacean and thecidean brachiopods and rare species from museum collections.

The present study is based on washed and sieved chalk bulk samples, typically weighing 10 kg and in many cases 2.5 kg and 5 kg (Surlyk 1972). The samples were first broken down into cm-sized fragments and subsequently dried at about 30°C and weighed. They were then heated in a supersaturated solution

of Glauber's Salt (sodium sulphate), followed by deep-freezing. This was typically repeated about 15 times, resulting in a total disintegration of the sample into chalk mud and shelly fossils. The sample was washed through a 0.25 mm sieve. The residue was dried and hand-sieved into three fractions: 0.25–0.5 mm, 0.5–1 mm and >1 mm. The brachiopods were picked under a binocular microscope from the upper two fractions, the lowest containing practically none.

The brachiopods comprising mainly early growth stages were subsequently determined to species level. The number of individuals is estimated by adding the number of whole specimens to whichever the greater number of ventral or dorsal valves, giving a minimum number of individuals (MNI). The number of fragments is also counted to assess if the calculated MNI is representative. High numbers of fragments show that the chalk sample in question was relatively hard, such as samples obtained from boreholes, representing relatively deep burial. The term 'individual' is used in the way described above in contrast to the term 'specimen', which is used for any whole shell, dorsal and ventral valve or fragment. A sample weight of 5 kg is ideal as larger samples rarely result in retrieval of additional species but only in more individuals. Further details on the methodology are given in Surlyk (1972). The material obtained by washing of bulk samples is supplemented by the much rarer medium- and large-sized specimens hand-picked in the field. In addition, material housed at the Natural History Museum of Denmark and Geomuseum Faxe has been examined (Table 1). Some larger specimens from these collections are photographed, but the museum material is not included under Material in the taxonomic section, which is based on the sample material except for the rare, larger species. Many of the specimens

in the museum collections lack precise stratigraphic location and are commonly only labelled as e.g. Møns Klint, which is not very useful for this 7 km long shoreline cliff exposing a long series of glacially thrust chert successions, 13 of which were sampled for the present study.

All colour photographs were made by Sten Lennart Jakobsen. Almost all drawings of growth stages were made by Erna Nordmann, of *Rugia spinosa* by Christian Rasmussen and of spicular skeletons by the author. In the scatter diagrams L=length, W=width, T=thickness, R=number of ribs/costae/costellae. A, B etc. in the scatter diagrams are not explained in the captions as they just show the relations between e.g. L/W and W.

The material is housed at the Natural History Museum of Denmark (MGUH numbers) and Geomuseum Faxe (OESM numbers).

Stratigraphy

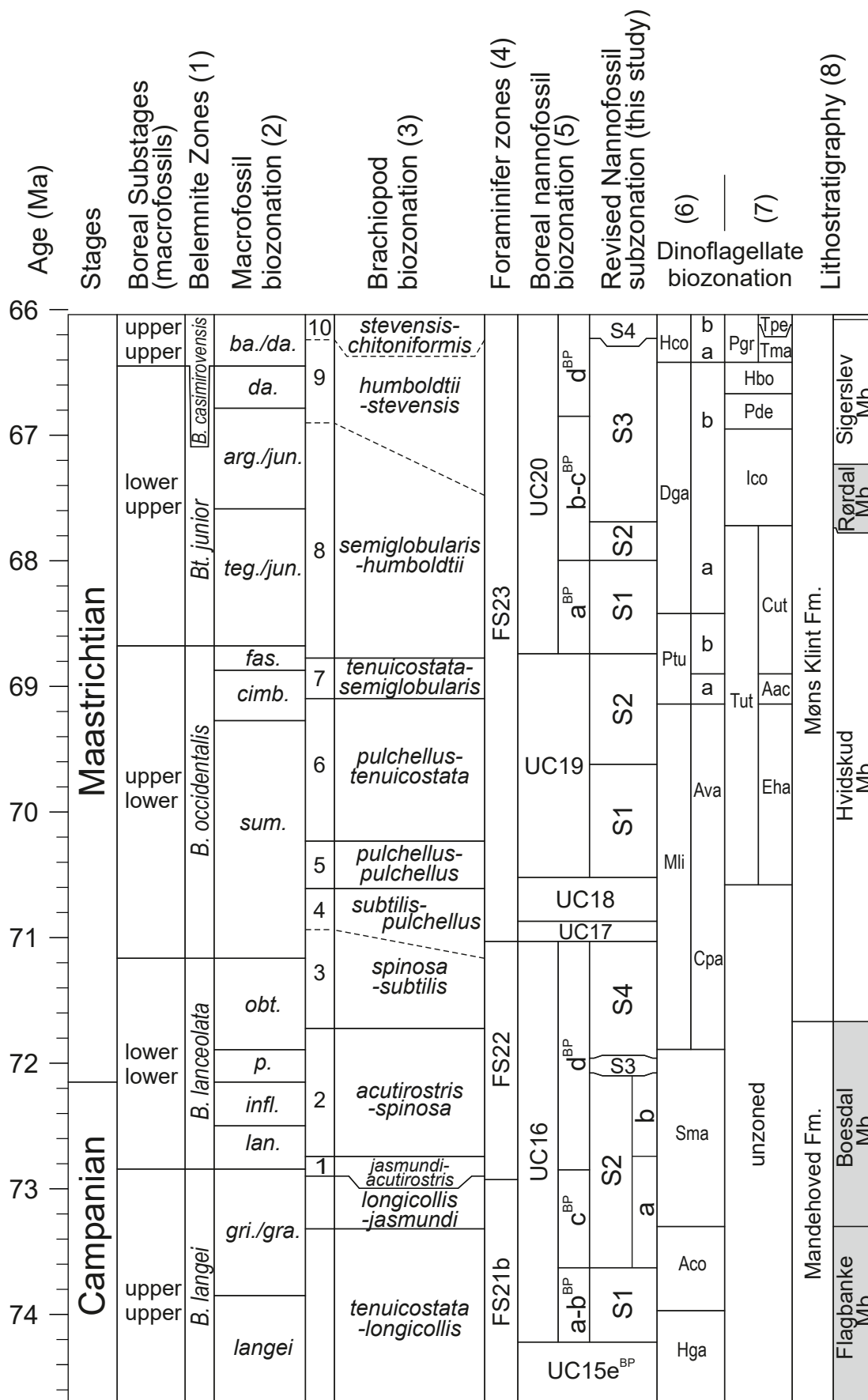
Steinich (1965) was the first to demonstrate that brachiopods obtained by washing of bulk samples were stratigraphically very useful, allowing the recognition of 3 full and 2 partial zones in the lower Maastrichtian chalk of the island of Rügen in NE Germany. Studies of the brachiopods from the Danish Maastrichtian resulted in a subdivision of the Maastrichtian into 10 zones based on material from 42 localities (Surlyk 1969, 1970a, 1984). The zones were originally numbered 1–10 from below (Surlyk 1970a) but were subsequently given binomial names based on the names of the species defining the lower and upper boundary, respectively (Surlyk 1982). This system was introduced by Murphy (1977) and each zone is defined by its boundaries in a stratotype. Only one species is used to define the lower zonal boundary; the upper boundary is then defined by the species defining the base of the next overlying zone. In this way gaps and overlaps of zones are avoided, following the principles used in the definition of stages. Note that only species names are given, using the names of the species defining the lower and upper boundary, respectively, e.g. *humboldtii-stevensi* Zone. This zonation was correlated with the earlier belemnite zonation of Birkelund (1957), resulting in a major revision of the position of the lower–upper Maastrichtian bound-

ary in Denmark, which is exposed in belemnite-poor relatively deep-water chalk exposed in northern Jylland, notably in the large Rørdal quarry in Aalborg (17 in Fig. 2). Washed samples from a cored borehole, Rørdal-1, extended about 100 m down from the floor of the quarry allowed a precise correlation with the lower Maastrichtian chalk at Rügen and Møns Klint (Surlyk 1970a, fig. 1). Brachiopods obtained in a similar way from the large quarries in Hemmoor and Krons Moor in northern Germany and from small sections in Norfolk in eastern England were then used to establish a brachiopod zonation for the Danish, German and British upper Campanian – Maastrichtian chalk (Surlyk 1970a, 1982, 1984; Johansen & Surlyk 1990).

The 456.1 m deep fully cored borehole Stevns-1 was drilled in the southern part of Stevns Klint (2 in Fig. 2). It penetrated 12.8 m of lower Danian bryozoan limestone and 443.3 m of upper Campanian – Maastrichtian chalk. The Stevns-1 borehole formed the basis for the definition of the upper Campanian – lowermost Maastrichtian Mandehoved Formation subdivided from below into the Flagbanke and Boesdal Members and the Maastrichtian Møns Klint Formation subdivided into the Hvidskud, Rørdal, Sigerslev and Højerup Members (Fig. 3; Surlyk *et al.* 2013). The upper Maastrichtian chalk exposed in the coastal cliff Stevns Klint is subdivided into the Sigerslev Member composed of pure chalk, mounded in the lower part and topped by a double incipient hardground overlain by mound-bedded bryozoan-rich chalk of the Højerup Member which is topped by the Cretaceous–Palaeogene boundary clay, the Fiskeler Member of the Rødvig Formation (Surlyk *et al.* 2006).

The brachiopod zones and their chronostratigraphic and lithostratigraphic positions are shown in Figure 3 (Surlyk *et al.* 2013; Thibault *et al.* 2024b) and in Table 2. They are defined as formal zones with stratotypes and are accordingly indicated with an upper-case Z in Zone (Surlyk 1984). The zonal scheme is extended downwards to include four zones belonging to the uppermost Campanian based on the successions at Krons Moor in northern Germany (Surlyk 1982, 1984) and Norfolk in eastern England (Johansen & Surlyk 1990). The definition of the Campanian–Maastrichtian boundary has been in some kind of a flux over the years, and this is one of the reasons for abandonment of the number system of Surlyk

Fig. 3. The uppermost Campanian – Maastrichtian brachiopod zones of the Danish Basin as recognized in Rasmussen & Surlyk (2012), Surlyk *et al.* (2013) and correlated with international standards. Modified from Thibault *et al.* (2024b, fig. 5). (1) Birkelund (1957) and Surlyk & Birkelund (1977); (2) Schulz *et al.* (1984) amended by Niebuhr *et al.* (2011) for the Campanian–Maastrichtian boundary interval; (3) Surlyk (1984); (4) King *et al.* (1989); (5) Burnett (1998); (6) Slimani (2011); (7) Schiøler & Wilson (1993); (8) Surlyk *et al.* (2013) – members in grey correspond to marly chalk and chalk–marl alternations; members in white correspond to chalk. Belemnite zones: B.: *Belemnella*; Bt: *Belemnitella*. Macrofossil biozonation (from below): *Belemnitella langei*, *Micraster grimensis*/*Cardiaster granulatus*, *Belemnella lanceolata*, *Belemnella inflata*, *Belemnella pseudobtusa*, *Belemnella obtusa*, *Belemnella sumensis*, *Belemnella cimbrica*, *Belemnella fastigata*, *Spyridosera tegulatus*/*Belemnitella junior*, *Tenuipteria argentea*/*Belemnitella junior*, *Tylocidaris baltica*/*Oxytoma danica*.



(1970a). The binomial system is open-ended and can be extended far downwards based on new data from older successions. In addition, new zones can easily be inserted without having to complicate a number system e.g. with adding 'a' and 'b' for new zones in a finer subdivision.

In the binomial zonal nomenclature both the lower and the upper boundary of the *pulchellus*–*pulchellus* Zone is defined by the lowest and highest occurrence of the same species. It is the only brachiopod range zone, whereas the other zones are concurrent range zones, e.g. the *humboldtii*–*stevensis* Zone. An upper Campanian – Maastrichtian holostratigraphy based on the Stevns-1 borehole, comprising new litho-, isotope and biostratigraphic subdivisions, based on petrophysical logs, stable carbon isotope, nannofossil, dinoflagellate and brachiopod data was presented by Rasmussen & Surlyk (2012) and Surlyk *et al.* (2013). Recently, an updated chronostratigraphy of the upper Campanian – Maastrichtian of the Boreal Realm was presented by Thibault *et al.* (2024b, fig. 5). It combines the biostratigraphic data with new carbon isotope records allowing correlation to the Tethyan bio-magnetic reference Gubbio in Italy and to the astronomically calibrated ODP site 762C in the Indian Ocean. The most up-to-date definition of the Campanian–Maastrichtian boundary is used based on the stratotype at Tercis les Bains in southern France. The position of the boundary in the Danish chalk remains unchanged following this definition and is still placed at the boundary between the *acutirostris*–*spinosa* and the *spinosa*–*subtilis* brachiopod Zones (Surlyk 1984; Thibault *et al.* 2024b, fig. 5). The lower–upper Maastrichtian boundary as used in Thibault *et al.* (2024b) also follows Surlyk (1970a, 1984) and Surlyk *et al.* (2013). It corresponds to the subdivision used in northern Germany (Schulz *et al.* 1984) and is placed just above the boundary between the *tenuicostata*–*semiglobularis* and the *semiglobularis*–*humboldtii* Zones.

Localities

The main sample localities in Denmark are situated on the islands of Sjælland (Stevns Klint) and Møn (Møns Klint) and in north-central Jylland (large quarries in, south and north of Aalborg), and in NW Jylland (Fig. 2). The localities are described in varying degrees of detail in Surlyk (1969). Published descriptions and measured logs of some key sections are indicated in the list below. The stratigraphy of the exposed sections is dealt with in some detail. I have experienced that this aspect is neglected in many taxonomic studies of Upper Cretaceous brachiopods. This practice hampers the interpretation of morphological changes as representing phyletic speciation through time or ecophenotypes, reflecting adapta-

tions to different contemporaneous environmental conditions. The stratigraphically most important species are listed for each locality. The author names of these species are not included here for simplicity but are given in the taxonomic descriptions.

Sjælland

Karlstrup (Surlyk 1969, 1984). This abandoned quarry is situated about 30 km SW of Copenhagen (1 in Fig. 2). The deepest part of the quarry exposed uppermost Maastrichtian chalk of the *stevensis*–*chitoniformis* Zone. The chalk is mounded (Fig. 5) as seen in parts of the contemporaneous Sigerslev and especially in the Højerup Members at Stevns Klint (Fig. 2; Surlyk *et al.* 2006). The mounded chalk is topped by the Cretaceous–Palaeogene boundary clay, the Fiskeler Member, marking the base of the Danian. The clay rests conformably on and drapes the mounds. It is overlain by lower Danian bryozoan limestone. The lowermost Danian Cerithium Limestone Member known from Stevns Klint (Surlyk *et al.* 2006) and its top erosion surface and associated hardground is absent and in this way the boundary succession is more like the boundary successions from the deeper parts of the Danish Basin, such as Nye Kløv and Kjølbygård (24 in Fig. 2). Several early attempts to describe the succession at Karlstrup have not added to the understanding and are difficult to follow possibly due to poor exposure at the time of study (Rosenkrantz & Rasmussen 1960; Gravesen 1983).

Seven samples are investigated for brachiopods (Fig. 5). The sample 'Karlstrup no number' was taken immediately below the boundary clay, and has together with Karlstrup 1–4 yielded stratigraphically important brachiopods, and they are listed here from below:

Karlstrup 1: *Meonia semiglobularis*; *stevensis*–*chitoniformis* Zone; upper upper Maastrichtian.

Karlstrup 2: *Rugia stenius* n. sp., *Ruegenella humboldtii*; *stevensis*–*chitoniformis* Zone; upper upper Maastrichtian.

Karlstrup 3: *M. semiglobularis*, *Bronnothyris stevensis*, *R. humboldtii*; *stevensis*–*chitoniformis* Zone; upper upper Maastrichtian.

Karlstrup 4: *R. stenius* n. sp., *B. stevensis*; *R. humboldtii*; *stevensis*–*chitoniformis* Zone; upper upper Maastrichtian.

'Karlstrup no number': *R. stenius* n. sp., *B. stevensis*; *stevensis*–*chitoniformis* Zone; upper upper Maastrichtian.

Stevns Klint (2 in Fig. 2; Figs 6, 7). (Surlyk 1984; Surlyk & Håkansson 1999; Surlyk *et al.* 2006, 2013; Anderskov *et al.* 2007; Rasmussen & Surlyk 2012; Hansen & Surlyk 2014). This 14.5 km long coastal cliff was appointed UNESCO World Heritage in 2016 due to the unbroken Cretaceous–Paleogene boundary succession



Fig. 4. **A.** Aerial photograph of the southern part of the coastal cliff, Møns Klint (Fig. 2). The cliff exposes a long series of stacked thrust sheets of mainly lower Maastrichtian chalk. The key section for sampling is Hvidskud (Surlyk 1970a, 1972; Surlyk & Birkelund 1977; Jelby *et al.* 2014). **B.** The upper part of the Hvidskud section; MF: master flint band; HG: Hardground.

(Damholt & Surlyk 2012). It exposes chalks of the upper Maastrichtian Sigerslev and Højerup Members (Møns Klint Formation), the lowermost Danian Fiskeler and Cerithium Limestone Members of the Rødvig Formation, overlain by lower Danian bryozoan limestone of the Stevns Klint Formation (Surlyk *et al.* 2006). Seven samples are investigated for their brachiopod fauna. Stevns 7 and 6 are from the northern part of the

cliff south of Sigerslev quarry (Fig. 6), whereas Stevns 5–1 are from the section due south of the stairs leading down to the beach from Højerup Old Church (Figs 2, 6, 7). The samples are listed from below with stratigraphically important species noted. Stevns 7–3 belong to the Sigerslev Member and Stevns 2–1 to the Højerup Member of Surlyk *et al.* (2006).

Stevns 7: Bronnothyris stevensis, Isocrania sendeni; ste-

vensis-chitoniformis Zone; upper upper Maastrichtian.

Stevns 6: *Meonia semiglobularis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

Stevns 5: *M. semiglobularis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

Stevns 4: *M. semiglobularis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

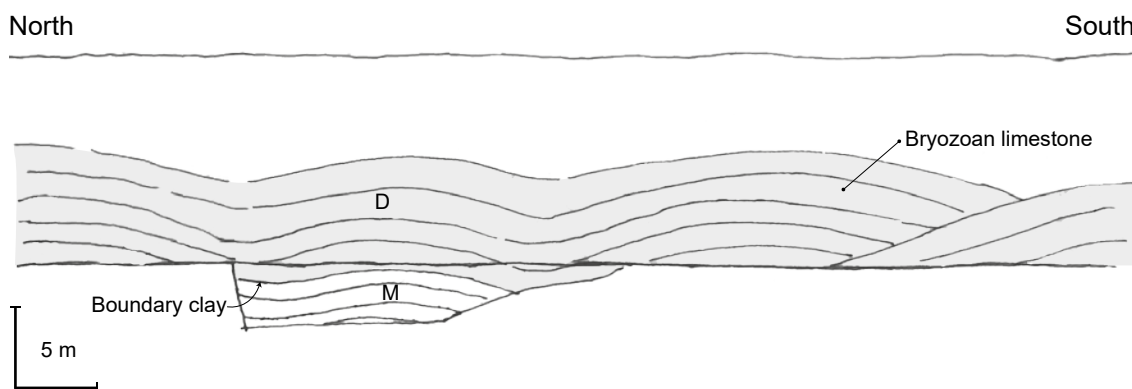
Stevns 3: *I. sendeni*, *Rugia stenius* n. sp., *M. semiglobularis*, *B. stevensis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

Stevns 2: *Ruegenella humboldtii*, *B. stevensis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

Stevns 1: *R. stenius* n. sp., *B. stevensis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

Kongsted (3 in Fig. 2). Abandoned quarry which exposed some of the oldest chalk in Denmark (outside Bornholm in the Baltic Sea), belonging to the uppermost Campanian or lowermost Maastrichtian mainly based on the presence of the crinoid *Austinocrinus bicoronatus* (Rasmussen 1961) and the belemnite *Belemnitella langei* (Birkelund 1957). One sample has been

A



B

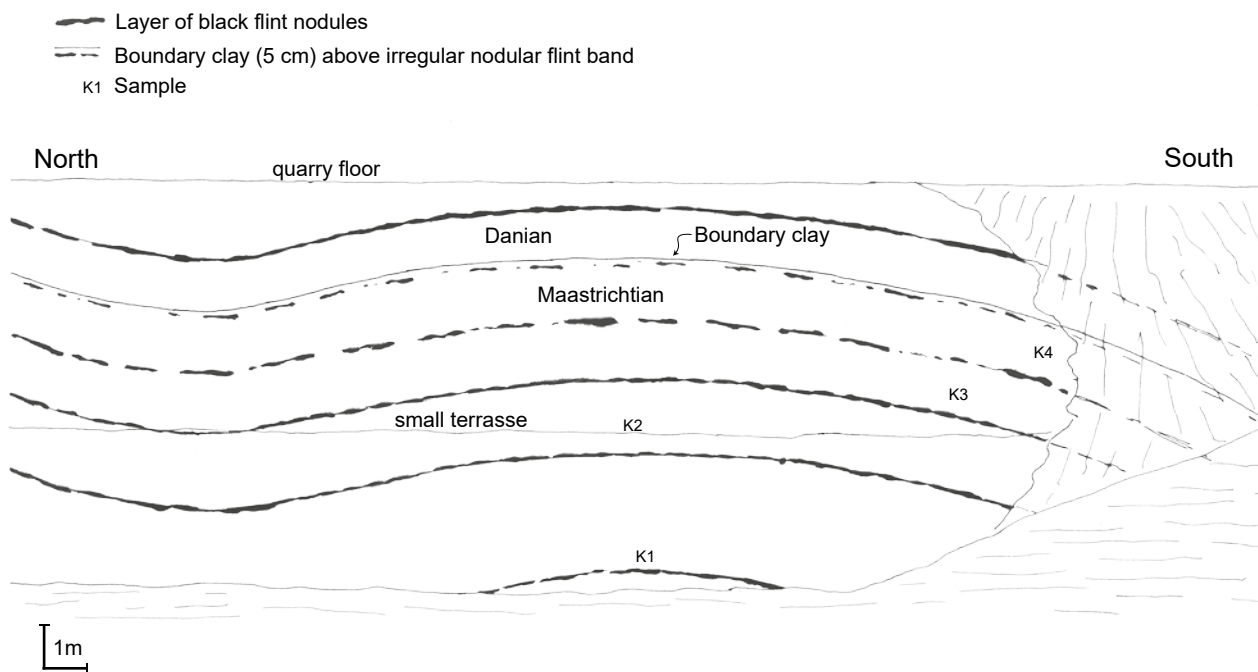


Fig. 5. Field sketches of the Maastrichtian–Danian (K–Pg) boundary at Karlstrup limestone quarry (1 in Fig. 2 and now abandoned). **A.** The lower non-shaded part is upper upper Maastrichtian chalk deposited in overlapping mounds (M). They are draped by the 5 cm thick boundary clay overlain by lower Danian bryozoan limestone mounds (D: shaded). **B.** Sample positions indicated with respect to the Maastrichtian–Danian boundary clay (K1–K4).

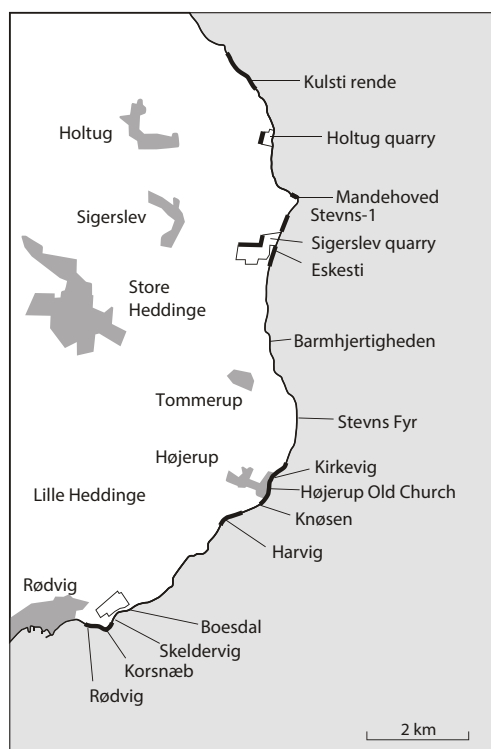


Fig. 6. Map showing the main sample localities along the coastal cliff, Stevns Klint (Fig. 2; From Hansen & Surlyk 2014).

studied and contained *Rugia acutirostris*, which is known from both the uppermost Campanian and lower lower Maastrichtian. The brachiopod content thus does not clearly indicate a Campanian or Maastrichtian age.

Falster

Gedser Fyr (7 in Fig. 2). *Rugia acutirostris*, *R. spinosa*; *spinosa–subtilis* Zone; lowermost Maastrichtian.

Gedser Odde (8 in Fig. 2). *R. acutirostris*, *R. spinosa*; *spinosa–subtilis* Zone; lowermost Maastrichtian

Møn

Hvide Klint (5 in Fig. 2). The low coastal cliff Hvide Klint on the south coast of Møn shows some of the oldest exposed chalk in Denmark (outside Bornholm in the Baltic Sea). The brachiopods indicate that the chalk belongs to the Campanian–Maastrichtian boundary interval. “The calcareous nannofossil assemblage of a few samples collected at the Hvide Klint locality is characterized by a high relative abundance of *Watznaueria barnesiæ* reaching up to >10% of all species, along with common *W. cf. W. manivitiae* and common *Reinhardtites levis*. Such an assemblage is typical in Denmark and NW Germany of the late Campanian warm optimum episode spanning sub-zones UC15e^{BP} to UC16S3 (Boussaha *et al.* 2016; Nyborg *et al.* 2020)” (N. Thibault, written communication 2025).

Hvide Klint 1: *Rugia tenuicostata*; *spinosa–subtilis*

Zone.

Hvide Klint 2: *Rugia acutirostris*; *spinosa–subtilis* Zone.

Hvide Klint 3: *R. acutirostris*; *spinosa–subtilis* Zone.

Hvide Klint 4: *R. tenuicostata*, *R. acutirostris*, *R. spinosa*; *spinosa–pulchellus* Zone

Lille Bissinge (5 in Fig. 2). Small, now overgrown outcrop, which probably exposed a glacial raft of chalk: *Rugia acutirostris*. Probably belonging to the *spinosa–subtilis* Zone; lowermost Maastrichtian (Surlyk 1984).

Møns Klint (4 in Fig. 2; Fig. 4). This 7 km long impressive coastal cliff exposes glacially upthrust anticlines and sheets of chalk. Listed from S to N they are named as Jættebrinken, Hvidskud, Hundefangsklint, Lille Stejlebjerg, Store Stejlebjerg, Gråryg, Nellerendenakke, Sommerspiret, Sandpynt, Maglevandspynt, Dronningestolen, Forchhammers Pynt, Vitmunds Nakke, Sættepileklint, Nylands Nakke, Store Taler, Lille Taler, and Slotsgravlene (Surlyk 1971, 1972, 1984; Surlyk & Birkelund 1977). The glacially overthrust anticline of Hvidskud (Fig. 7) is the key section for bulk sampling and formed the basis for the works of Surlyk (1969, 1970a, 1972) and Surlyk & Birkelund (1977) and especially for the correlation with the chalk of Rügen (Surlyk 1970a) and more recently for carbon isotope stratigraphy (Jelby *et al.* 2014). The sampled sections at Møns Klint is listed below in alphabetical order.

Forchhammers Pynt

Forchhammers Pynt 1: *Terebratulina subtilis*.

Forchhammers Pynt 2: *T. subtilis*, *Gisilina gisii*; *subtilis–pulchellus* or *pulchellus–pulchellus* Zone; upper

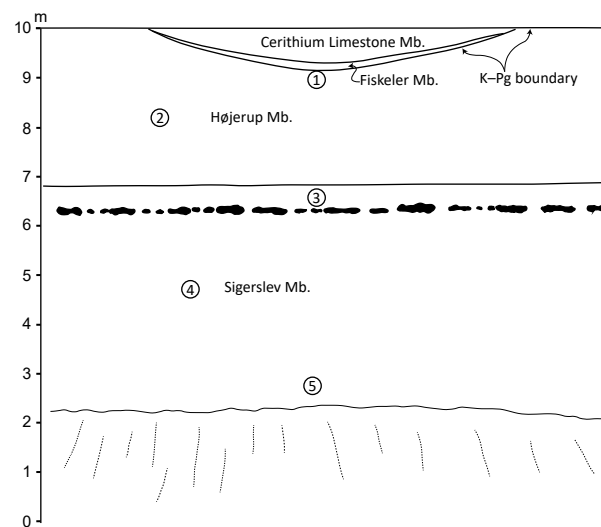


Fig. 7. Field sketch of the Maastrichtian–Danian (K–Pg) boundary succession exposed immediately south of the Højerup old church at Stevns Klint. This is the classical boundary location where Walter Alvarez in 1978 sampled the boundary clay, the Fiskeler Member to check if the iridium anomaly found at Gubbio, Italy was more than a local phenomenon. The encircled numbers indicate the position of bulk samples S1–S5.

lower Maastrichtian.

Hundefangsklint (Fig. 4). Six samples investigated out of a long sample series. Those with stratigraphically significant species are listed below.

Hundefangsklint 4: *Rugia tenuicostata*, *R. acutirostris*; *subtilis*–*pulchellus* or *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hundefangsklint 7: *Gisilina gisii*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hundefangsklint 22: *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hundefangsklint 26: *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud (Fig. 4). One of the key sections for the brachiopod zonation. A long sample series was investigated. Not all containing stratigraphically significant species.

Hvidskud 1: *Rugia tenuicostata*, *R. acutirostris*, *Gisilina gisii*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 2: *Terebratulina subtilis*, *G. gisii*, *R. tenuicostata*?; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 3: *T. subtilis*, *G. gisii*, *R. tenuicostata*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 4: *G. gisii*, *R. tenuicostata*, *T. pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 5: *T. subtilis*, *R. tenuicostata*, *T. pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 7: *T. subtilis*; upper lower Maastrichtian.

Hvidskud 9: *T. subtilis*, *R. tenuicostata*, *T. pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 14: *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Hvidskud 16: *G. gisii*, *R. acutirostris*, *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Hvidskud 18: *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Hvidskud 22: *R. acutirostris*; *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Hvidskud 25: *G. gisii*, *R. tenuicostata*; *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Hvidskud 26: *G. gisii*, *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Hvidskud 28: *R. tenuicostata*, *R. acutirostris*; *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Jættebrinken (Fig. 4). *Gisilina gisii*, *Rugia acutirostris*, *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Lille Taler. *Gisilina gisii*, *Rugia tenuicostata*; probably *pulchellus*–*tenuicostata* Zone; upper lower Maastrich-

tian.

Maglevandspynt. Three samples.

Maglevandspynt 1: *Rugia tenuicostata*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Maglevandspynt 2: *Gisilina gisii*, *R. tenuicostata*; *pulchellus*–*pulchellus* or *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian.

Maglevandspynt 3: *R. tenuicostata*; upper lower Maastrichtian.

Nylands Nakke. *Rugia tenuicostata*, *Gisilina gisii*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Sandpynten. *Terebratulina subtilis*; *subtilis*–*pulchellus* or *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Slotsgavlene. *Rugia tenuicostata*; upper lower Maastrichtian.

Sommerspiret. Four samples contain stratigraphically significant species.

Sommerspiret 1: *Gisilina gisii*, *Rugia tenuicostata*; upper lower Maastrichtian

Sommerspiret 2: *Terebratulina subtilis*, *G. gisii*, *R. tenuicostata*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Sommerspiret 5: *G. gisii*, *R. tenuicostata*, *R. acutirostris*; upper lower Maastrichtian

Sommerspiret 9: *G. gisii*; upper lower Maastrichtian.

Store Taler. *Gisilina gisii*, *Rugia tenuicostata*; upper lower Maastrichtian. A few loose finds of *Meonia semiglobularis* indicate the presence of the lower part of the upper Maastrichtian *semiglobularis*–*humboldtii* Zone. The finds possibly include the type specimen of *M. semiglobularis* (Posselt 1894), leading Steinich (1965) to erect the genus name *Meonia* – Latin for Møn, a locality where it is close to absent!

Sættepileklint. *Gisilina gisii*, *Rugia tegulata*; upper part of the *pulchellus*–*tenuicostata* Zone; upper lower Maastrichtian. *R. tegulata* may indicate the presence of the lower upper Maastrichtian.

Vitmunds Nakke. *Terebratulina subtilis*, *Gisilina gisii*?, cf. *Rugia tenuicostata*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Central Jylland

Large quarries have been or are in operation in and north of the town of Aalborg and a number of smaller quarries south and south-east of Aalborg were active at the time of sample collection.

Aalborg (17 and 18 in Fig. 2). Three large quarries have exposed the *tenuicostata*–*semiglobularis* and *semiglobularis*–*humboldtii* Zones, the former only at Rørdal. The stratigraphic key succession of the Rørdal quarry is extended downwards with a ca. 100 m long fully cored borehole, Rørdal-1 that enabled correlation with the chalk at Møns Klint, Rügen and Hemmoor for the first time (Surlyk 1970a).

The combined borehole-outcrop section at Rørdal is thus a key section in the brachiopod zonation (Surlyk 1982, 1984; Surlyk *et al.* 2013). The top part of the succession exposed in the quarry is characterized by a succession of alternating pure and marly chalk beds, the Rørdal Member of Surlyk *et al.* (2010). This member has been the subject of detailed studies of faunal successions, climatic changes and orbital stratigraphy (Lauridsen & Surlyk 2008; Lauridsen *et al.* 2011; Thibault *et al.* 2024b). The lowest marl band was the only one exposed at the time of sampling and was correlated with a marl layer at Rügen and the ‘Tonband’ at Hemmoor, a marl bed interpreted as a bentonite by Valetton (1960) and as a residue after dissolved chalk by Ernst (1982). None of these interpretations seems to be correct and the German marl bands are probably the southernmost expression of the Rørdal Member in Denmark. A southwards decrease in the number of marl bands of the Rørdal Member is thus documented by comparison with the Stevns-1 borehole and 5 other boreholes (Thibault *et al.* 2024b, fig. 3).

Danmark (18 in Fig. 2). Three samples contained stratigraphically significant species.

Danmark 1: *Meonia semiglobularis*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Danmark 3: *M. semiglobularis*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Danmark 7: *M. semiglobularis*, *Rugia tegulata*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Lindholm (19 in Fig. 2). Six samples contained stratigraphically significant species.

Lindholm 1: *M. semiglobularis*, *Rugia tegulata*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Lindholm 2: *M. semiglobularis*, *R. tegulata*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Lindholm 7: *M. semiglobularis*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Lindholm 6: *M. semiglobularis*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Lindholm 5: *M. semiglobularis*, *R. tegulata*; *semiglobularis*–*humboldtii* Zone; lower upper Maastrichtian.

Rørdal quarry (17 in Fig. 2). Eight samples investigated. Only the two highest, Rørdal 7 and 8 contain a stratigraphically significant species, *M. semiglobularis* (Rørdal 7), indicating the base of the *semiglobularis*–*humboldtii* Zone (Fig. 3). This marks a level immediately below the lower–upper Maastrichtian boundary as currently defined (Surlyk 1970a; Surlyk *et al.* 2013; Thibault *et al.* 2024a) and allows correlation of the lowest marl layer of the Rørdal Member (Surlyk 1970a; Surlyk *et al.* 2010) with marl layers at Hemmoor and Rügen in northern Germany. Rørdal 1–6 are referred to the *tenuicostata*–*semiglobularis* Zone; uppermost lower Maastrichtian.

Rørdal-1 borehole (17 in Fig. 2). 22 samples ana-

lyzed, but not all contained stratigraphically significant species. The samples are listed from below in correct stratigraphical order.

Rørdal core sample 84: *Rugia spinosa*; *spinosa*–*subtilis* Zone; lowermost Maastrichtian

Rørdal core sample 74: *R. spinosa*; *spinosa*–*subtilis* Zone; lowermost Maastrichtian.

Rørdal core sample 70: *Ruegenella* sp. (non *humboldtii*)

Rørdal core sample 57: *Terebratulina subtilis*, *Rugia tenuicostata*, *Trigonosemus pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Rørdal core sample 46: *R. tenuicostata*, *T. pulchellus*?; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Rørdal core sample 42: *T. subtilis*, *R. tenuicostata*, *T. pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Rørdal core sample 38: *T. subtilis*, *Gisilina gisii*, *T. pulchellus*; *pulchellus*–*pulchellus* Zone; upper lower Maastrichtian.

Rørdal core sample 34: *G. gisii*?, *R. tenuicostata*; *tenuicostata*–*semiglobularis* Zone; uppermost upper lower Maastrichtian.

Rørdal core sample 31: *G. gisii*, *R. tenuicostata*; *tenuicostata*–*semiglobularis* Zone; uppermost upper lower Maastrichtian.

Rørdal core sample 29: *R. tenuicostata*; *tenuicostata*–*semiglobularis* Zone; uppermost upper lower Maastrichtian.

Rørdal core sample 24: *G. gisii*; *tenuicostata*–*semiglobularis* Zone; uppermost upper lower Maastrichtian.

South of Aalborg

Medium-sized to small mostly abandoned quarries including Dania, Ellidshøj, Ferslev, Gudumholm, Linds, Mjels, Nørre Flødal, Smidie, Spentrup, Sønder Kongerslev. Most or all of these localities exposed chalk of the lower upper Maastrichtian *humboldtii*–*stevensis* Zones (Surlyk 1984). The section at Dania, however, is clearly placed in the *stevensis*–*chitoniformis* Zone, upper upper Maastrichtian.

Dania (10 in Fig. 2). 16 samples, D23–D2 have been investigated for brachiopods, but the order of the numbers is not stratigraphically systematic and all except four contain *M. semiglobularis*, which, however occurs in both the lowest and highest sample. *B. stevensis* occurs in D19, D7 and D5, placing the succession in the *stevensis*–*chitoniformis* Zone, upper upper Maastrichtian. The Maastrichtian–Danian (K–Pg) boundary is located in the upper part of the succession, supporting this interpretation for the whole section.

Ellidshøj (14 in Fig. 2). One sample: *Meonia semiglobularis* and *Ruegenella humboldtii*; lower upper Maastrichtian.

Ferslev (16 in Fig. 2). One sample: *Meonia semiglobularis*; upper Maastrichtian.

Gudumholm (13 in Fig. 2). Four samples, all containing *Meonia semiglobularis*; upper Maastrichtian.

Linds (15 in Fig. 2). One sample: *Meonia semiglobularis*, *Ruegenella humboldtii*; probably the lowermost part of the *humboldtii*–*stevensis* Zone; transition between the lower upper and upper upper Maastrichtian.

Mjels (14 in Fig. 2). One sample: *Meonia semiglobularis*; upper Maastrichtian.

Nørre Flødal (15 in Fig. 2). Two samples both containing *Meonia semiglobularis* and one also *Ruegenella humboldtii*; probably the lowermost part of the *humboldtii*–*stevensis* Zone; transition between the lower upper and upper upper Maastrichtian.

Smidie (11 in Fig. 2). One sample: No age-diagnostic species, probably *humboldtii*–*stevensis* Zone; transition between the lower upper and upper upper Maastrichtian.

Spentrup (9 in Fig. 2). One sample: *Ruegenella humboldtii*; upper Maastrichtian.

Sønder Kongerslev (12 in Fig. 2). One sample: *Meonia semiglobularis*; upper Maastrichtian.

The relatively closely situated sections south of Aalborg are all referred to the upper Maastrichtian based on *M. semiglobularis*. Only two samples contained *R. humboldtii* (1 in each) and none of the species characterizing the upper upper Maastrichtian are found, so these sections probably all belong to the *semiglobularis*–*humboldtii* Zone and the transition into the *humboldtii*–*stevensis* Zone.

Mors

Eerslev (22 in Fig. 2). *Meonia semiglobularis*, *Bronnothyris stevensis*; *stevensis*–*chitoniformis*; upper upper Maastrichtian.

NW Jylland

Mainly small quarries and slope sections at Aggersund, Batum, Bjerre, Hillerslev, Hov, Kjølbygård, Nye Kløv, and Svinkløv (Fig. 2). These successions mainly belong to the upper upper Maastrichtian *stevensis*–*chitoniformis* Zone (Surlyk 1984; Surlyk *et al.* 2013) and Nye Kløv is a key section to the understanding of the faunal succession across the Maastrichtian–Danian, K–Pg boundary (Surlyk & Johansen 1984; Johansen 1987; Håkansson & Thomsen 1999).

Aggersund (20 in Fig. 2). Two samples have both yielded *Meonia semiglobularis*, indicating the upper Maastrichtian.

Bjerre (26 in Fig. 2). One sample: *Meonia semiglobularis*, upper Maastrichtian, but the position of the sample immediately below the Maastrichtian–Danian boundary clay narrows it down to the *stevensis*–*chitoniformis* Zone, upper upper Maastrichtian.

Hillerslev (25 in Fig. 2). Two samples, both containing *Meonia semiglobularis*; upper Maastrichtian.

Hov (23 in Fig. 2). One sample: *Meonia globularis*; up-

per Maastrichtian.

Kjølbygård (24 in Fig. 2). Four samples, three of which containing *Meonia globularis*, indicating the upper Maastrichtian. However, the Maastrichtian–Danian boundary clay is exposed at the top of the rather small section, which can be safely placed in the *stevensis*–*chitoniformis* Zone, upper upper Maastrichtian.

Nye Kløv (24 in Fig. 2). This locality is generally regarded as exposing the most complete Maastrichtian–Danian (K–Pg) boundary succession in Denmark and the brachiopods and not least their stratigraphic distribution have been studied in detail (Surlyk & Johansen 1984; Johansen 1987). *Gisilina jasmundi*, *Meonia semiglobularis*, *Rugia tenuicostata*, *Rugia stenius* n. sp. (listed as *Rugia acutirostris* by Johansen 1987), *Bronnothyris stevensis*.

Svinkløv (21 in Fig. 2). Three samples, two with *Meonia semiglobularis*, indicating the upper Maastrichtian.

Taxonomy

All brachiopod species retrieved from bulk samples of the Maastrichtian chalk of the Danish Basin are described below using the terminology and diagnoses of the Treatise on Invertebrate Paleontology Part H Brachiopoda (Williams *et al.* 1997; Baker 2006; Bassett 2000; Holmer & Popov 2000; Lee & Smirnova 2006; Lee *et al.* 2006, 2007; MacKinnon & Lee 2006; Mancenido *et al.* 2002, 2007). Rare species are included for the sake of completeness even if they have not been found in the washed bulk samples. The larger species in particular are shown in a series of colour photographs, and the growth stages of most of the common micromorphic species are shown in drawings.

Most of the species are well known and many have been described in detail in the literature, notably by Backhaus (1959), Steinich (1965, 1967, 1968a,b), Surlyk (1970b, 1972, 1973, 1974), Asgaard (1972, 1975), Bitner & Pisera (1979), Johansen (1987), Johansen & Surlyk (1990), Simon (1998, 2000, 2011), Schröder & Surlyk (2020) and Machalski & Bitner (2024). I therefore refer to these works in terms of synonym lists and, in some cases, more detailed descriptions of large or rare species, which are only rarely found in the bulk samples. The inner morphology plays little role in the species identifications and are described in detail for most species notably by Steinich (1963, 1965, 1967, 1968a, b), Surlyk (1970b, 1972, 1974, 1982), Bitner & Pisera (1979), Johansen (1987), Johansen & Surlyk (1990), Simon (1998, 2011), Sklenár & Simon (2009) and Machalski & Bitner (2024).

Emphasis is placed on the differences to closely related species, especially as regards the juvenile specimens and to the dimensions illustrated in scat-

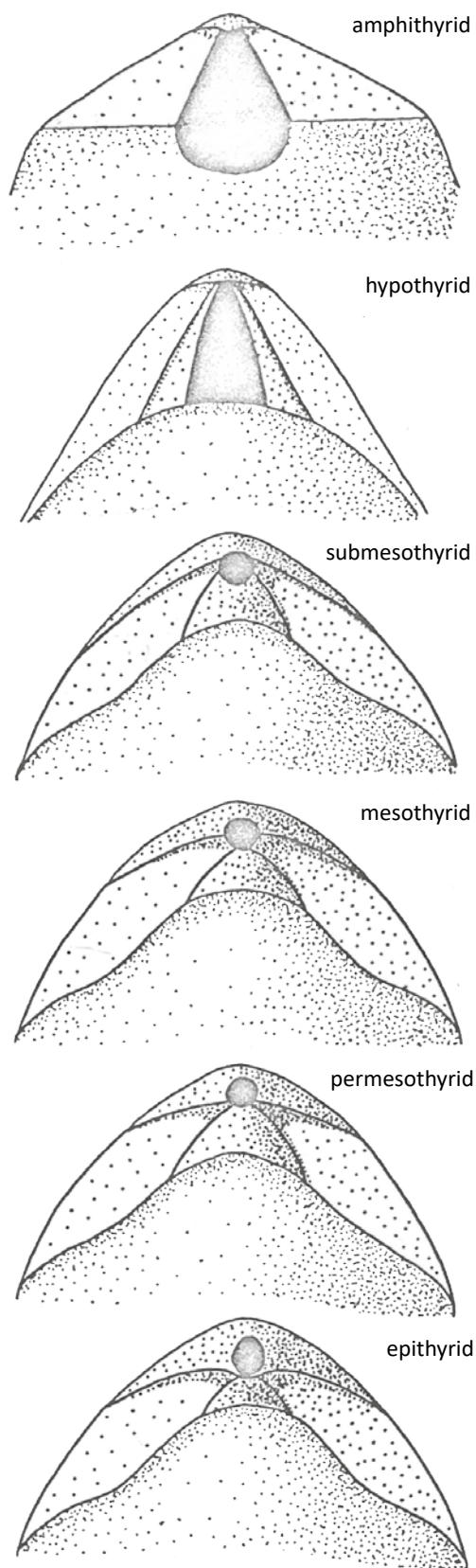


Fig. 8. Terminology describing the relative position of the pedicle opening and the beak ridges. Modified from Williams *et al.* (1997, fig. 318).

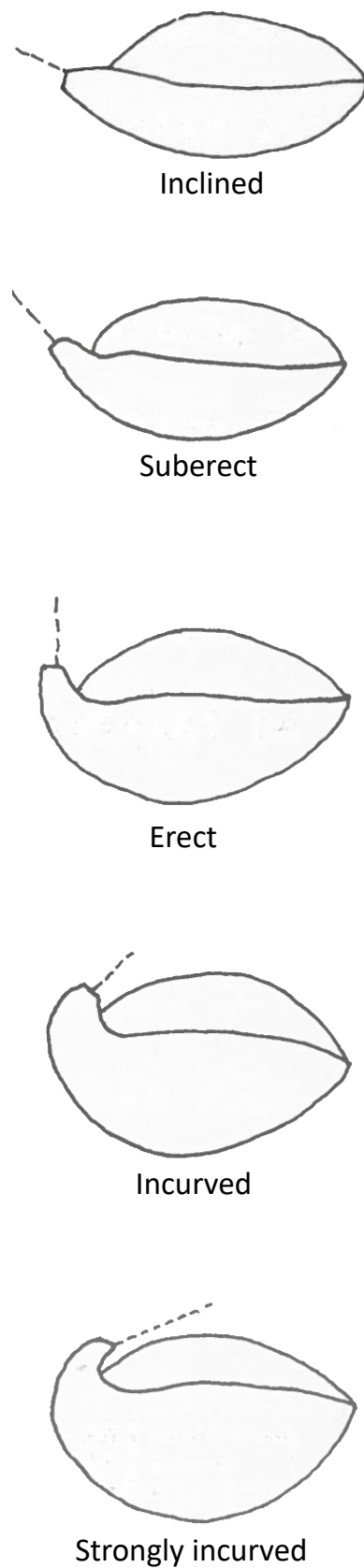


Fig. 9. Terminology describing the position of the pedicle openings relative to the beak ridges. Modified from Williams *et al.* (1997, fig. 318).

ter plots, showing the ontogenetic development of most of the species. The following abbreviations are used in the text and in the scatter plots: L=length, W=width, T=thickness and R=number of ribs (costae and costellae). All ratios such as length/width = L/W are ca. values but 'ca.' is omitted throughout for clarity. The size of the species is given as 'micromorphic' for species with an adult length of $\in [0;5]$ mm, small-sized $\in [5;10]$ mm, medium-sized $\in [10;20]$ mm, and large-sized $\in [20;100]$ mm. These assignments should be considered approximations only. The somewhat cumbersome terminologies describing the morphology of the foramen and its relations to the two valves and the lateral profile of the shell and beak are illustrated in Figure 8 and 9.

Number of individuals of all species found in the sample series are mentioned under 'Material' and the most relevant literature is listed under the heading 'Pertinent references' in the descriptions of the individual species. The numbers given are minimum number of individuals (MNI), calculated as the sum of whole specimens and whichever the greater number of ventral or dorsal valves following Surlyk (1972). An exception is the numbers from Nye Kløv, which are the sum of whole specimens, ventral and dorsal valves taken from Johansen (1987).

Under the heading 'Chronostratigraphy in Denmark' special attention is paid to the stratigraphic distribution of those species that form the basis for the brachiopod zonation (Surlyk 1970a, 1982, 1984; Surlyk *et al.* 2013). The definition of the Campanian–Maastrichtian boundary in the chalks of northern Europe has been in a state of flux over the years. The classical boundary in the Boreal Realm was placed at the lowest occurrence of the belemnite *Belemnella lanceolata*, but the definition of this species has been revised. In addition, the micro- and nannofossil defined boundary as currently understood differs from the belemnite-defined boundary (see Thibault *et al.* 2024a). The boundary as now defined at Tercis les Bains in southern France and rectified by the International Commission of Stratigraphy is marked by the lowest occurrence at this locality of the ammonite *Pachydiscus neubergicus* (von Hauer, 1858) supported by several other so-called guide-events (e.g. Odin & Lamaurelle 2001). The Global Boundary Stratotype Section and Point (GSSP) is thus defined at Tercis les Bains by a combination of several stratigraphic criteria, quite clearly not an ideal situation.

It is important to note that the stage mentioned for each species under the heading Chronostratigraphy in Denmark only refers to its occurrence in the Maastrichtian in Denmark. Thus, quite a few species are known also to occur in the upper Campanian as demonstrated for e.g. Krons Moor in northern Germany and Norfolk in eastern England (Surlyk 1982, 1984; Johansen & Surlyk 1990). Also, under occur-

rences 'outside Denmark' only those localities are listed where I find the assignment convincing, preferably with descriptions and illustrations of growth stages in Figures 8 and 9.

The material is kept in the collections of the Natural History Museum of Denmark (MGUH numbers), Geomuseum Faxe (OESM numbers) and in private collections (indicated in the text). This information is shown in Table 1.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams & others, 1997

Class Lingulata Gorjansky & Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus *Lingula* Bruguière, 1797

Type species *Lingula anatina* Lamarck, 1801

'*Lingula*' *cretacea*, Lundgren 1885

Fig. 10

The inverted comma around '*Lingula*' indicates that the generic assignment awaits further study. At the time of writing, a project has been initiated to solve the taxonomic identity of this species hopefully once and for all. The species is rare, but easy to locate both in the field and in the washing residues due to its chitinophosphatic light brown shell. It is almost always fragmented by compaction or during sample preparation due to the delicate nature of the thin shell. The studied material comprises only relatively

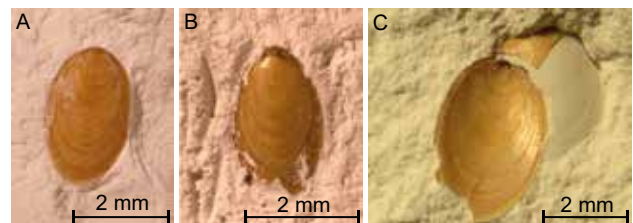


Fig. 10. '*Lingula*' *cretacea* Lundgren, 1885 ventral (A and B) and partially preserved dorsal valve (C). The specimens do not show enough detail of the posterior part around the hinge to allow a safe determination of the genus. Upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone, Sigerslev quarry, Stevns Klint (Figs 6, 7).

few specimens housed at Geomuseum Faxe and at the National History Museum of Denmark.

The species is small, elongate, oval and the umbo is located at the posterior end of the shell, but a small distance from the shell margin.

Material. Jylland. Dania, Rørdal-1 (found in 4 samples in the lower Maastrichtian part).

Sjælland. Sigerslev chalk quarry at Stevns Klint (Fig. 6; Gravesen & Jakobsen 2013, p. 93, no. 7)

Chronostratigraphy in Denmark. Lower and uppermost Maastrichtian. The very sparse material does not allow any precise statements as regards the stratigraphic distribution of this species.

Pertinent references. Lundgren (1885), Surlyk (1972), Gravesen & Jakobsen (2013).

Order Craniida Waagen, 1885

Superfamily Cranioidea Menke, 1828

Family Craniidae Menke, 1828

Genus *Crania* Retzius, 1781

Type species *Crania craniolaris* Linnaeus, 1758

Crania craniolaris Linnaeus, 1758

Fig. 11

C. craniolaris has not been found in the washing residues and this description is based mainly on material housed at Geomuseum Faxe.

The shell is medium-sized and the outline is subcircular to subquadrangular. The maximum width lies anterior to the midline. The ventral valve was attached to a hard substrate by the posterior part and the attachment surface is rather large, about 5 mm long. The dorsal valve is conical and smooth with faint growth laminae. The cicatrix is placed on the posterior part of the valve. The inner side of this valve is planar or slightly concave. It has deeply incised subcircular to oval muscle scars in the posterior part. The anterior muscle scars are located centrally in the valve, in connection to a rounded median ridge. The remaining part of the ventral floor has tubercles or radiating ridges. The limbus is thickened, wide and tuberculate.

Material. *C. craniolaris* is rare and lived attached to large, hard shelly substrates such as tests of irregular echinoids, belemnites and large brachiopods. Specimens available for study are housed at Geomuseum Faxe, the National History Museum of Denmark and own collections housed at the University of Copenhagen.



Fig. 11. *Crania craniolaris* Linnaeus, 1758 showing two ventral valves attached to the dorsal valve of the brachiopod *Carneithyris subcardinalis* (Sahni, 1925). The longitudinal axes of the two specimens are directed towards the anterior and lateral margin of the shell of *C. subcardinalis*. This fits well with the interpreted life position of this free-living brachiopod with the heavy umbo buried in chalk and the anterior margin and thus access to food-bearing currents pointing upwards – the self-righting “tumbler” of Surlyk (1972, fig. 4). If this interpretation is correct then the attachment of *C. craniolaris* probably took place while *C. subcardinalis* was still alive. Lower Maastrichtian. Dronningestolen, Møns Klint.

Dronningestolen, Møns Klint (Gravesen & Jakobsen 2013, p. 92, nos. 1, 5), Stevns Klint (Hansen & Surlyk 2013).

Chronostratigraphy in Denmark. Maastrichtian. The rarity of the species precludes precise information on stratigraphic distribution. The specimens from Møns Klint are lower Maastrichtian and those from Stevns Klint are upper upper Maastrichtian. A single poorly preserved specimen probably belonging to *C. craniolaris* was described from Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Lee & Brunton (1986), Gravesen & Jakobsen (2013), Robinson (2018).

***Crania antiqua* DeFrance, 1818**

Fig. 12

This species is rare in the Danish chalk and has not been found in the washing residues. Specimens from the Natural History Museum of Denmark, Geomuseum Faxe and the private collection of S.L. Jakobsen form the basis for the description.

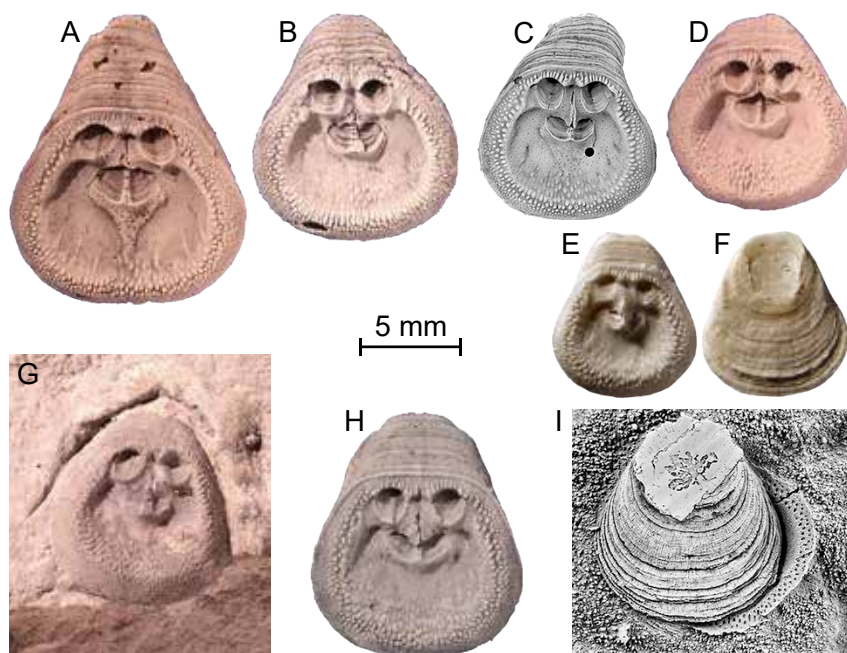


Fig. 12. *Crania antiqua* Defrance, 1818. A, B, C, D, E, G, H. Inside of ventral valve. Note the impressive adductor and pedicle muscle scars, giving the brachiopod a face-like appearance. C. Note the circular gastropod boring. F. External view of same specimen as E, showing attachment scar at posterior end. I. Ventral view of rare complete specimen, probably the only one known from the Danish chalk and designated a Danekræ fossil trope. The irregular furrows on the attachment scars were probably etched by organic acids from bryozoans. All except E and F from the Sigerslev quarry, E and F, Holtug quarry. Upper upper Maastichtian, *stevensis*–*chitoniformis* Zone, Stevns Klint (Figs 2, 6).

Crania antiqua is small to medium sized. The outline of the ventral valve is elongate pear-shaped with a more or less strongly extended posterior margin. The dorsal valve is similar except for the lack of the extended margin. The shell is thick and the attachment surface on the ventral valve is situated in the posterior part of the valve and is rather large, up to about half the length of the valve. It may show imprints after the subject of attachment, including etchings probably produced by bryozoans. The outer surface of the valve shows very fine radial striations, in some case very weak costellae and numerous crude growth lines. The inner side of the valve is characterized by deep, oval posterior muscle scars and two oblique closely spaced anterior scars. The valve has a relatively wide tuberculate margin where the tubercles become progressively smaller towards the valve margin. This is also the case with the dorsal valve. The inner margin of the tuberculated belt is not sharply delimited. *C. antiqua* differs from *Crania craniolaris* in the posterior extension of the ventral valve and in the very deep muscle scars.

Material. A number of specimens are housed at the Natural History Museum of Denmark, Geomuseum Faxe and in the private collection of S.L. Jakobsen, Stevns Klint (Holtug and Sigerslev quarries). Nielsen (1909) lists two specimens from Stevns Klint.

Chronostratigraphy in Denmark. Upper upper Maastichtian, *stevensis*–*chitoniformis* Zone.

Pertinent reference. Gravesen & Jakobsen (2013).

Genus *Ancistrocrania* Dall, 1877

Type species *Ancistrocrania parisiensis* Defrance, 1818

Ancistrocrania parisiensis Defrance, 1818

Fig. 13

This species is rare in the Danish chalk and has not been found in the washing residues. Specimens from the Natural History Museum of Denmark, Geomuseum Faxe and own collection housed at the University of Copenhagen form the basis for the description.

The species is small to medium sized. It is attached with the complete ventral valve to large, hard substrates such as shells of inoceramid bivalves and irregular echinoids. It has deeply incised subcircular to oval muscle scars in the posterior part, giving the valve its eponymic name. The outline is subangular to subcircular but with a rather straight posterior margin. The greatest width is anterior to the midline. The ventral valve is thick, and the rim is slightly pustulose and has an outwards inclined margin. The ventral valve is internally concave to conical with deeply sunken muscle scars. The dorsal valve is thin, and the outside is smooth but with numerous growth lines and in some cases with a pustulose ornamentation. The inner surface and muscle scars are described in detail by Robinson (2018) and Schröder *et al.* (2019).

Material. A few specimens from collections at Geomuseum Faxe, the National History Museum of Denmark and own collections housed at the University of Copenhagen.

Nylands Nakke at Møns Klint, Dania and Sigerslev chalk quarry, Stevns Klint (Gravesen & Jakobsen

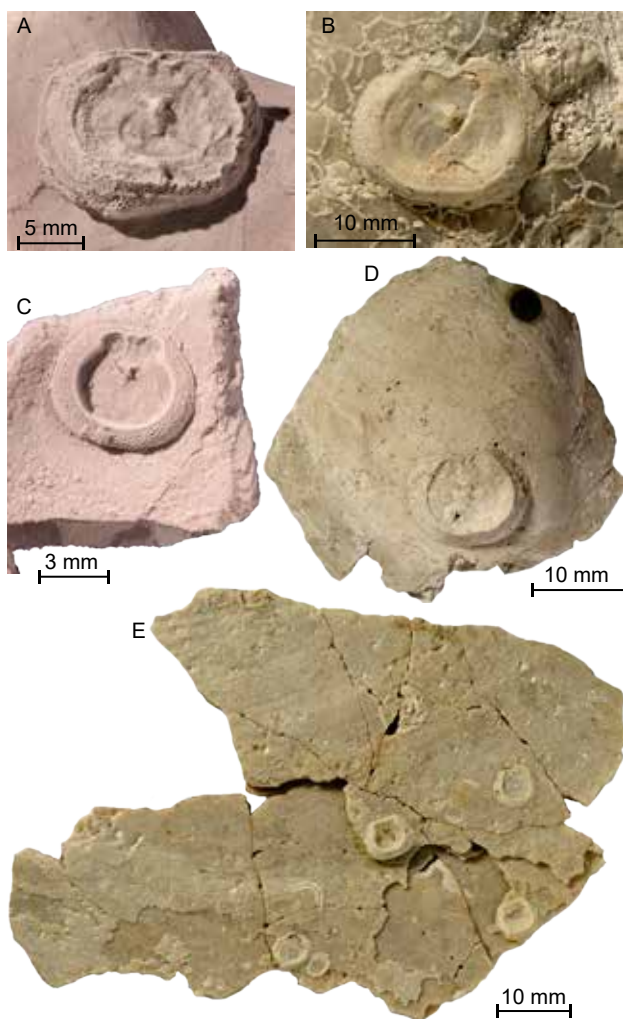


Fig. 13. *Ancistrocrania parisiensis* (DeFrance, 1819). Ventral valves attached with the whole valve to the hard skeletal substrates. A, B, C, Sigerslev quarry, Stevns Klint. D. Attached to oyster *Pycnodonte vesicularis* (Lamarck, 1806), Dania. E. Five specimens attached to inoceramid shell, Nylands Nakke, Møns Klint. Upper lower Maastrichtian (Fig. 2). All except E, Upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone (Figs 2, 6).

2013, p. 92, nos. 2, 3, 4, 7).

Chronostratigraphy in Denmark. Maastrichtian. Lower Maastrichtian at Nylands Nakke at Møns Klint and upper upper Maastrichtian at Dania and Stevns Klint. Outside Denmark, it is well known from the upper lower Campanian at Ivö Klack in southern Sweden.

Pertinent references. Lee & Brunton (1986), Gravesen & Jakobsen (2013), Robinson (2018), Schröder *et al.* (2019).

Ancistrocrania tubulosa Nielsen, 1909

Fig. 14

This species is rare and poorly known. In the various collections, it is sometimes labelled as *Ancistrocrania parisiensis*, and Nielsen (1909) wrote that it possibly should be referred to this species. However, he also noted that it possessed some persistent features that distinguished it from *A. parisiensis*. The specimens I have examined support this observation and it is undoubtedly a well-defined, independent species.

The species is small-sized, up to 7.5 mm in length, and the outline of the ventral valve is oval to rounded quadrangular and is attached with almost all of its

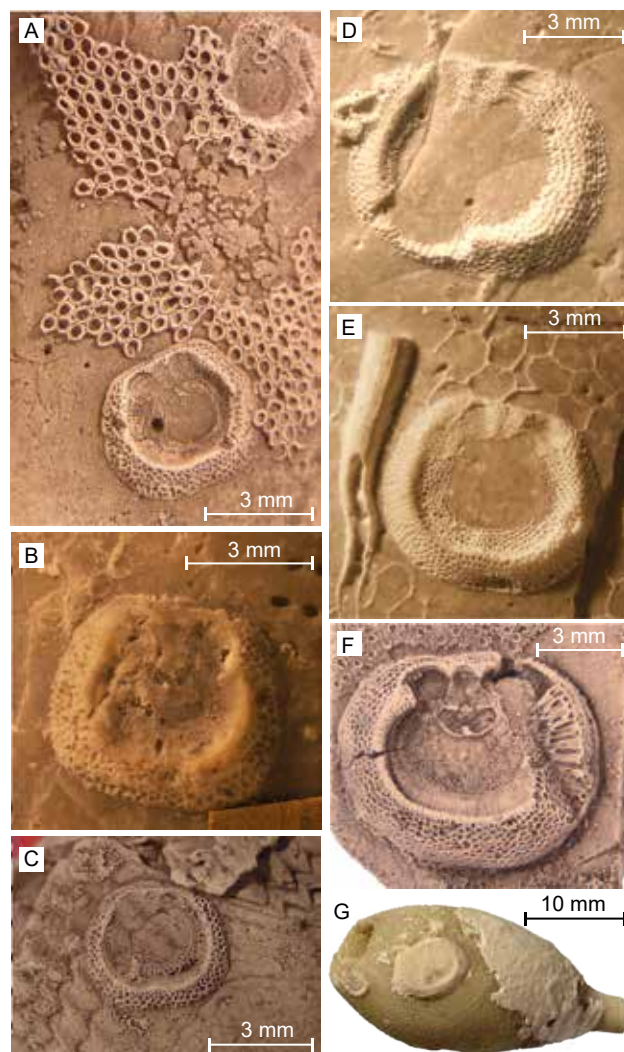


Fig. 14. *Ancistrocrania tubulosa* (Nielsen, 1909). A–G. Ventral valves attached to large hard substrates. Note the tubular pores of shell margin. G. Attached with the whole valve to the bulbous spine of the regular echinoid *Tylocidaris baltica* together with a microporid cheilostome bryozoa, probably *Micropora* sp., to the right (E. Håkansson, pers. comm. 2024). Upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6). A–F. Maastrichtian, Denmark.

outer surface to the substrate, normally a large bivalve shell or an echinoid test. The posterior muscle scars are oval and not very clearly marked. The anterior muscle scars are weak or missing. The shell consists almost only of the thickened margin and the inner, central part is not calcified. The most characteristic feature of the species is that the margin consists of parallel, radial calcareous tubes, which touch each other and have a narrow inwards opening towards the lumen of the shell, whereas the outer opening is wider. This feature clearly distinguishes *A. tubulosa* from related species.

Material. Møns Klint: 1; Nielsen (1909) mentions 1 specimen from Møns Klint, 6 from Stevns Klint, 1 from Aalborg, 8 from Rørdal and 1 from Dania. Gravesen & Jakobsen (2013, p. 92, no. 6) figure a fine specimen from Stevns Klint attached to the club-shaped spine of the regular echinoid *Tylocidaris baltica*. I have examined the collection of the Natural History Museum of Denmark which houses a total of 19 mainly well-preserved specimens, Aalborg: 2; Dania: 1; Møns Klint: 2; Rørdal: 7; Stevns Klint: 7.

Chronostratigraphy in Denmark. The species probably occurs throughout the Maastrichtian of Denmark in spite of lack of detailed locality information. However, almost all chalk at Møns Klint is lower Maastrichtian, the chalk at Aalborg and Rørdal exposed at the time of Nielsen's (1909) paper is upper lower Maastrichtian, the chalk at Dania and Stevns Klint is upper upper Maastrichtian.

Pertinent references. Nielsen (1909), Gravesen & Jakobsen (2013).

Genus *Isocrania* Jaekel, 1902

Type species *Isocrania egnabergensis* Retzius, 1781

Isocrania costata (Sowerby, 1823)

Fig. 15

The taxonomy, morphology and autecology of *I. costata* (Sowerby, 1823) was presented by Surlyk (1973). The morphological description given below is essentially repeated here as no new data on the morphology and ontogeny of the Danish material have been obtained since then. I have avoided the use of "..." for direct quotes in the description of this species to ease reading. The holotype has not been traced, but Surlyk (1973) gave an account on authorship and presumed type locality.

The shell is small and thick. The outline is subrectangular to subcircular, and the shell is normally a bit wider than long. The dorsal valve has a low conical shape with a smooth, pointed protegulum. The first costae are formed at $L=0.5$ mm and the number varies between 10 and 30. New costellae are formed by intercalation. A stratigraphic increase in number took place through the Maastrichtian. The costellae are strong, prominent and protrude somewhat beyond the shell margin. The lateral costellae show a slight backwards curvature. Coarse, radially directed small spines are normally present between the costellae. The posterior adductors of the dorsal valve are separated by a low septum, whereas the anterior adductor scars are closely spaced. A broad median ridge extends from the anterior adductors towards the limbus, which is wide and has a finely pustulose sculpture.

The outline and sculpture of the ventral valve is similar to the dorsal valve except for larger, widely spaced adductor scars, and the protegular node, which is flat and may show imprints of tiny hard substrates, such as bryozoan fragments. The anterior adductors are relatively small and situated closer to the midline. They are separated by a prominent, short, pointed septum.

The differences between *I. costata* and the closely related *I. egnabergensis* (Retzius, 1781) are described in Surlyk (1973). Simon (2007) discussed the difference between these two species and other representatives of *Isocrania* in detail in connection with his de-

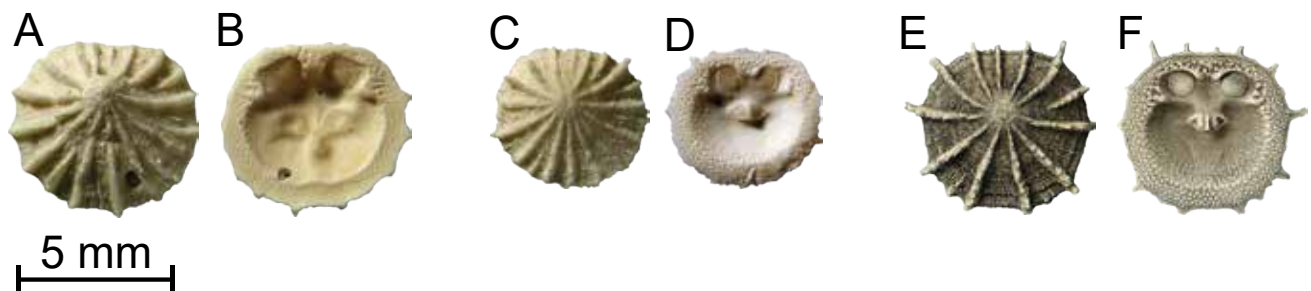


Fig. 15. *Isocrania costata* (J. Sowerby, 1823). External and internal views of ventral valves. Note the low number of laterally curving costellae which extend somewhat beyond the margin of the valve. The interstices have a sculpture of elongate knobs, each ending at a growth line. Note that the protegulum is situated more anteriorly than in *I. barbata*. Upper lower Maastrichtian, Møns Klint: A, B. Store Taler; C, D. Sommerspiret; E, F. Hvidskud (Figs 2, 4).

scription of the new species *Isocrania sendeni* Simon, 2007. This species differs from *I. costata* in a heavy, flat disc-shaped ventral valve, a backwards curved umbo and a high number of costellae. Surlyk (1973, p. 241) suggested that what was later erected as *I. sendeni* by Simon (2007) was a new species of *Isocrania*, representing a late Maastrichtian offshoot of *I. costata* rather than a direct descendant of *I. egnabergensis*, an interpretation that was “entirely corroborated by the present study” (Simon 2007, p. 151).

Material. Jylland. Danmark: 20; Ferslev: 11; Gudumholm: 17; Hillerslev: 6; Lindholm: 21; Linds: 3; Mjels: 7; Nørre Flødal: 4; Rørdal: 68.

Møn. Hundefangs Klint: 22; Hvide Klint: 3; Hvidskud: 97; Jættebrinken: 2; Lille Taler: 1; Maglevandspynt: 5; Nylands Nakke: 2; Sommerspiret: 4; Store Taler: 1; Sætpeleklinten: 1.

Sjælland. Kongsted: 1.

Outside Denmark *I. costata* is known from eastern Poland (Bitner & Pisera 1979; Machalski & Bitner 2024), Rügen (e.g. Nestler 1965, 1975), Hemmoor and Krons-moor (Surlyk 1982, 1984; Ernst 1984) in northern Germany, the Netherlands (Simon 2007) and Norfolk in England (Johansen & Surlyk 1990).

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones possibly except the *stevensi*–*chitoniformis* Zone. The uppermost Maastrichtian forms with a relatively large number of costellae are thus referred to *Isocrania sendeni* Simon, 2007.

Pertinent references. Surlyk (1973), Ernst (1984), Johansen & Surlyk (1990), Simon (2007), Lauridsen & Surlyk (2008), Hansen & Surlyk (2014).

Isocrania sendeni Simon, 2007

Fig. 16

Surlyk (1973) recognized a systematic change in some morphological characters of *Isocrania costata* through the transition from the lower to the upper Maastrichtian, especially in material from the upper upper Maastrichtian at Stevns Klint. Surlyk (1973, p. 241) thus wrote: “Forms very close to *I. egnabergensis* and from the same type of facies occur in the Maastrichtian of Holland” ... “Tentatively I would suggest that this form is an Upper Maastrichtian off-shoot of the *I. costata* line rather than a direct descendent of *I. egnabergensis*, corresponding to the stratigraphical increase in number of ribs by *I. costata* (fig. 7)”. Somewhat unusual, this form was erected as a new species *Isocrania sendeni* n. sp. by Simon (2007) who wrote (p. 151): “The suggestion formulated by Surlyk (1973, p. 241)....is thus corroborated entirely by the present study”. This is not so strange as stated by Surlyk (1973, p. 237): “In the uppermost Maas-

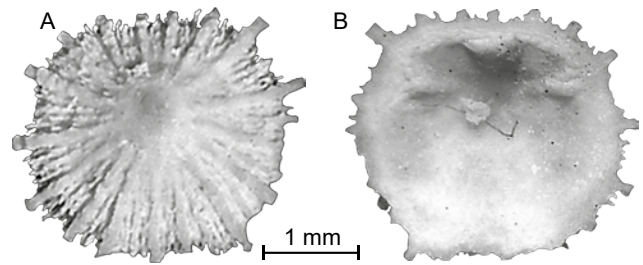


Fig. 16. *Isocrania sendeni* Simon, 2007. A. Dorsal valve, external view. Note large number of costellae and small size. B. Internal view of same specimen. Upper upper Maastrichtian, *stevensi*–*chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Fig. 2, 6).

trichtian (Zone 10) the species has changed so much that a new species of *Isocrania* has formed by phyletic speciation”“which will be described elsewhere”.

Isocrania sendeni is very well illustrated in several plates by Simon (2007). The preservation of the present material is not suited for illustrations of a similar quality and reference is thus made to these excellent figures. The shell is small-sized, the outline is subcircular and slightly wider than long with the greatest width at the midline of the shell. The ventral valve is flat with a very small attachment surface. The valve has up to 15 costae and new costellae are added by intercalation. The maximum number of costellae is about 35. The lateral costellae show a slight backwards curvature and they extend somewhat beyond the margin of the valve. The wide interspaces between the costellae are covered with small spines. The posterior adductor muscle scars are wide and subcircular, whereas the anterior muscle scars are very small and elongated. The dorsal valve is subconical and the umbo is situated in the posterior part and is somewhat curved in a posterior direction. The costellae are similar to those of the ventral valve. The posterior adductor muscle scars are situated close to the posterior valve margin.

Isocrania sendeni can be distinguished from *I. costata* by the relatively small size, the flat ventral valve, the backwards curved umbo of the dorsal valve and the large number of costellae in adult specimens. *I. egnabergensis* has a subrectangular outline, is longer than wide, the costellae are very fine and their number is much higher.

Material. Jylland. Dania: 6; Kjølbygård: 3. Sjælland. Stevns Klint: 17.

Chronostratigraphy in Denmark. Upper upper Maastrichtian, *stevensi*–*chitoniformis* Zone (Surlyk 1984; Surlyk *et al.* 2013).

Pertinent references. Surlyk (1973), Ernst (1984), Simon (2007).

***Isocrania barbata* (von Hagenow, 1842)**

Fig. 17

Isocrania barbata is rare in the Danish chalk and has not been found in the washing residues. The description is based on specimens housed at Geomuseum Faxe. The outline of *I. barbata* is subquadrangular to subcircular with a relatively straight posterior margin. The attachment surface on the ventral valve is small. The cicatrix of the valve is situated in the posterior half, which is high and triangular in lateral view. The costellae are well defined and thin in the early growth stages but becomes stronger during growth. The number reaches about 70, greater than in any other species of *Isocrania* found in the Maastrichtian chalk. They are straight or gently backwards curved. The adductor muscle scars are well developed.

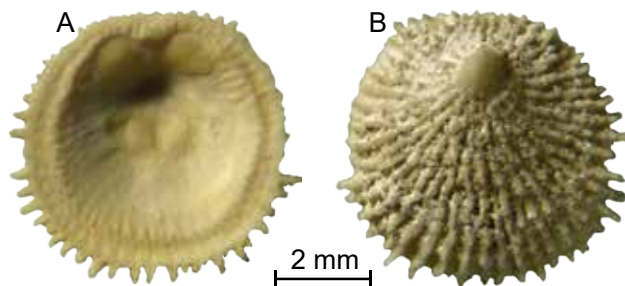


Fig. 17. *Isocrania barbata* (von Hagenow, 1842). Dorsal valve. A. Internal view. B. External view. Note the large number of laterally curved costellae, which extend beyond the valve margin and possess a characteristic saw-like knobby ornamentation. Lower Maastrichtian. Møns Klint (Fig. 2).

Material. Only a few specimens have been available for study. They are housed at the Natural History Museum of Denmark and Geomuseum Faxe. Møns Klint: a single specimen is illustrated in Gravesen & Jakobsen (2013, p. 93, no. 4).

Chronostratigraphy in Denmark. Lower Maastrichtian. The rarity of the species precludes more detailed information on the stratigraphic distribution. Outside Denmark the species is known from Rügen, Lägerdorf-Kronsmoor and Höver in northern Germany (Ernst 1984) and south-eastern England (Lauridsen

et al. 2009)

Pertinent references. Posselt (1894), Ernst (1984), Gravesen & Jakobsen (2013).

Order Rhynchonellida Kuhn, 1949

Superfamily Hemithiridoidea Rzhonsnitskaia, 1956

Family Tetrarhynchiidae Ager, 1965

Subfamily Cretirhynchiinae Katz, 1974

Genus *Cretirhynchia* Pettitt, 1950

Type species *Cretirhynchia plicatilis* (J. Sowerby, 1816)

***Cretirhynchia* sp.**

Figs 18, 19

The material comprises a large number of juvenile forms, which can be referred to the genus *Cretirhynchia* because of the presence of all growth stages, and they commonly occur together with adult specimens of *C. retracta* (Roemer, 1841). However, it cannot be excluded that a few of the juvenile forms belong to *Homaletarhynchia limbata* (von Schlotheim, 1813), previously referred to *Cretirhynchia* (Simon & Owen 2001; Motchurova-Dekova & Simon 2007). Accordingly, the juvenile forms are here described under the name *Cretirhynchia* sp. and only adult specimens are described under *C. retracta* and *Homaletarhynchia limbata*, respectively.

The outline of specimens at $W < 2.0$ mm is pointed oval. At $W < 1.5$ mm the anterior commissure is rounded in dorsal view but rapidly turns into straight and slightly incurved during further growth. L/W decreases rapidly from 1.4 to 1.6 at $W = 0.6$ mm to 1.2–1.3 at $W = 1.5$ mm. The greatest width is at the shell midline for specimens < 1.5 mm, but becomes closer to the anterior margin at $W = 1.5$ – 2.0 mm. The shell is flattened biconvex at $W < 2$ mm but the ventral valve is more inflated than the dorsal valve. The shell is very thin in small specimens. The lateral margins pass evenly into the posterior shell margin. The shell has no ears. The beak is suberect in small forms. The foramen is large and triangular at $W < 1$ mm

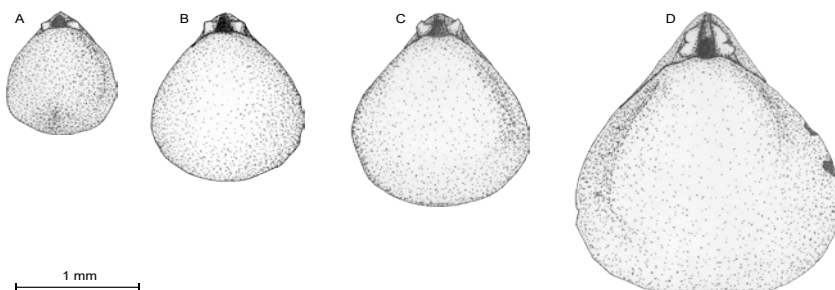


Fig. 18. *Cretirhynchia* sp. Juvenile specimens, probably all belonging to *C. retracta*. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

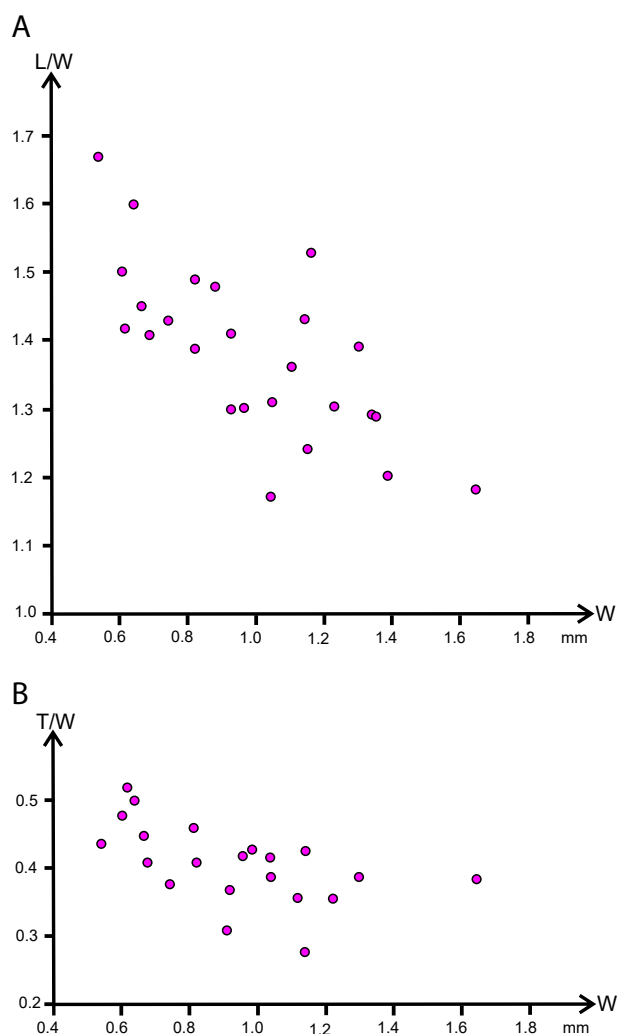


Fig. 19. *Cretirhynchia* sp. Scatter diagrams.

and is limited by two long, narrow deltidial plates that grow slightly upwards and then outwards. At $W=1.0\text{--}1.2$ mm the plates meet posteriorly to form a long and tubular pedicle collar. The hinge in young specimens consists dorsally of relatively strong low inner socket ridges and ventrally of teeth and strong tooth plates. There is no cardinal process. The inner socket ridges pass anteriorly directly into the crura, which are present in even the smallest specimens ($W=0.5$ mm). They diverge slightly and are strong, straight, long and gently ventrally directed.

Distinctions between small, rounded smooth specimens in the material belonging to *Carneithyris subcardinalis* (Sahni, 1925), *Magas chitoniformis* (von Schlotheim, 1813), *Scumulus inopinatus* Steinich, 1968, *Leptothyrelloopsis polonicus* Bitner & Pisera, 1979 and *Dalligas nobilis* Steinich, 1968 is far from straightforward. The morphology of the deltidial plates is the most characteristic feature distinguishing *Cretirhynchia* sp. from the other small, smooth species.

Material. Falster. Gedser Fyr: 1.

Jylland. Danmark: 28; Ferslev: 11; Gudumholm: 30; Kjølbygård: 1; Lindholm: 10; Linds: 24; Mjels: 3; Nye Kløv: 40 (Johansen 1987); Nørre Flødal: 13; Rørdal: 57; Smidie: 1; Spentrup: 3.

Møn. Forchhammers Pynt: 3; Hvide Klint: 17; Hvidskud: 556; Hundefangsklint: 131; Maglevandspynt: 5; Nylands Nakke: 2; Store Taler: 18; Sættelekklint: 4. Sjælland. Karlstrup: 16; Stevns Klint: 20.

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones.

Pertinent reference. Steinich (1965).

Cretirhynchia retracts (Roemer, 1841) Fig. 20

The small specimens are described under *Cretirhynchia* sp. which may also cover small forms of other rhynchonellids but mainly includes *C. retracts*, as this is by far the most common among the larger species. Large specimens are housed in the collections of Geomuseum Faxe, the National History Museum of Denmark and own collections housed at the University of Copenhagen. According to the comprehensive revision of the genus *Cretirhynchia* initiated by Simon & Owen (2001) the present species is one of the few still included in *Cretirhynchia*.

C. retracts is wider than long in outline, commonly subpentagonal and rarely subtriangular. The anterior commissure is denticulate and uniplicate. The shell is biconvex, and the greatest thickness is situated posterior to the shell midline. The ventral valve is less inflated than the dorsal valve. A wide, rather

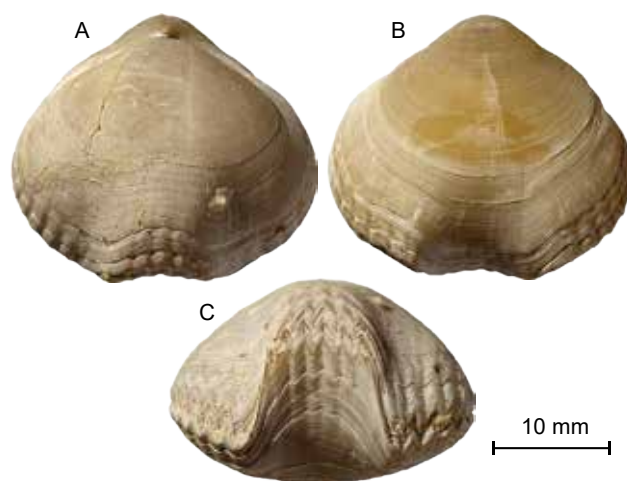


Fig. 20. *Cretirhynchia retracts* (Roemer, 1841). A, B, C. Dorsal, ventral and anterior views, respectively of the same specimen. Note the closed foramen (A), indicating a free-living mode-of-life (Surlyk 1972). Upper upper Maastrichtian, *stevensis*-*chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6).

deep sinus occurs in the ventral valve. Flat and wide costellae separated by 60–70 sharp, narrow furrows are formed at $W=4$ mm. They do not branch and no new costellae are formed by intercalation. A reduction in number to about 20–30 may occur at growth lines.

The beak is short and pointed and erect to slightly incurved. The foramen is small and hypothyril (Figs 8, 9). The deltidial plates are initially long and narrow but they fold in the middle and develop an ear-like extension already at $W=1$ mm (see Steinich 1965, fig. 5). During growth they form a long pedicle collar. The pedicle opening is in adult forms closed by a plug from the inside (Steinich 1965, Pl. 3, fig. 1a, b). The hinge is strongly developed and comprises parallel to slightly diverging inner socket ridges. The sockets are deep and crenulated. The hinge teeth are stump, triangular and strongly crenulated. The crura are raduliform and become broader and ventrally bent during growth.

Material. Almost all of the juvenile specimens described above under *Cretirhynchia* sp. are assumed to belong to *C. retracta*. Most of the larger specimens are from Møns Klint and Stevns Klint (Hansen & Surlyk 2014), in most cases without further indications of sample location.

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones. Outside Denmark, *C. retracta* has been safely recorded from Poland and Rügen in northern Germany (Steinich 1965). It is clearly more widespread, but the great variability of species referred to *Cretirhynchia* in the literature does not easily allow further information on the geographic distribution of *C. retracta*.

Pertinent references. Steinich (1965), Surlyk (1972, 1984), Simon & Owen (2001), Gravesen & Jakobsen (2013), Hansen & Surlyk (2014).

Cretirhynchia plicatilis (J. Sowerby, 1816)

Fig. 21

C. plicatilis has not been safely identified in the washing residues and the description is based on a few specimens housed at Geomuseum Faxe and the Nat-

ural History Museum of Denmark. The species is medium-sized, up to about 13 mm long. The outline is subpentagonal to transversely oval. The shell is thin, and the maximum width lies roughly at the midline. The length and width are of approximately the same size, but the ratio varies so that some specimens are markedly wider than long. The shape is bilobate. The shell is dorso-biconvex and has an ornamentation of up to 35 rounded costellae, which may extend from the umbo to the anterior margin. The presence of the costellae results in a denticular commissure. The dorsal fold is high and wide and the ventral sulcus is low and trapezoidal with 7–8 rounded costellae. The growth lines are indistinct. The beak is small and erect. The hinge teeth are subquadrangular and supported by subparallel to slightly converging hinge plates. The sockets are deep and the hinge plates are triangular and short. A median septum is present.

C. plicatilis differs from *Cretirhynchia retracta* and *Homaletarhynchia limbata* in having costellae, which may extend along the whole length of the shell from the umbo to the anterior margin. In addition, it has a more clearly subpentagonal outline.

Material. A few specimens housed at Geomuseum Faxe and at the Natural History Museum of Denmark.

Chronostratigraphy in Denmark. The rarity of this species in the Danish chalk precludes any detailed information on the stratigraphic distribution. It is known from the upper upper Maastrichtian, *stevensis-chitoniformis* Zone at Stevns Klint (Gravesen & Jakobsen 2013, p. 91, no. 6).

Pertinent references. Pettitt (1950), Simon & Owen (2001), Motchurova-Dekova *et al.* (2008), Gravesen & Jakobsen (2013).

Superfamily Pugnacoidea Rzhonsnitskaia, 1956

Family Basiliolidae Cooper, 1959

Subfamily Aphelesiinae Cooper, 1959

Genus *Homaletarhynchia* Simon & Owen, 2001

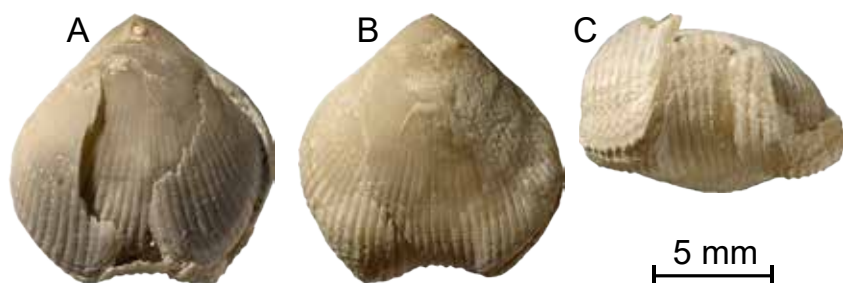


Fig. 21. *Cretirhynchia plicatilis* (J. de C. Sowerby, 1818). Dorsal, ventral, and anterior views, respectively of the same specimen. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6).

Type species *Homaletarhynchia limbata* (von Schlotheim, 1813).

***Homaletarhynchia limbata* (von Schlotheim, 1813)**

Figs 22, 23

The genus *Cretirhynchia* was considered prone to major revision by Simon & Owen (2001). Motchurova-Dekova & Simon (2007) transferred *C. limbata* to the genus *Homaletarhynchia* Simon & Owen, 2001 based on serial sections, study of the umbonal part and shell ultrastructure. This new genus was at the same time placed in the family Basiliolidae, superfamily Pugnacoidea.

H. limbata has not been safely identified in the washing residues forming the basis for the present study and small specimens may be covered under *Cretirhynchia* sp. Description of larger specimens is based on material housed at the Natural History Museum of Denmark, Geomuseum Faxe and own collection housed at the University of Copenhagen. The number of specimens is small and does not allow a detailed description of the inner morphology.

The species is medium-sized. *H. limbata* is in most cases wider than long, ovate to subtriangular and the anterior margin is denticulate and uniplicate. The shell is biconvex with a strongly convex dorsal valve and a rather flat ventral valve. The greatest thickness is at the anterior margin of the shell. A marked ventral sinus is formed close to the shell midline. The surface of the shell is smooth but may have a sculpture of faint and narrow radial grooves. According to Motchurova-Dekova & Simon (2007) a few costae are developed at the anterior margin, whereas Steinich (1965) indicates that 12–16 strong costae occur, being restricted to the shell margin, where they form a zig-zag tooth-like pattern. The material at my disposal fits better with Steinich's (1965) description, but the degree of external ornamentation is quite variable. The beak is short and pointed and becomes gradually more incurved during growth. The minute foramen is hypothryid (Fig. 8) and surrounded by a collar-like deltidium but is apparently not closed like in *Cretirhynchia retracta*. Large specimens have strong inner socket ridges and the crura are subfalciform. The hinge plates are strongly reduced. An euseptoidum is well developed (Motchurova-Dekova & Simon 2007).

Material. Stevns Klint (Hansen & Surlyk 2014), Møns Klint.

Outside Denmark *H. limbata* has been recorded from Rügen in northern Germany (Steinich 1965), Belgium (Motchurova-Dekova & Simon 2007), who also indicate a wide distribution in northern, central and eastern Europe without providing any details, and Norfolk in eastern England (Johansen & Surlyk 1990).



Fig. 22. *Homaletarhynchia limbata* (von Schlotheim, 1813), **A.** Dorsal view. Note very small foramen which may have been closed in larger specimens, indicating a free-living mode-of-life (Surlyk 1972). **B.** Same specimen in ventral views. **C.** Dorsal view of another specimen. Lower Maastrichtian. Møns Klint (Fig. 2).

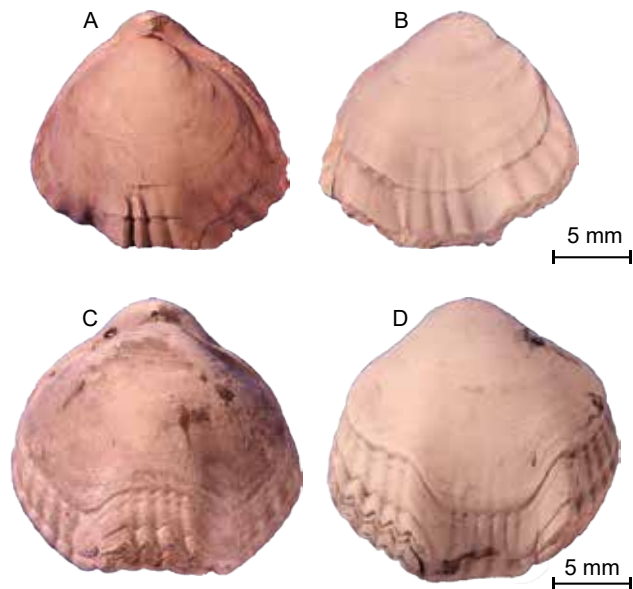


Fig. 23. *Homaletarhynchia limbata* (von Schlotheim, 1813), **A, B:** Dorsal and ventral views, respectively. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6). **C, D:** Dorsal and ventral views, respectively. Sigerslev quarry. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6), OESM 4611. F-G: OESM 4616.

Chronostratigraphy in Denmark. Maastrichtian.

Pertinent references. Steinich (1965), Motchurova-Dekova & Simon (2007), Johansen & Surlyk (1990).

Order Thecideida Elliott, 1958

Superfamily Thecideoidea Gray, 1840

Family Thecideidae Gray, 1840

Subfamily Thecideinae Gray, 1840

Genus Thecidea Defrance, 1822

Type species *Thecidea papillata* (von Schlotheim, 1813)

Thecidea papillata (von Schlotheim, 1813)

Fig. 24

T. papillata has not been found in the washing residues and the description is based mainly on specimens housed at Geomuseum Faxe. The species is medium-sized. The outline is elongate oval-ellipsoidal, and the length is greater than the width. Both valves are rather flat, and the dorsal valve is almost quadrangular in small forms, while the associated ventral valve is pointed posteriorly. The beak becomes gradually more incurved during growth and the ventral valve becomes deeper to allow space for the brachidium. The dorsal valve becomes somewhat heart-shaped in some specimens, while it is almost perfectly circular in others. The margin of the dorsal

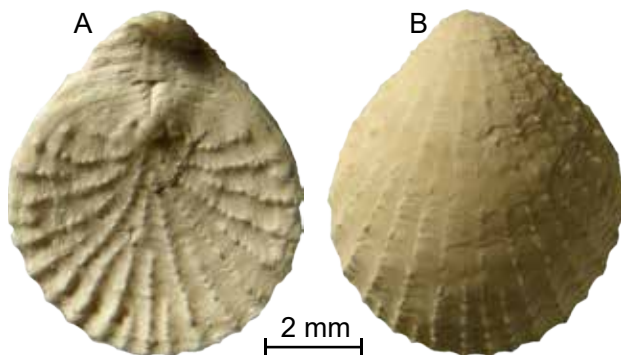


Fig. 24. *Thecidea papillata* (von Schlotheim, 1813). A. Dorsal view. B. Ventral view of same specimen. Note the circular outline of the dorsal valve and the laterally curved costellae. New ones added by intercalation. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

shell is inclined towards the ventral valve and has a granulate sculpture. The outer surface of the valves has radial, laterally curved costellae, which extend outwards from the slightly elevated protegulum. They have fine knobs where new costellae are initi-

ated. The number of costellae increases by intercalation gradually from 16 to 20 in the early stages. The pseudodeltidium is pointed triangular and there is a low median septum. A detailed description of the inner morphology is given by Backhaus (1959).

Material. *T. papillata* is rare in the Danish chalk. Hand-picked specimens are known mainly from Kulsti Rende and Eskesti at Stevns Klint (Fig. 5; Hansen & Surlyk 2014; S.L. Jakobsen, pers. comm. 2024).

Chronostratigraphy in Denmark. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Outside Denmark *T. papillata* is known from Hemmoor (own data: Hemmoor sample 140 u, ca. 63 m above the 'Tonband', which roughly indicates the position of the lower-upper Maastrichtian boundary), Ilten, both in northern Germany (Backhaus 1959), the Netherlands where it occurs in great numbers in the shallower marine carbonate facies and in France (Backhaus 1959; Simon 1998).

Pertinent references. Backhaus (1959), Simon (1998), Hansen & Surlyk (2014).

Thecidea recurvirostra (Defrance, 1828)

Figs 25, 26

This species is rare in the Danish Maastrichtian except for the locality Eskesti at Stevns Klint (4 in Fig. 2; Fig. 5), which has yielded a large number of specimens housed at Geomuseum Faxe. The description is supported by information in Schröder (2013) and a detailed description was given by Backhaus (1959). The species is small and elongate, up to 7.6 mm long. The ventral valve is convex, whereas the dorsal valve is slightly concave and subcircular in outline. The largest width lies in the anterior part of the shell, which is thick and smooth but with marked growth lines. The beak is strongly incurved, and there is no foramen. The interarea has marked growth lines

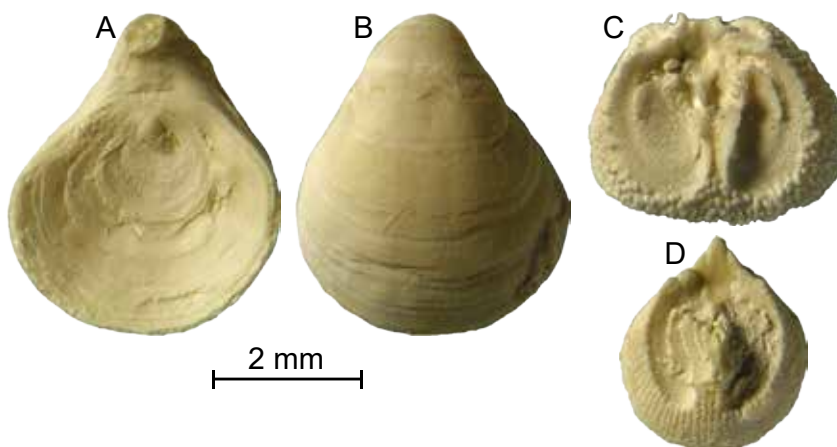


Fig. 25. *Thecidea recurvirostra* Defrance, 1828. A. Dorsal view. Note the incurved beak, smooth shell surface and the circular outline of the dorsal valve. B. Same specimen in ventral view. C, D. Inner side of ventral valves. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Holtug quarry, Stevns Klint (Figs 2, 6).

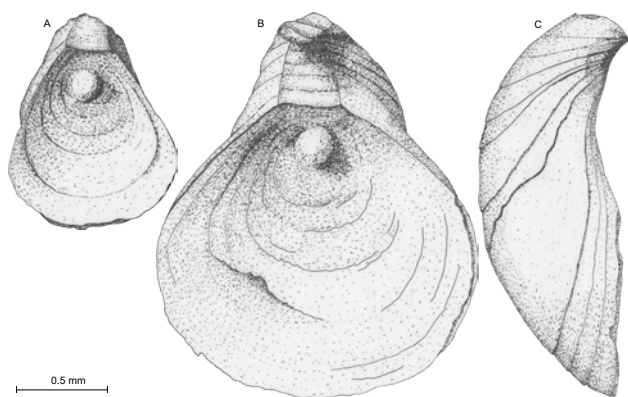


Fig. 26. *Thecidea recurvirostra* Defrance, 1828. Two growth stages. **A.** Dorsal view. **B, C.** Dorsal and lateral views. Uppermost Maastrichtian, *stevensi*–*chitoniformis* Zone. Højerup, Stevns Klint (Figs 2, 6).

and a narrow convex pseudodeltidium with a longitudinal ridge. The cicatrix on the rostral extremity varies in shape and is not always present. *T. recurvirostra* lived attached to a hard substrate during early growth stages but subsequently became free-living. The species resembles *Vermiculothecidea vermicularis* (von Schlotheim, 1813) but differs in its smooth surface of the shell and the morphology of the interarea and pseudodeltidium. It can be distinguished from *Thecidea papillata* in the lack of costellae and the elongate outline.

Material. Jylland. Eerslev: 1. Sjælland. Stevns Klint: Holtug: 28; Eskesti: 121; Sigerslev quarry: 3. All housed at Geomuseum Faxe.

Chronostratigraphy in Denmark. Upper upper Maastrichtian, *stevensi*–*chitoniformis* Zone.

Pertinent references. Backhaus (1959), Simon (1998).

Genus *Praelacazella* Smirnova, 1969

Type species *Praelacazella valangiense* de Loriol, 1868

***Praelacazella wetherelli* (Morris, 1851)**

The material only includes a few fragments which are not of a quality allowing good photographs and the reader is referred to Backhaus (1959) and Schröder *et al.* (2024) for additional details. *P. wetherelli* is cemented to the substrate with the entire surface of the ventral valve. The outline is elongate to rounded subtriangular with a rounded anterior margin, which may have a slight median emargination on the rectimarginate commissure as seen in dorsal view. The largest width is between the midline and the anterior margin. The shell is thick, and the surface is smooth with steep margins. The anterior

commissure is rectimarginate. The interarea is weak and has a convex pseudodeltidium. The hinge line is straight. The ventral valve has thick, robust teeth and a well-developed median septum supporting the hemispondylium, which has two plate-like prongs. The inside has a sculpture of radiating ridges. The interarea is weak and has a convex pseudodeltidium. The brachial lobes are reniform. The anterior margin has an ornamentation of minute pustules

Material. Møn. Hvidskud: 10; Sandpynten: 1?

Chronostratigraphy in Denmark. Upper lower Maastrichtian, *pulchellus*–*pulchellus* Zone. Outside Denmark the species is known from northern Germany (Backhaus 1959; Steinich 1965), Belgium (Simon 2000), Norfolk in eastern England (Johansen & Surlyk 1990), Spain (Muñoz 1990) and Western Australia (Schröder *et al.* 2024). The latter occurrence shows that the species reached a circumpolar distribution in the Maastrichtian.

Pertinent references. Backhaus (1959), Steinich (1965), Surlyk (1972), Johansen & Surlyk (1990), Schröder *et al.* (2024).

Genus *Vermiculothecidea* Elliott, 1953

Type species *Vermiculothecidea vermicularis* (von Schlotheim, 1813)

***Vermiculothecidea vermicularis* (von Schlotheim, 1813)**

Fig. 27

The material only includes fragments and the reader is referred to Backhaus (1959) for a detailed description. The description is supported by information in Schröder (2013) based on her own collections. *V. vermicularis* is up to about 7.5 mm long and has an irregular elongate outline and the greatest width lies in the anterior part of the shell. The length is greater than the width. The outline of the dorsal valve is sub-circular to oval. The shell is thick and planoconvex to concavoconvex. The ventral valve in large specimens has prominent, uneven concentric folds which probably represent growth lines. The anterior commissure is rectimarginate. The beak is more or less strongly incurved. There is no foramen. The interarea and the triangular pseudodeltidium are weakly differentiated. Some specimens possess a cicatrix on the rostral extremity. The outer part of the inner margin of the dorsal valve is finely granulate with granules arranged in lines. The species was attached to a hard substrate in the early growth stages but eventually developed a free-living mode-of-life. It is rather similar to *V. recurvirostra* in the outer morphology but deviates in the length of the pseudodeltidium and in

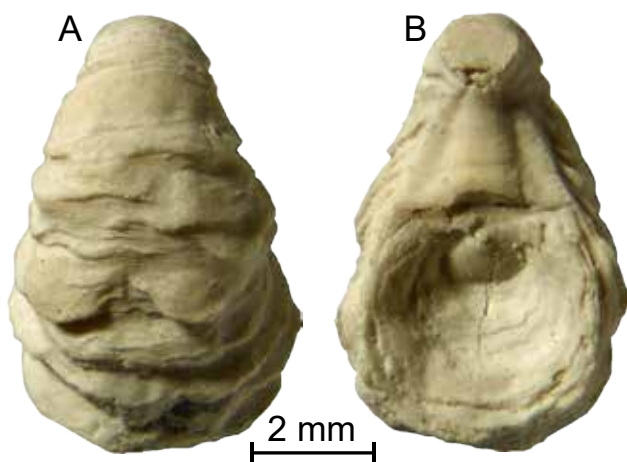


Fig. 27. *Vermiculothecidea vermicularis* (von Schlotheim, 1813). **A.** Ventral view, showing marked step-like growth lines. **B.** Dorsal view of same specimen. Note the strongly posteriorly extended rostrum making the ventral valve almost the double length of the dorsal valve. Both valves are very thick. Lower Maastrichtian. Møns Klint (Fig. 2).

the surface of the shell.

Material. Jylland. Gudumholm: 1; Lindholm: 1; Rørdal: 2.

Møn. Hvidskud: 23; Hundefangsklint: 3.

Sjælland. Stevns Klint (Hansen & Surlyk 2014).

Chronostratigraphy in Denmark. Upper lower Maastrichtian, *acutirostris*–*spinosa* to *pulchellus*–*pulchellus* Zone and upper Maastrichtian, *semiglobularis*–*humboldtii* and *stevensis*–*chitoniformis* Zones. Outside Denmark, it occurs in the Netherlands and Romania (Pajaud & Patruilius, 1964).

Pertinent references. Backhaus (1959), Pajaud & Patruilius (1964), Gravesen & Jakobsen (2013), Hansen & Surlyk (2014).

Superfamily Terebratulioidea Gray, 1840

Family Sellithyrididae Muir-Wood, 1965

Subfamily Rectithyridinae Muir-Wood, 1965

Genus *Neolothyrina* Sahni, 1925

Type species *Neolothyrina obesa* Davidson, 1852

***Neolothyrina obesa* Sahni, 1925**

Fig. 28

In the washed samples, *N. obesa* has only been recognized at Hvidskud at Møns Klint and at Stevns Klint but is elsewhere known from relatively rare outcrop finds and from museum collections. It is possible, however, that smooth rather featureless juvenile specimens have been lumped with minute smooth juveniles of other species. It has a very thin shell and is usually severely deformed or broken by compaction of the chalk. The description is supported by information in Steinich (1965).

N. obesa is the largest brachiopod found in the Danish Maastrichtian and the largest specimen I have seen is 78 mm long (private collection of Torbjørn H. Madsen). Juveniles of *N. obesa* have an elongate outline and poorly defined ears. The relative width increases markedly from $W=2.5$ mm and becomes subpentagonal in large specimens to reach values around 1.4 in L/W . The inflation of the biconvex shell increases during growth, although the dorsal valve is less inflated than the ventral valve. The anterior commissure is rectimarginate in small forms but becomes sulcinate during growth. Fine radial capillae occur on the otherwise smooth shell already in small specimens but are restricted to the lateral margins throughout the growth of the shell. They are, however, not always present and the shell is commonly completely smooth. The beak is almost erect and

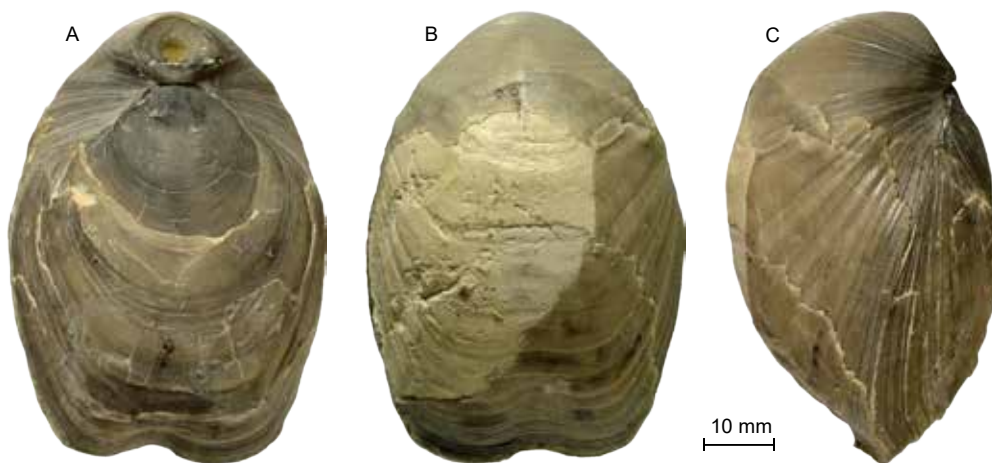


Fig. 28. *Neolothyrina obesa* Sahni, 1925. **A.** Dorsal view of an unusually well-preserved specimen of this thin-shelled species. *N. obesa* is the largest brachiopod species found in the Danish chalk. Note medial anterior sinus. **B** and **C.** Same specimen in ventral and lateral views, respectively. Lower Maastrichtian. Møns Klint (Fig. 2).

stump from $W=4$ mm. The foramen is submesothyrid to mesothyrid and becomes permesothyrid in large specimens (Fig. 8). The deltidial plates are discrete and pass posteriorly into the strong pedicle collar. They fuse to form a symphytium during growth. In large specimens, the symphytium is very short and difficult to recognize. The beak becomes gradually somewhat incurved. The hinge teeth are narrow and pointed. Crura and descending branches are straight from the outset and form a transverse bridge already in small specimens.

Material. A few specimens have been examined from own collection housed at the University of Copenhagen, private collections and specimens housed at Geomuseum Faxe and the Natural History Museum of Denmark.

Møn. Hundefangs Klint: 2; Hvidskud: 2; Store Taler: 1; Maglevandspynt: 1 (the two latter: S.L. Jakobsen, pers. comm. 2024).

Sjælland. Stevns Klint: 1; 5 are housed at Geomuseum Faxe (3 from Sigerslev chalk quarry, 1 south of Kulsti Rende, 2 just labelled Stevns Klint). Recently, two perfectly preserved specimens were found at Sigerslev chalk quarry by Peter Bennicke. They were collected from the hardened chalk, immediately below the K–Pg boundary and are the youngest known specimens of this species. The excellent preservation is undoubtedly due to the fact that the chalk was hardened before an overburden corresponding to the lower Danian bryozoan limestone was deposited, thus protecting the shells from compaction fracturing.

Chronostratigraphy in Denmark. Upper lower Maastrichtian, probably *pulchellus*–*tenuicostata* and *tenuicostata*–*semiglobularis* Zones and upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone. Outside Denmark it is reported from Rügen in northern Germany (Steinich 1965).

Pertinent references. Steinich (1965), Hansen & Surlyk (2014), Schröder & Surlyk (2020).

Neoliothyryna fittoni (von Hagenow, 1842)

Fig. 29

This species is in many respects similar to *Neoliothyryna obesa* but reaches some characters at a markedly smaller size. There are also important internal differences aiding proper determination.

The shell is small to medium in size. The outline of juvenile specimens is elongate oval, but has changed to circular already at $W=5$ mm. Subsequently the shape again changes to a longer L/W ratio and adult forms have a subpentagonal outline. The largest width is at the shell midline. The shell is biconvex with a somewhat flatter dorsal valve, which at $W=8$ mm becomes flat in the anterior part, where it later develops a gentle sinus. The anterior commissure accordingly changes from rectimarginate to a gentle ventral unisulcate depression. The surface of the shell is smooth, but shows numerous growth lines, which become very strong anteriorly, forming a step-like morphology. The beak is short and erect to slightly incurved. The foramen is permesothyrid. The hinge is relatively strongly developed and the brachidium is usually crushed, reflecting the very thin, fragile shell, but according to Steinich (1965), it is probably similar to that of *N. obesa*. The shell of *N. fittoni* lacks the fine lateral ribs or striations characterizing some specimens of *N. obesa* and the outline of adult specimens is also clearly subpentagonal. Excellent drawings of outer and inner morphology are given in Asgaard (1972).

Material. Jylland. Nørre Flødal: 1; Bjerre: 1; Udbyovre: 1; Vive: 1 (All from Asgaard 1972).

Møn. Hundefangs Klint: 2; Hvidskud: 1 (both localities from Asgaard 1972); Store Stejlebjerg: 1.

Sjælland. Stevns Klint: 20 (Asgaard 1972), 5 (Geomuseum Faxe. Sigerslev Kridtbrud: 2, Holtug Kridtbrud: 2; Mandehoved: 1).

Chronostratigraphy in Denmark. Lower Maastrichtian, *subtilis*–*pulchellus* Zone and upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone. Outside Denmark

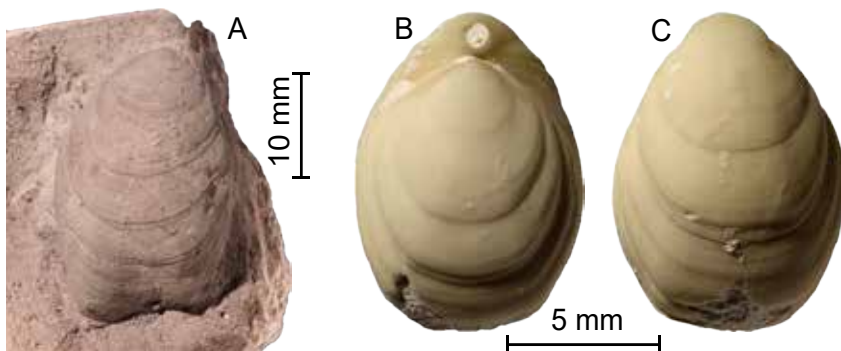


Fig. 29. *Neoliothyryna fittoni* (von Hagenow, 1842). A. Ventral view. B and C. Another specimen in dorsal and ventral views, respectively. Note the marked growth lines. Lower upper Maastrichtian. Store Stejlebjerg, Møns Klint (Fig. 2).

N. fittoni is reported from the Netherlands, Belgium and Norfolk in eastern England (see Asgaard 1972).

Pertinent references. Steinich (1965), Asgaard (1972).

Family Gibbithyrididae Muir-Wood, 1965

Subfamily Carneithyridinae Muir-Wood, 1965

Genus *Carneithyris* (Sahni, 1925)

Type species *Carneithyris subcardinalis* (Sahni, 1925)

Carneithyris subcardinalis (Sahni, 1925)

Figs 30, 31, 32

The material from the washed bulk samples comprises mainly juvenile specimens, $W < 2$ mm. Description of larger specimens is based on own collection housed at the University of Copenhagen, material housed at Geomuseum Faxe and the Natural History Museum of Denmark supplemented with data from Steinich (1965).

The adult shell is large-sized. The outline of the juvenile specimens is strongly elongate and pointed oval. The shell is very thin and small specimens are commonly deformed by sediment compaction. The largest width is situated anterior to the shell midline in juvenile forms and the hinge line forms a sharp angle with the lateral shell margins. In specimens < 1.7 mm the L/W varies between 1.26 and 1.6. The shell is biconvex and the largest thickness in large specimens lies posterior to the midline. The dorsal valve has poorly delimited shell ears. The anterior commissure is rectimarginate and the surface of the shell is smooth. The beak is pointed, suberect with a small, sharply delimited area. The posterior part of the beak in specimens at $W = 0.6\text{--}0.8$ mm is curved into a small, pointed hook. The foramen is hypothyrid, triangular, laterally limited by two triangular deltidial plates,

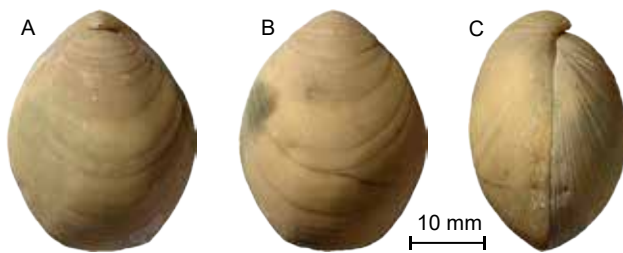


Fig. 30. *Carneithyris subcardinalis* (Sahni, 1925), an unusually well-preserved specimen of this thin-shelled species. Note the very small, essentially closed foramen, indicating a free-living mode-of-life of the older stages of this species (Surlyk 1972). **A, B, C.** Dorsal, ventral and lateral views of same specimen, showing the perfect biconvex shape. Uppermost Maastrichtian, *stevensis*–*chitoniformis* Zone. Holtug quarry, Stevns Klint (Figs 2, 6).

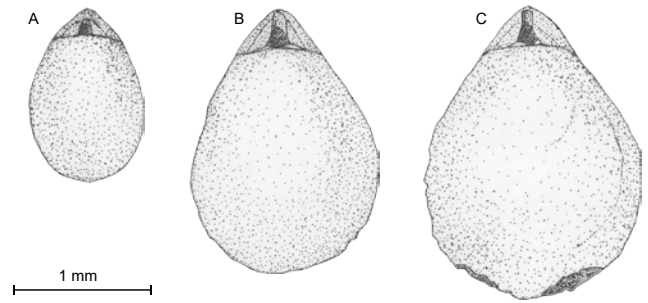


Fig. 31. *Carneithyris subcardinalis* (Sahni, 1925). **A, B, C.** Juvenile growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

which are separate in the earliest growth stages, but are fused already at $W = 10$ mm (Steinich 1965). The diameter of the foramen is very small in large specimens and the otherwise thin shell becomes markedly thickened in the umbonal region. The area and deltidial plates are both smooth and pass evenly into each other only separated by a weak furrow. The hinge is poorly developed. The dental sockets are flat and a cardinal process is missing. The teeth are small and do not have dental plates. The brachidium consists of short, anteriorly directed crura. The descending branches are developed on the dorsal side of the

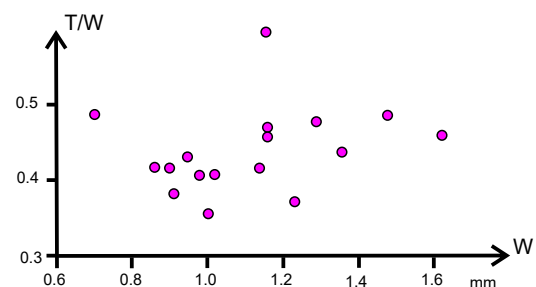
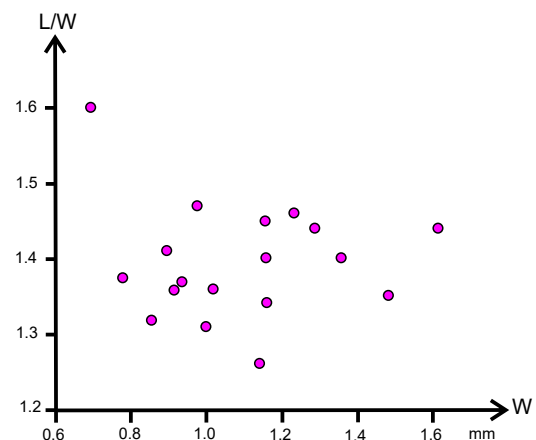


Fig. 32. *Carneithyris subcardinalis* (Sahni, 1925), scatter diagrams of juvenile specimens. L=length, W= width, T=thickness.

crura and are fused to form a bridge at $W=1.5$ mm. *C. subcardinalis* does not possess a coherent spicular skeleton, but isolated spicules are present already at $W=1$ mm (Steinich 1963). The juvenile specimens are characterized by the large, smooth and triangular field formed by the area and deltidial plates, which delimits the foramen laterally.

Material. Jylland. Danmark: 2; Ferslev: 4; Gudumholm: 22; Kjølbygård: 7; Lindholm: 3; Linds: 3; Nye Kløv: 19 (Johansen 1987); Nørre Flødal: 21; Rørdal: 2. Møn. Hvide Klint: 5; Hvidskud: 249; Hundefangs Klint: 31; Sættepileklint: 2; Maglevandspynt: 4. Nylands Nakke: 3; Store Taler: 4. Sjælland. Karlstrup: 29; Stevns Klint: 38.

Chronostratigraphy in Denmark. Maastrichtian. *C. subcardinalis* is recorded in all brachiopod zones except the *tenuicostata*–*semiglobularis* Zone. Outside Denmark it is reported from Poland (Bitner & Pisera 1979; Machalski & Bitner 2024), Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982, 1984) and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1972), Asgaard (1975).

Superfamily Cancellothyridoidea Thomson, 1926

Family Cancellothyrididae Thomson, 1926

Subfamily Cancellothyridinae Thomson, 1926

Genus *Terebratulina* d'Orbigny, 1847

Type species *Terebratulina retusa* Linnaeus, 1758

Terebratulina chrysalis (von Schlotheim, 1813)

Figs 33, 34, 35

T. chrysalis commonly occurs in great numbers in all investigated sections of the Maastrichtian chalk in Denmark. It also occurs in the lower Danian bryozoan mounds at Stevns Klint. In the middle Danian coral-bryozoan mound complex at Faxe and has recently been described from the lower Selandian Kerteminde Marl Formation (Schröder & Surlyk 2024). It is one of the few Cretaceous brachiopods that survived the mass extinction at the Cretaceous–Palaeogene boundary (Surlyk & Johansen 1984; Johansen 1987; Schröder & Surlyk 2024).

T. chrysalis is small to medium-sized, and the outline is elongate-subpentagonal. Young specimens are relatively thick-shelled, whereas adults are thin-shelled. The greatest width is anterior to the midline in juvenile specimens and at the shell midline in large

forms. The anterior shell margin is rectimarginate and truncated or even slightly uniplicate in very large specimens. The shell ears are large and well defined in small specimens. In larger forms they become relatively small and less well defined. The shell is biconvex and thickest posterior to the midline. The surface is finely costellate and six to eight costae with small tubercles are formed at $W=0.4$ mm. New costellae are added by intercalations, reaching a number of about 100. In juvenile stages below $W=3$ mm, the costellae are rather wide and possess transverse tubercles of a half-ring shape. At $W=3$ mm the morphology of the costellae changes markedly to very narrow, delicate and only weakly tuberculate. This change normally takes place at a growth line with the formation of a large number of densely spaced costellae.

The beak is short and suberect with well-developed keels. The area is small and sharply delimited. The foramen is hypothyriform below $W=1$ mm, and changes to submesothyriform and further to mesothyriform in large forms. It is delimited laterally by two triangular deltidial plates, which converge anteriorly during growth, whereby the outline of the foramen changes from subtriangular to circular.

The hinge is not strongly developed. The inner socket ridges are rather shallow, and the teeth are small and triangular. A cardinal process is only present in large specimens where it is low, concave and ellipsoidal in outline. The first brachial stages are formed at $W=0.7$ mm. They consist of short lamellae, which sit directly on the inner valve without crura. At $W=1$ mm they have become slightly concave medially and the initial stages of crura, crural processes and descending branches are formed. The latter fuse at $W=2$ mm and the crural processes fuse shortly later with the development of a brachial loop which develops into a tube shape during growth as the

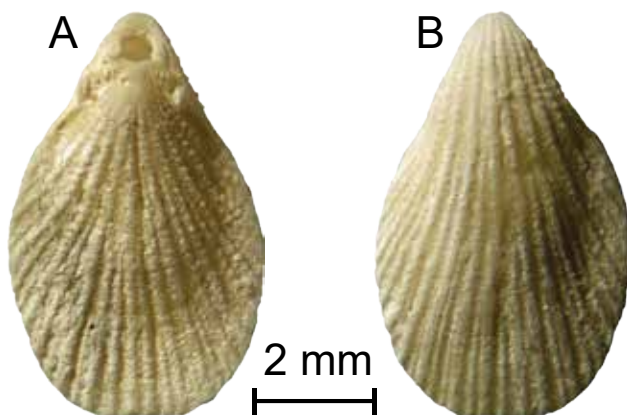


Fig. 33. *Terebratulina chrysalis* (von Schlotheim, 1813). **A.** Dorsal view. **B.** Same specimen in ventral view. Note the numerous fine costellae where new ones are formed by intercalation. Uppermost Maastrichtian, *stevensi*–*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

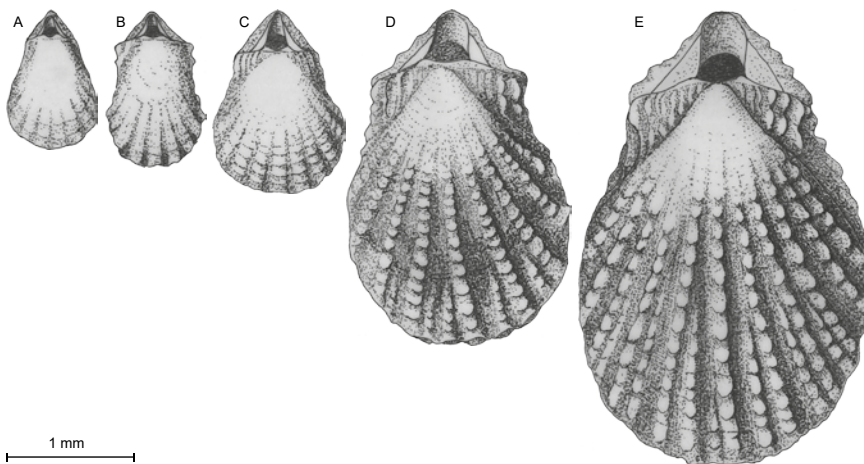


Fig. 34. *Terebratulina chrysalis* (von Schlotheim, 1813). A–E. Growth stages, showing the formation of new costellae by intercalation (D, E). Upper lower Maastrichtian. Hundefangsklint, Møns Klint (Figs 2, 4).

transverse band becomes ventrally arched. The inner surface of the shell is smooth.

A strongly developed spicular skeleton occurs in the mantle, the anterior body wall and the arms of the lophophore. The skeleton of the anterior body wall forms a collar, which drapes the brachidial ring on the dorsal side of the crura. The dorsal mantle skeleton is more strongly developed than the ventral. A well-developed plectolophe is already present in specimens larger than $W=2.5\text{--}3\text{ mm}$. The filament skeletons are narrow and there are 10 filaments/mm arm.

T. chrysalis is easy to distinguish on the basis of the large number of intercalated costellae. Young forms where new costellae have not yet been formed may, however, be difficult to distinguish from specimens of *Gisilina gisii* (Roemer, 1841) and *Gisilina jasmundi* Steinich, 1965 of the same size. *T. chrysalis* is normally more elongate and has fewer costellae in those stages with a sculpture that is less strong compared to *G. jasmundi*.

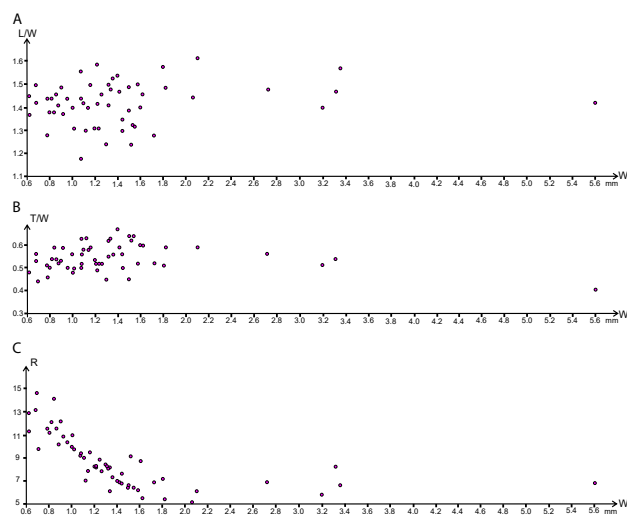


Fig. 35. *Terebratulina chrysalis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width, R=number of ribs/costellae.

Material. Falster. Gedser Fyr: 56; Gedser Odde: 11. Jylland. Danmark: 75; Eerslev: 34; Ferslev: 127; Gudumholm: 72; Hillerslev: 10; Kjølbygård: 10; Lindholm: 45; Linds: 71; Mjels: 73; Nye Kløv: about 200 (Johansen 1987); Nørre Flødal: 136; Rørdal: 98; Smidie: 12; Spentrup: 23; Sønder Kongerslev: 2. Møn. Forchhammers Pynt: 33; Hundefangs Klint: 662; Hvide Klint: 64; Hvidskud: 3311; Lille Taler: 4; Maglevandspynt: 4; Nylands Nakke: 7; Store Taler: 4; Sættepileklint: 16. Sjælland. Karlstrup: 143; Stevns Klint: 120.

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark, it has been recorded from Skåne in southern Sweden (Surlyk 1969), eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1965), Hemmoor (Surlyk 1970a; Surlyk & Schröder unpublished data) and Krons Moor (Surlyk 1982) in northern Germany, Norfolk in eastern England (Johansen & Surlyk 1990), Belgium (Simon 2000) and southern Limburg in the Netherlands (Simon 2011).

Pertinent references. Steinich (1965), Surlyk (1972, 1984), Surlyk & Johansen (1984), Johansen (1987), Johansen & Surlyk (1990), Simon (2000, 2011), Schröder & Surlyk (2020).

***Terebratulina longicollis* Steinich, 1965** Figs 36, 37, 38, 39, 40

T. longicollis is micromorphic, the outline is markedly elongate subpentagonal and the L/W varies between 1.5 and 1.8. The greatest width is situated at the gently rounded anterior margin in small forms. During growth, it moves close to the midline of the shell but is always anterior to this line. The shell is relatively thick and biconvex, the dorsal valve being slightly flatter than the ventral valve. The shell ears are small, but well defined. Six to eight radial costae are formed at $W=0.3\text{ mm}$. They become stronger dur-

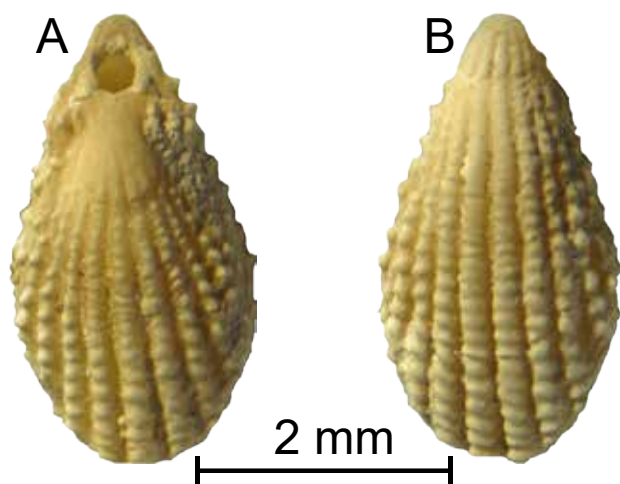


Fig. 36. *Terebratulina longicollis* Steinich, 1965. A. Dorsal view. B. Same specimen in ventral view. Note the coarse, undivided, straight, strongly ornamented, costae. Lower Maastrichtian. Møns Klint (Fig. 2).

ing growth and larger specimens normally have 8–10 costae, and the few new costae are formed laterally at the ears. There are no intercalated ribs. The costae are straight and have a sculpture of small knobs formed as transverse half-rings. The shell has only few and only rarely more than two growth lines.

The beak is suberect and short. The area is very narrow but sharply delimited. The foramen is initially hypothryid and becomes mesothryid in later growth stages. The deltidial plates converge slightly anterior to the foramen during growth, resulting in the formation of a circular foramen. The pedicle collar is well developed. The hinge is of the same type as in *Terebratulina chrysalis* (von Schlotheim, 1813) and *T. faujasii* (Roemer, 1841). The inner socket ridges are thin and long, while the outer socket ridges are shallow. A cardinal process is only found in larger forms. It is shaped as a transversal process with a concave posterior surface. The teeth are triangular, pointed and relatively strong.

The first brachidial stages can be recognized at $W=0.6\text{--}0.7$ mm. Small processes are formed at the anterior end of the inner socket ridges. They are rapidly differentiated into posteriorly directed crural processes and anteriorly directed descending branches. Crura form at $W=1.0$ mm and the descending branches are fused at $W=1.3$ mm. The crural processes are fused at $W=1.5$ mm. The brachidium is very strongly developed in adult forms and have long, thick anteriorly directed crura. The dorsal transverse bridge has a dorsally directed median ridge. The inner side of the valve margins has strong furrows.

A well-developed spicular skeleton occurs in the mantle, the anterior body wall and the lophophore arms. The adult lophophore was a plectolophe. The skeleton of the body wall forms a collar, which drapes the anterior dorsal margins of the brachidium. The ventral mantle skeleton is particularly strongly developed. The filament skeletons are long. The circular mouth penetration has a diameter of 0.2 mm in large specimens. The brachial furrow is wide and limited by a strongly developed brachial lip.

T. longicollis is easy to distinguish from *T. chrysalis* on the basis of its undivided costae and the relatively higher L/W also in small specimens. The transverse half-ring sculptures of the costae are also much weaker in *T. chrysalis*. It can always be distinguished from *T. faujasii* on the basis of its much higher L/W ratio.

Material. Jylland. Danmark: 106; Gudumholm: 337; Kjølbygård: 8; Lindholm: 133; Linds: 3; Nye Kløv: 106 (Johansen 1987); Nørre Flødal: 45; Rørdal: 44; Smidie: 4; Spentrup: 3.

Møn. Forchhammers Pynt: 7; Hundefangs Klint: 32; Hvide Klint: 11; Hvidskud: 679; Lille Taler: 3; Maglevands Pynt: 5; Store Taler: 6; Sættepileklint: 1.

Sjælland. Stevns Klint: 116; Karlstrup: 131.

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark it is recorded in eastern Poland

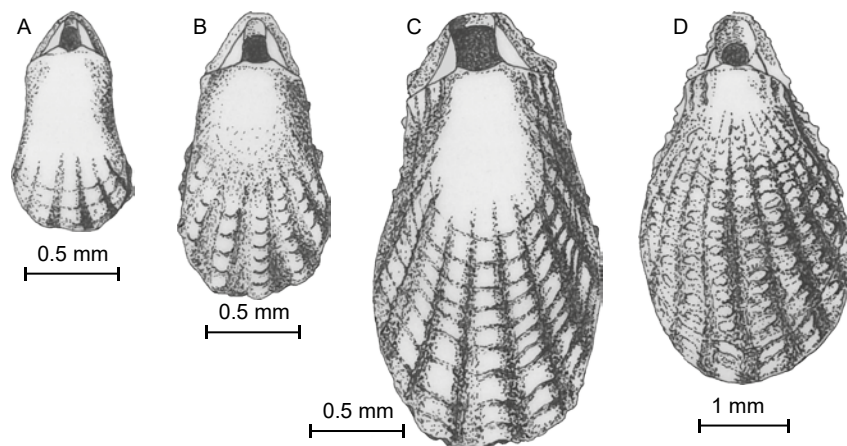


Fig. 37. *Terebratulina longicollis* Steinich, 1965. A–D. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

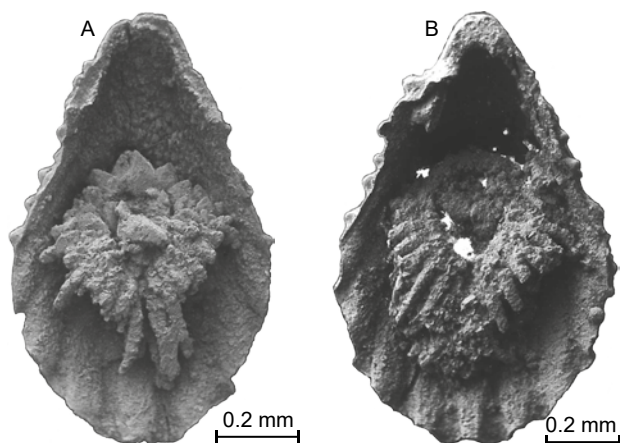


Fig. 38. *Terebratulina longicollis* Steinich, 1965. SEM photographs of opened ventral valves, showing the well-preserved spicular skeletons of the lophophore arms. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

(Bitner & Pisera 1979; Machalski & Bitner 2024), Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982; Surlyk & Schröder unpublished data) and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1972, 1982, 1984), Johansen & Surlyk (1990), Surlyk & Schröder (unpublished data).

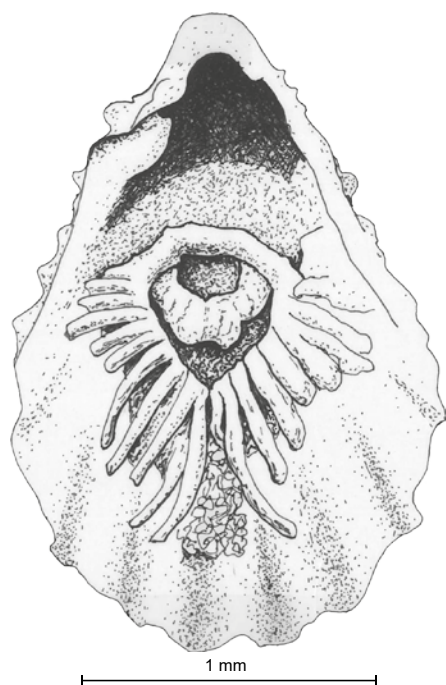


Fig. 39. *Terebratulina longicollis* Steinich, 1965. Opened ventral valve, showing the spicular skeleton of the plectolophous lophophore, Lower upper Maastrichtian, Gudumholm (Fig. 2).

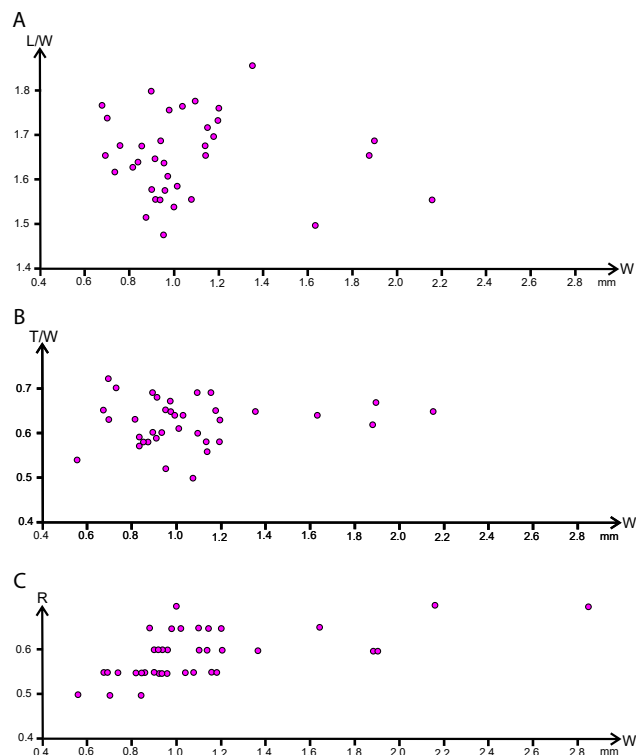


Fig. 40. *Terebratulina longicollis* Steinich, 1965. Scatter diagrams. L=length, W=width, R=number of ribs/costae. *T. longicollis* can always be distinguished from the other species of the Danish chalk by the high L/W.

Terebratulina faujasii (Roemer, 1841)

Figs 41, 42, 43, 44

T. faujasii is micromorphic and the outline is subtriangular. The shell is relatively thick. The largest width is situated anterior to the midline of the shell. The L/W decreases slowly during ontogenesis, but the shell is always clearly elongate. The shell is biconvex to planoconvex, and the dorsal valve is always considerably flatter than the highly convex ventral valve.

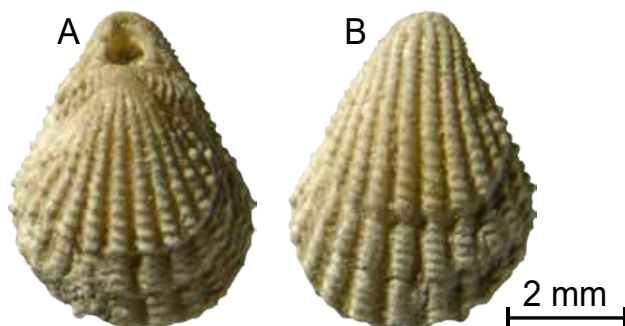


Fig. 41. *Terebratulina faujasii* (Roemer, 1841). A. Dorsal view. B. Same specimen in ventral view. Note the straight undivided costae with a strong sculpture of half-ring tubercles. The tubercles are somewhat similar to, but much stronger than those of *Gisilina jasmundi* Steinich, 1965. Lower Maastrichtian. Møns Klint (Fig. 2).

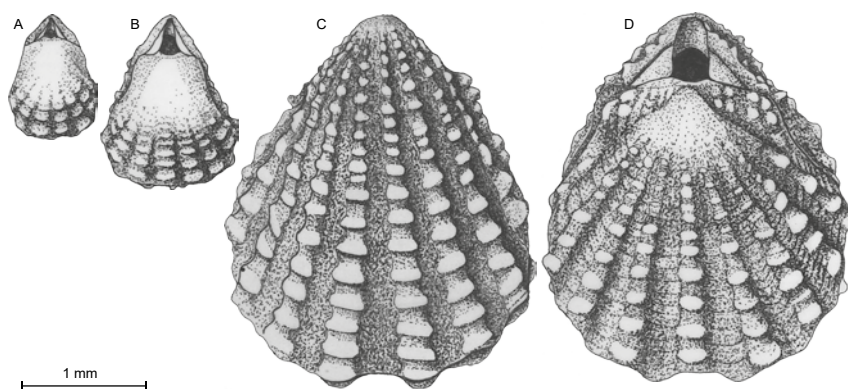


Fig. 42. *Terebratulina faujasii* (Roemer, 1841). A–D. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

The anterior commissure is almost rectimarginate in subadult forms, while it is slightly uniplicate in fully grown specimens. The ears are large and clearly limited. The lateral margin forms a stump angle with the shell margin. The costae start to be formed at $W=0.4$ mm and the number varies between 7 and 10, 8 or 9 being most common. They are strong, straight and undivided with a marked sculpture of transverse half-rings. The interspaces between the costae are smooth. There are few indistinct growth lines.

The beak is suberect and pointed in juveniles but becomes short and blunt during growth. The shell ears have irregular knobs, which in rare cases are arranged in rows to form very short costae. The foramen is large, initially hypothyrud and later submeso- to mesothyrid. The pedicle collar is short and strongly developed. The deltidial plates are tri-

angular and approach each other slightly anterior to the foramen. The hinge is formed like in *Terebratulina chrysalis*, but the outer sockets are somewhat deeper. The crura start as two short, blunt ventrally directed processes at $W=0.5$ mm. The processes are markedly wider at $W=0.9$ – 1.0 mm. Real crura are first developed at $W=1.1$ – 1.3 mm but are still very short. The descending branches fuse at $W=2$ mm to form a connecting bridge. The crural processes are connected at a width of 2.3–3.0 mm to form a complete brachidial ring. The inner valve margins are strongly furrowed.

A well-developed spicular skeleton is formed in the arms of the lophophore, in the anterior body wall and in the mantle. The adult lophophore was a plectolophe. The filament skeletons are very short and there are 4.5 filaments per 0.5 mm of arm. The brachial furrow is wide and inwards delimited by a

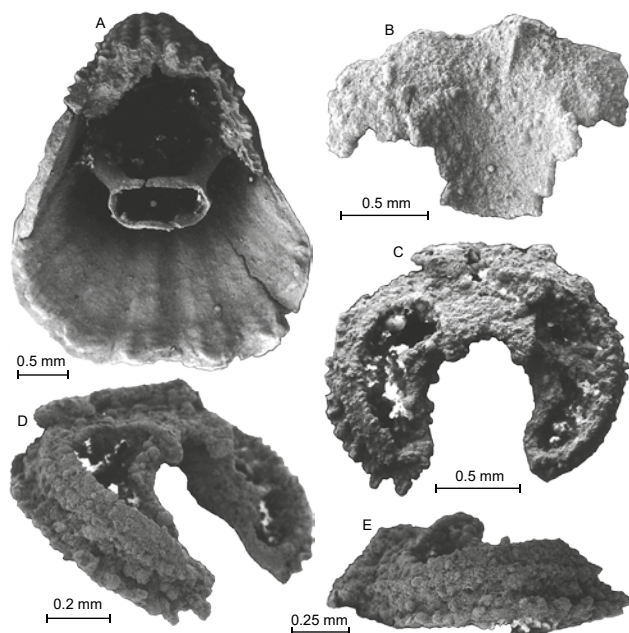


Fig. 43. *Terebratulina faujasii* (Roemer, 1841). A. Opened specimen, showing the ring of the brachidium. B. Spicular skeleton of the anterior body wall. C, D and E. Spicular skeleton of the plectolophous lophophore in dorsal, oblique and lateral views, respectively. Møns Klint (4 in Fig. 2).

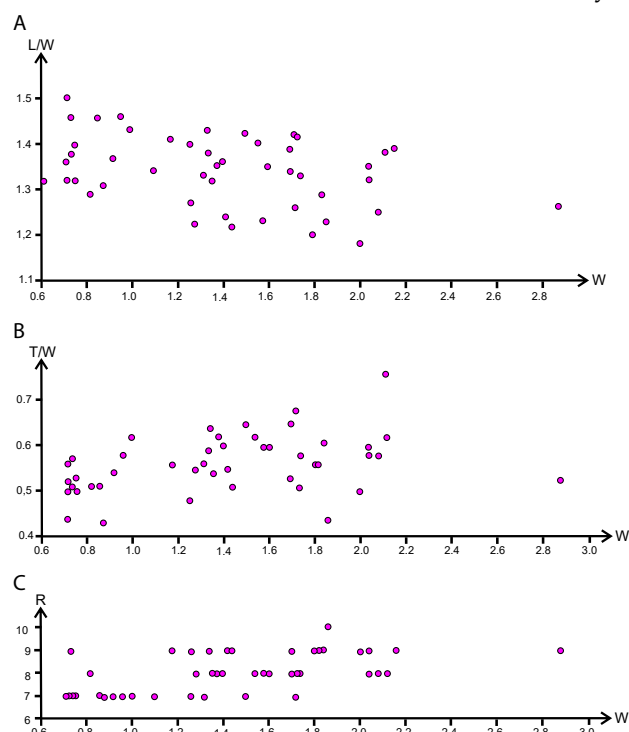


Fig. 44. *Terebratulina faujasii* (Roemer, 1841). Scatter diagrams. L=length, W= width, T=thickness, R=number of ribs/costae.

well-developed brachial lip.

T. faujasii is characterized by the low number of costae with a sculpture of strong transverse half-ring knobs. Young forms are difficult to distinguish from *Gisilina jasmundi*, but they always have a smaller number of more strongly sculptured ribs.

Material. Jylland. Eerslev: 2; Gudumholm: 3; Nye Kløv: 40 (Johansen 1987); Rørdal: 4; Spentrup: 6; Sønder Kongerslev: 3.

Møn. Forchhammers Pynt: 9; Hvide Klint: 31; Hvidskud: 1910; Hundefangs Klint: 167; Lille Taler: 6; Maglevandspynt: 3.

Sjælland. Karlstrup: 299; Stevns Klint: 805.

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones in Denmark (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark, it has been found in Skåne in southern Sweden (own data), Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982, 1984, Surlyk & Schröder unpublished data).

Belgium (Simon 2000) and Norfolk in eastern England (Johansen & Surlyk 1990),

Pertinent references. Steinich (1965), Surlyk (1972, 1982, 1984), Johansen (1987), Johansen & Surlyk (1990), Simon (2000), Surlyk & Schröder (unpublished data).

Terebratulina subtilis Steinich, 1965

Figs 45, 46, 47

T. subtilis is micromorphic and the outline is initially highly elongate subpentagonal to subtriangular. The L/W is about 1.80–1.85 in very small specimens but decreases to 1.23–1.40 during growth and the outline changes correspondingly to pointed oval. The greatest width is almost at the anterior margin in small specimens and at the shell midline in adult specimens. The shell is thin, and biconvex to almost plano-convex. The shell ears are indistinctly delimited, and the anterior commissure is rectimarginate. A large number of very fine radial costellae occurs. Three to

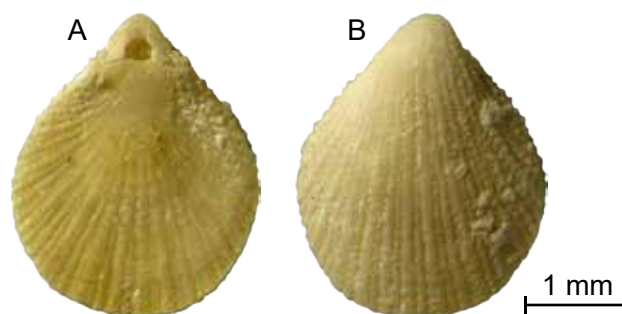


Fig. 45. *Terebratulina subtilis* Steinich, 1965. A. Dorsal view. B. Same specimen in ventral view. Note the large number of very fine costellae with only a weak knobby ornamentation. New costellae are formed by intercalation. Lower Maastrichtian. Møns Klint (Fig. 2).

ten costae are formed at $W=0.45$ mm and new costellae are rapidly formed during growth by intercalation, and a characteristic alternation between wide and narrow costellae is formed. Specimens at $W>2$ mm possess 40–50 costellae, which have a sculpture of very small tubercles. The interspaces between the costellae are very narrow and the costellae are low. In small specimens they are only visible if the incident light forms a very low angle to the surface of the shell. Growth lines are absent or indistinct.

The beak is short and suberect. The area is small and sharply defined. The foramen is laterally limited by two narrow, triangular deltidial plates. It is initially hypothyril but changes to submesothyril during growth. The pedicle collar is long and well developed. The hinge is rather weak. The inner socket ridges are thin, and the sockets are flat. The crura start to form at $W=0.4$ mm and crural processes and descending branches form at $W=0.75$ – 0.80 mm. The descending branches fuse at $W=1.0$ – 1.1 mm and the crural processes fuse at $W=1.35$ mm so that a complete brachidial ring is formed. The brachidium is rather slender in all growth stages.

A strongly developed spicular skeleton is developed in the arms but is almost always recrystallized. The lophophore was a plectolophe. The mantle does not seem to have possessed a spicular skeleton.

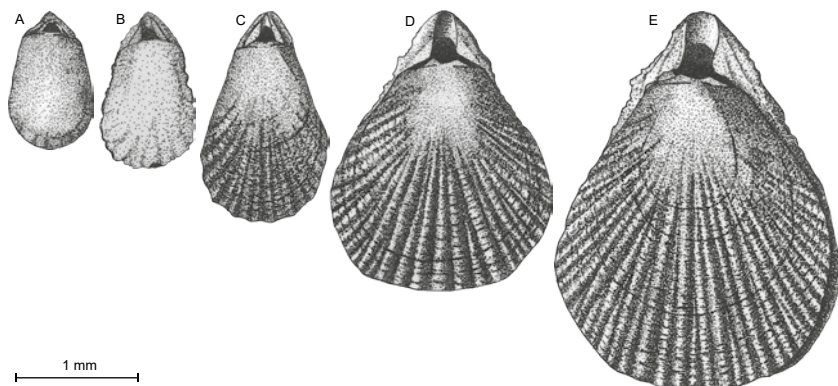


Fig. 46. *Terebratulina subtilis* Steinich, 1965. A–E. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

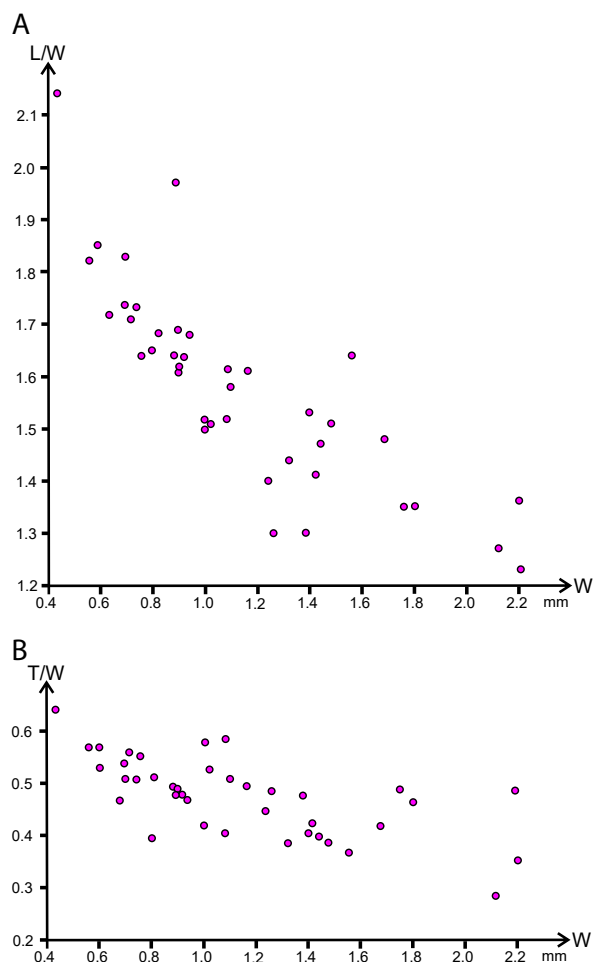


Fig. 47. *Terebratulina subtilis* Steinich, 1965. Scatter diagrams. L=length, W= width, T=thickness.

T. subtilis is somewhat similar to *Rugia tenuicostata* in the early growth stages. It has always a higher number of more densely spaced costellae and a less pointed beak. Particularly characteristic is the difference in the details of the ornamentation of the costellae, which enables correct identification of even small valve fragments. *R. tenuicostata* has relatively high, widely spaced costellae with a sculpture of small triangular tubercles, giving the costellae a fretsaw-like appearance, while *T. subtilis* has flat, densely spaced costellae with a sculpture of low, rounded tubercles.

Material. Jylland. Rørdal: 17.

Møn. Forchhammers Pynt: 6; Hundefangsklint: no numbers; Hvidskud: 236; Sandpynten: 19; Sommer-spiret: no numbers; Vitmunds Nakke: 18

Chronostratigraphy in Denmark. Lower Maastrichtian, *subtilis*–*pulchellus* Zone, where its lowest occurrence defines the base of the zone, and in the *pulchellus*–*pulchellus* Zone. Outside Denmark it is found at Balsvik, Skåne, southern Sweden (own data), Rügen (Steinich

1965) and Krons Moor in northern Germany (Surlyk 1982) and in Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1972, 1982), Johansen & Surlyk (1990).

Genus *Gyrosoria* Cooper, 1973

Type species *Gyrosoria gracilis* (von Schlotheim, 1813)

Gyrosoria gracilis (von Schlotheim, 1813)

Figs 48, 49, 50

This species is in most of the literature referred to the genus *Terebratulina*. It was subsequently designated type species for a new genus *Gyrosoria* by Cooper (1973). This was considered unjustified museum-type splitting by Surlyk (1982) who preferred to keep it in *Terebratulina* but the new genus has since been generally accepted and I have thus also later referred it to *Gyrosoria* (Surlyk 1984). This practice is followed here.

The species is small to medium-sized. The shell is relatively thick. The outline of juveniles is elongate oval and is subcircular to circular in adults. The hinge margin passes evenly into the lateral margins and only in specimens with $W < 2$ mm do they form a blunt, but sharp angle. Poorly defined ears also occur in these small forms. The L/W decreases very strongly to $W = 3$ mm. This ratio is almost constant from $W = 3$ – 8 mm and increases slightly above this size. Species smaller than $W = 2$ mm are biconvex, but large specimens are planoconvex or even slightly concavoconvex. At $W = 0.5$ mm 5–10 radial costae are formed. They are initially straight and rapidly become strongly developed. The formation of new costellae by intercalation is initiated at $W = 1.5$ – 2 mm. The costellae are curved laterally in specimens larger than $W = 1.5$ mm. New costellae normally start at growth lines and the number of costellae thus increase in a stepwise manner during growth. The final number of costellae varies between 40 and 60. They have an ornamentation of small grain-like tubercles, which gives them a string-of-pearl-like appearance

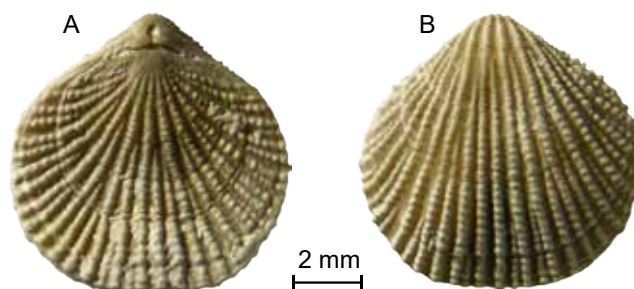


Fig. 48. *Gyrosoria gracilis* (von Schlotheim, 1813). A. Dorsal view. B. Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

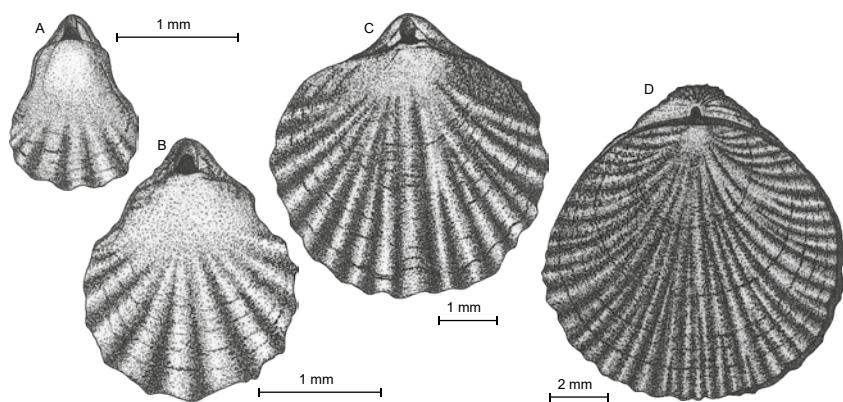


Fig. 49. *Gyrosoria gracilis* (von Schlotheim, 1813). A–D. Growth stages.

especially in small specimens. Growth lines are clearly marked and commonly occur in densely spaced groups.

The beak is short and pointed and becomes incurved during growth. Only very small specimens possess an area, and in larger forms the triangular deltidial plates sit directly on the area margins. The foramen is small and moves into the ventral valve during progressive incurving of the beak. The deltidial plates gradually approach each other anterior to the foramen but never fuse. The pedicle collar is strong (wrongly described as absent in Lee *et al.*, 2006, p. 2148) and becomes extended during growth. In large specimens, it forms a tube or gutter on the inner side of the ventral valve. The hinge is very strongly developed. The inner socket ridges are well defined and laterally delimited by deep sockets. The cardinal process is low and only fully developed in large specimens. It has a posteriorly crenulated surface. The teeth are strong and pointed. Short, thin, ventrally directed crura are formed at $W=1.1\text{--}1.3$ mm. At $W=1.6\text{--}1.8$ mm the descending branches fuse into a transverse bridge, and the crural processes fuse at $W=2.0\text{--}2.1$ mm, so that a complete brachidial ring is formed. The crura become relatively stronger built during growth. The median part of the branch formed by the fused descending branches becomes

strongly ventrally curved and a small posterior extension is formed. The internal part of the shell is smooth, except at the shell margin which has strong furrows. The dorsal valve has two large triangular to pointed oval adductor scars in large forms. The ventral valve has very weak muscle scars in the posterior part of the valve. The arms, mantle and anterior body wall have a strong spicular skeleton, which in the body wall is sharply delimited from that of the dorsal mantle. The body wall skeleton has two medial penetrations, corresponding to the median vascula. The adult lophophore is a plectolophe.

Small biconvex specimens of *G. gracilis* below $W=2$ mm are difficult to distinguish from specimens of *Gisilina gisii* of the same size. However, already in the early stages the costellae show a tendency to a lateral outwards curvature, whereas the costae of *G. gisii* are always straight and more anteriorly directed.

Material. Jylland. Rørdal: 135; Lindholm: 39; Danmark: 7; Gudumholm: 41; Nørre Flødal: 64; Linds: 22; Ferslev: 7; Mjels: 19; Smidie: 7; Sønder Kongerslev: 4. Møn. Hvide Klint: 2; Hvidskud: 35; Maglevandspynt: 5; Lille Taler: 2; Store Taler: 11; Sættepileklint: 2. Sjælland. Karlstrup: 11; Stevns Klint: 14.

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark it has been found at Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982, 1984; Surlyk & Schröder unpublished data), Belgium and the Netherlands (Sklenár & Simon 2009), and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1972, 1984; Sklenár & Simon (2009), Surlyk & Schröder (unpublished data).

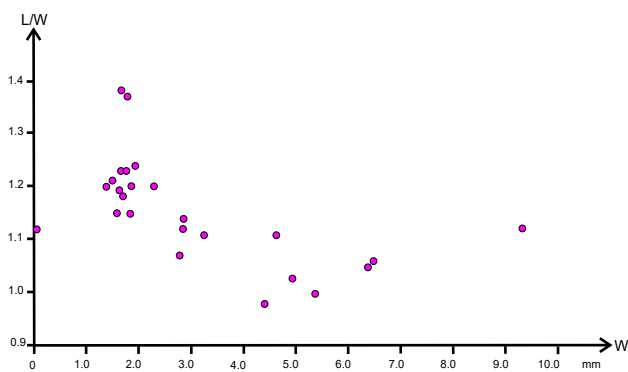


Fig. 50. *Gyrosoria gracilis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width.

Family Chlidonophoridae Muir-Wood, 1959

Subfamily Chlidonophorinae Muir-Wood, 1959

Genus *Gisilina* Steinich, 1963

Type species *Gisilina gisii* (Roemer, 1841)

Gisilina gisii (Roemer, 1841)

Figs 51, 52, 53

G. gisii is micromorphic to small. The outline is rounded to somewhat triangular and the L/W does not change markedly during growth above L=1.0 mm. The largest width lies slightly anterior to, or at the shell midline. The shell is strongly biconvex and relatively thick. The anterior commissure is rectimarginate. The shell ears are small and not clearly delimited. About 10 costae are formed at W=0.3 mm. They are strong, straight, and smooth or have a sculpture of small, weak knobs and their width increase during growth. New costae are formed laterally at the shell ears and the total number may reach 20. Five to six growth lines are present on large specimens. The beak is pointed and suberect during the early growth stages but becomes more incurved and erect during growth. The foramen is likewise indented into

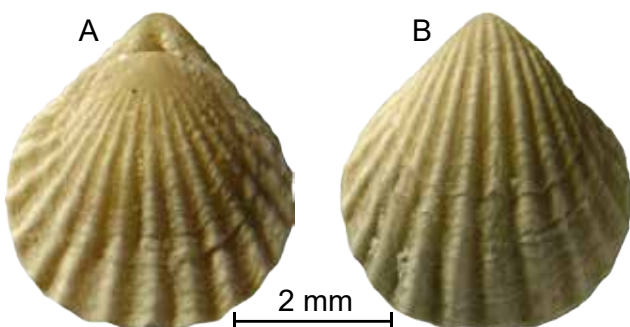


Fig. 51. *Gisilina gisii* (Roemer, 1841). A. Dorsal view. Note the straight only weakly knobbed costae where new costae are formed at the shell ears. B. Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

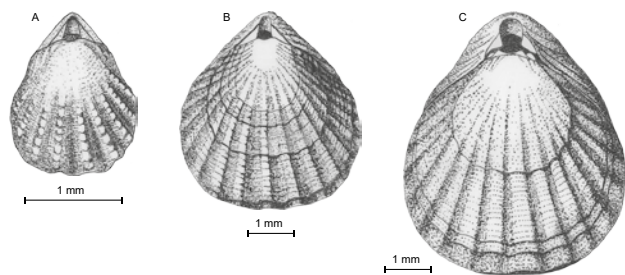


Fig. 52. *Gisilina gisii* (Roemer, 1841). A–C. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

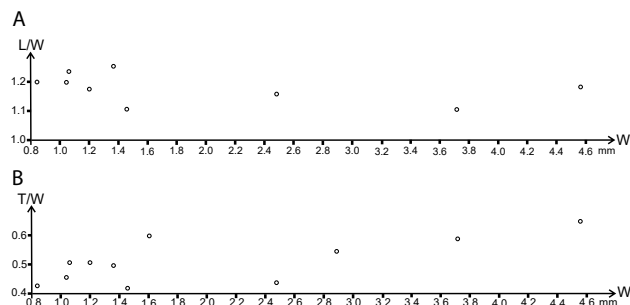


Fig. 53. *Gisilina gisii* (Roemer, 1841). Scatter diagrams. L=length, W=width, T=thickness.

the ventral valve during growth. It is initially hypothryid, but changes to submesothryid and finally to mesothryid. The deltidial plates are triangular. The pedicle collar is long and strongly developed. Very short crura are formed at W=2 mm. The crural processes are also short, but the descending branches are somewhat longer and rapidly grow and fuse together forming a thin bridge that is slightly ventrally curved. The brachidium is fully developed at W=2.4–2.5 mm. The margin of the inner side of the shell is strongly furrowed corresponding to the costae on the outer side.

The arms of the lophophore possess a strong spicular skeleton and a specimen with W=1.14 mm had a schizolophe, whereas large forms with a fully developed brachidium had a plectolophe.

Large specimens of *G. gisii* are distinguished from *G. jasmundi* in being more biconvex, in having smooth to only weakly knobbed costae and by the mesothryid foramen. Small specimens can be difficult to distinguish from *G. jasmundi* and *T. chrysalis* of the same size but normally differ from the former by the lack of half-ring ornamentation of the costae, and from the latter in having a lower number of costae and a more biconvex shell.

Material. Jylland. Rørdal-1: 37.

Møn. Hvide Klint: 2; Hvidskud 98; Hundefangsklint: 48; Store Taler: 24; Lille Taler 2; Maglevandspynt: 1; Nylands Nakke: 4; Forchhammers Pynt: 6.

Chronostratigraphy in Denmark. Lower Maastrichtian, *acutirostris*–*spinosa* to *pulchellus*–*pulchellus* Zones. Outside Denmark *G. gisii* is found in Skåne, southern Sweden (own data), at Rügen and Krons Moor in northern Germany (Steinich 1965; Surlyk 1982) and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1969, 1982), Johansen & Surlyk (1990), Surlyk & Schrøder (unpublished data).

Gisilina jasmundi Steinich, 1965

Figs 54, 55, 56

G. jasmundi is micromorphic and the outline is pointed oval to subtriangular. The largest width is at the shell midline. The ears are large and clearly delimited. The shell is relatively thick, biconvex, but rather flat. The commissure is mainly rectimarginate. Nine to 10 straight costae are formed at $W=0.4$ mm. In a few cases up to 4 new costae are formed at the ears, reaching a total of about 13. The costae are strongly

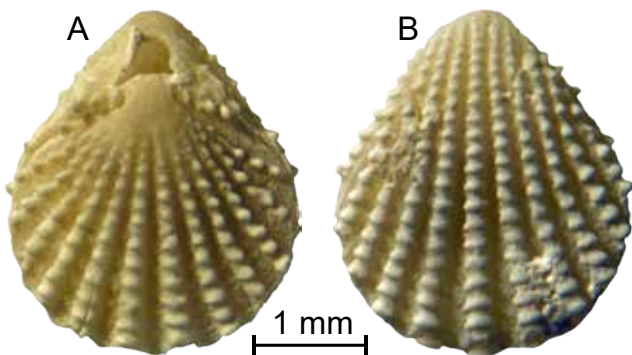


Fig. 54. *Gisilina jasmundi* Steinich, 1965. A. Dorsal view. Note the straight costae with a characteristic knobby sculpture, which are not as strongly developed than the half-ring knobs of rather similar *Terebratulina faujasii*. B. Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

developed and have a sculpture of transverse half-rings much like *Terebratulina faujasii* but not quite as strong. The half-rings are always oriented obliquely to the length of the costae, the medial side pointing back towards the beak. Large specimens have 2–3 rather poorly defined growth lines.

The beak is suberect and the area is small. The foramen is relatively large and submesothyrid. The deltidial plates are triangular and the pedicle collar is well developed. The inner socket ridges are high and bent slightly outwards in a posterior direction. Large

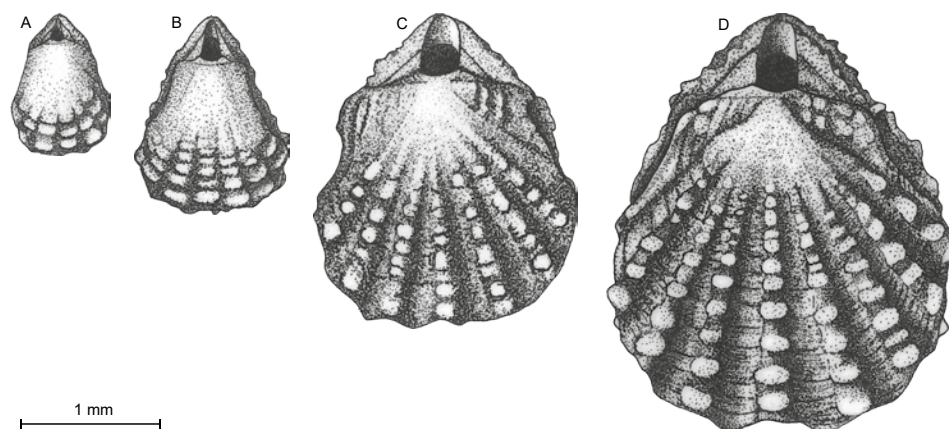


Fig. 55. *Gisilina jasmundi* Steinich, 1965. A–D. Growth stages. Upper lower Maas-trichtian. Hvidskud, Møns Klint (Figs 2, 4).

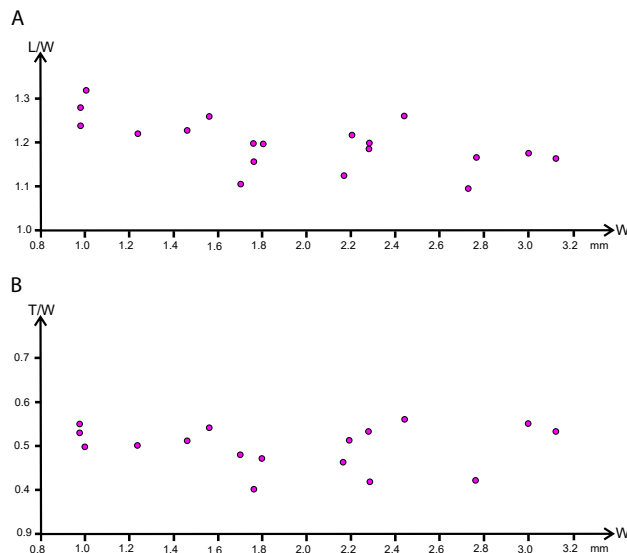


Fig. 56. *Gisilina jasmundi* Steinich, 1965. Scatter diagrams. L=length, W=width, T=thickness.

specimens have a low cardinal process. The teeth are short. The brachidium is very delicate and is formed in a similar way as in *Gisilina gisii*. The descending branches fuse into a long, thin, slightly ventrally directed bridge at $W=1.8$ mm. The crura are short and the crural processes are pointed and commonly oriented obliquely towards each other but never meet. The internal part of the shell has strong furrows corresponding to the costae on the external side.

The arms have a strong, well-developed spicular skeleton. A specimen with $W=2.72$ mm had a well-developed plectolophe. The skeletons of the filaments are strong and 13 filaments/mm arm is recorded.

Large specimens are difficult to distinguish from *Terebratulina faujasii* but can always be recognized by the larger number of costae and a flatter shell. Small specimens with relatively weakly sculptured costae may be difficult to distinguish from *Gisilina gisii* and *Terebratulina chrysalis* but differ from the former by

the knobs on the costae and from the latter by a less elongate outline and a smaller number of costae.

Material. Falster. Gedser Fyr: 21; Gedser Odde: 17. Jylland. Kjølbjergård: 3; Nye Kløv: 1, and possibly a few more (Johansen 1987); Rørdal: 100. Møn. Hvide Klint: 39; Hvidskud: 401; Hundefangsklint: 158; Maglevandspynt: 8; Nylands Nakke: 1; Forchhammers Pynt: 4. Sjælland. Karlstrup: 198; Stevns Klint: 8. Outside Denmark, *G. jasmundi* is recorded in Skåne, southern Sweden (own data), at Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982, 1984; Surlyk & Schröder unpublished data), and in Norfolk, eastern England (Johansen & Surlyk 1990),

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones.

Pertinent references. Steinich (1965), Surlyk (1972, 1982, 1984), Johansen & Surlyk (1990), Surlyk & Schröder (unpublished data).

Genus *Meonia* Steinich, 1963

Type species *Meonia semiglobularis* (Posselt, 1894)

Meonia semiglobularis (Posselt, 1894)

Figs 57, 58, 59, 60, 61

M. semiglobularis is micromorphic. The outline is elongate in the early juvenile stages, but L/W decreases rapidly during ontogeny and is essentially constant from a width of 1 mm. From then on it is on average 0.95. The hinge margin is straight and the anterior margin has an hemispherical outline in dorsal view. The lateral margins are straight and converge slightly in a posterior direction. The greatest width is situated anterior to the midline of the shell. Weakly defined ears are present in adult specimens. The shell is planoconvex and the ventral valve is almost hemispherical. A broad dorsal sinus is formed at $W=0.8-0.9$ mm and becomes more marked during

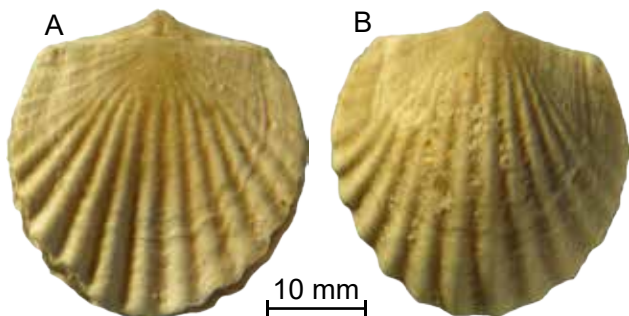


Fig. 57. *Meonia semiglobularis* (Posselt, 1894). A. Dorsal view. B. Same specimen in ventral view. Møns Klint (4 in Fig. 2).

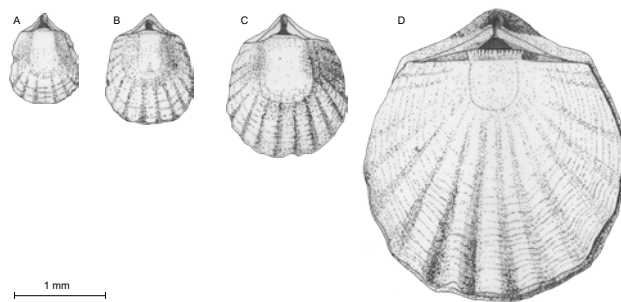


Fig. 58. *Meonia semiglobularis* (Posselt, 1894). A–D. Growth stages. Lower upper Maastrichtian. Nørre Flødal (Fig. 2).

growth. The anterior commissure is rectimarginate in juvenile forms but is slightly unisulcate in adults, reflecting the development of the dorsal sinus. 4–5 radial costae are formed at $W=0.3-0.4$ mm. The number increases rapidly to about 20 at $W=1.2$ mm. New costae form on the ears laterally to the first formed ones and none are added by intercalation. The costae are strong, smooth, straight and rounded in cross section in juvenile specimens, but become V-shaped in adults. Two to three growth lines are present in adults.

The beak is very short and becomes gradually more incurved during growth. The area is very small, but with sharp edges. The foramen is initially hypothyriform but becomes mesothyriform during growth and is permesothyriform in large specimens. The foramen is laterally limited by two initially triangular deltidial plates, which start to merge at $W=1.5$ mm and from then on restrict the foramen anteriorly. The pedicle collar is small. The hinge is strongly developed. The posterior half of the inner socket ridges are strongly curved in a median direction. They are connected by a broad, low cardinal process, which posteriorly has narrow dorso-ventrally oriented ridges. The dorsal

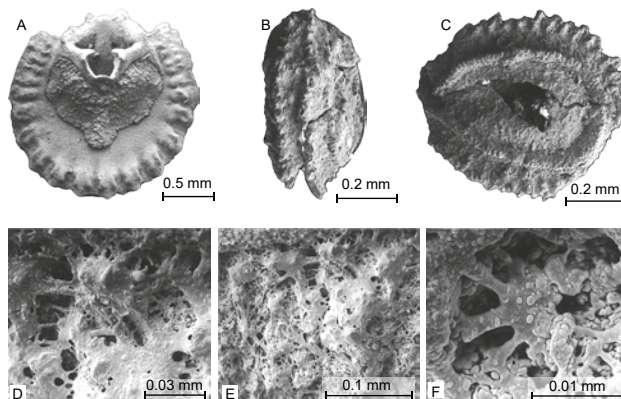


Fig. 59. *Meonia semiglobularis* (Posselt, 1894). Spicular skeletons. A. Anterior body wall. B and C. Frontal and lateral views of schizolophous lophophore. The lower panel shows details of spicular meshwork of the body wall.

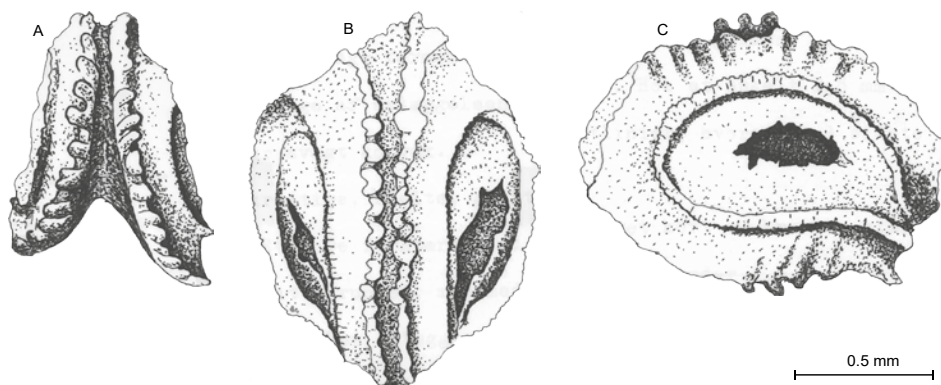


Fig. 60. *Meonia semiglobularis* (Posselt, 1894). Spicular skeletons of schizolophous lophophore. A, B and C. Frontal, dorsal and lateral views, respectively. Lower upper Maastrichtian, Gudumholm (Fig. 2).

cardinalia extend increasingly across the posterior shell margin during growth. The teeth are blunt, flat and medially directed. They carry dorsal narrow ridges, which are oriented in the length direction of the shell. The brachidium consists at $W=1$ mm of thin, long crura. They converge slightly and are strongly ventrally directed. At $W=1.7$ – 1.8 mm, ventro-medially directed stump crural processes are formed at the ends of the crura and the descending branches meet at $W=2.0$ mm and fuse into a bridge. The crura are very strongly developed in large, adult forms.

M. semiglobularis has a strongly developed spicular skeleton in the mantle, anterior body wall and arms. The mantle skeleton is highly reminiscent to those found in the species of *Terebratulina* and forms a thin drape of the inside of the shell. The lophophore was schizolophous even in the largest specimens and there is no sign of a median spiral part. There is also only one row of filaments, so there is no differentiation in ad- and ablabial filaments. The brachial furrow is very wide but strongly developed. The filaments have strong spicules, which are furrowed on the adlabial side. There are 9 filaments/mm of arm, and the arms are hollow, corresponding to the small and large brachial canal.

The inner surface of the shell is smooth except along the margin, which is strongly furrowed, corresponding to the costae on the outer surface. Two pairs of weak muscle scars are seen in the dorsal valve. Those of the anterior pair are subtriangular in outline and probably represent adductor muscle scars. The other pair is situated at the root of the cardinal process, are small and circular in outline and probably represent scars of the pedicle muscle.

Material. Jylland. Denmark: 70; Eerslev: 1; Ferslev: 256; Gudumholm 342; Hillerslev: 2; Kjølbygård: 7; Lindholm 188; Linds: 128; Mjels: 186; Nye Kløv: 394 (Johansen 1987); Nørre Flødal: 435; Rørdal 76; Sønder Kongerslev: 5.d

Sjælland. Karlstrup: 24; Stevns Klint: 58.

Chronostratigraphy in Denmark. All upper Maastrichtian brachiopod zones. The lowest occurrence is, however, immediately below the Boreal lower-up-

per Maastrichtian boundary as defined by belemnites (Surlyk 1970a, 1984; Schulz *et al.* 1984; Surlyk *et al.* 2013; Thibault *et al.* 2024b). It was therefore a somewhat misleading choice to name the genus after Møns Klint where almost only lower Maastrichtian chalk is exposed. However, the type specimen of Posselt (1894) may have been found at Møns Klint (2 out of his 5 specimens are from that locality) just like the specimen shown in Figure 57. The northern parts of the cliff at Store Taler exposes chalk that probably reaches up into the lowermost upper Maastrichtian (Surlyk 1984). Outside Denmark, it has been found at Rügen (Steinich 1965) and Hemmoor (Surlyk 1970a, 1984; Surlyk & Schröder unpublished data) in northern Germany and in Sicily (Surlyk & Dieni 1988).

Pertinent references. Posselt (1894), Steinich (1965), Surlyk (1972, 1984), Surlyk & Johansen (1984), Johansen (1987), Surlyk & Dieni (1988), Lauridsen & Surlyk (2008), Hansen & Surlyk (2014).

Genus *Rugia* Steinich, 1963

Type species *Rugia tenuicostata* Steinich, 1963

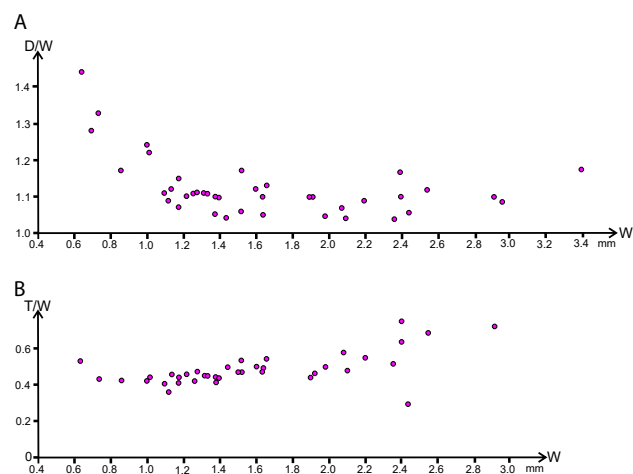


Fig. 61. *Meonia semiglobularis* (Posselt, 1894). Scatter diagrams. W=width, T=thickness, D=diameter of foramen.

Rugia tenuicostata Steinich, 1963

Figs 62, 63, 64

R. tenuicostata is micromorphic. The outline is highly elongate-subtriangular in young specimens and becomes more pointed ovate during growth. The L/W increases from 1.55–1.60 at $W=0.75$ mm to 1.3–1.5 at $W=1.5$ mm. The largest width is anterior to the midline of the shell throughout ontogeny. The shell is biconvex, but the dorsal valve is always slightly flatter than the ventral valve. The ears are indistinctly delimited and blunt. The anterior commissure is rectimarginate throughout growth. Both valves have straight costellae with a sculpture of small knobs. New costellae are formed by intercalation and increases from 6–7 to 28–30 during growth. The knobs are highly characteristic of this species. They are small, bluntly and obliquely triangular and sit on top of the costellae, which thereby obtains an easily recognizable fretsaw-like profile. Growth lines are uncommon.

The beak is short, suberect and pointed in small specimens and somewhat rounded in large specimens. The area is well delimited and narrow. The foramen is laterally limited by two narrow deltidial plates, which are developed in a special way. Initially they first grow in ventro-medial direction. At $W=0.6$

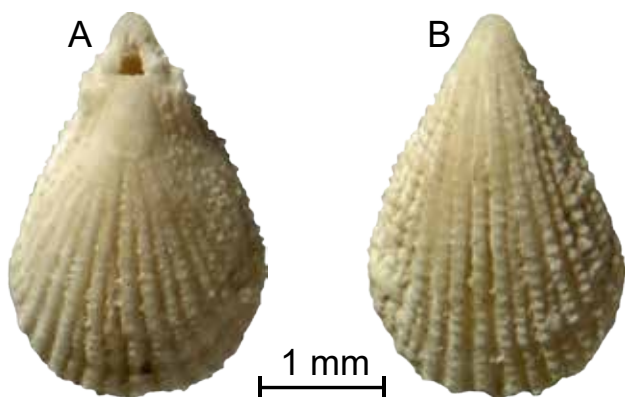


Fig. 62. *Rugia tenuicostata* Steinich, 1963. A. Dorsal view. B. Same specimen in ventral view, showing the scales on the costellae giving them a fretsaw like appearance. Lower Maastrichtian. Møns Klint (Fig. 2).

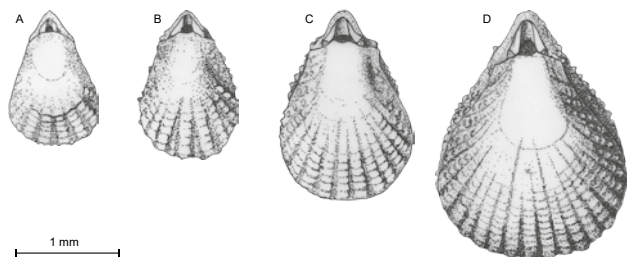


Fig. 63. *Rugia tenuicostata* Steinich, 1963. A–D. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 7).

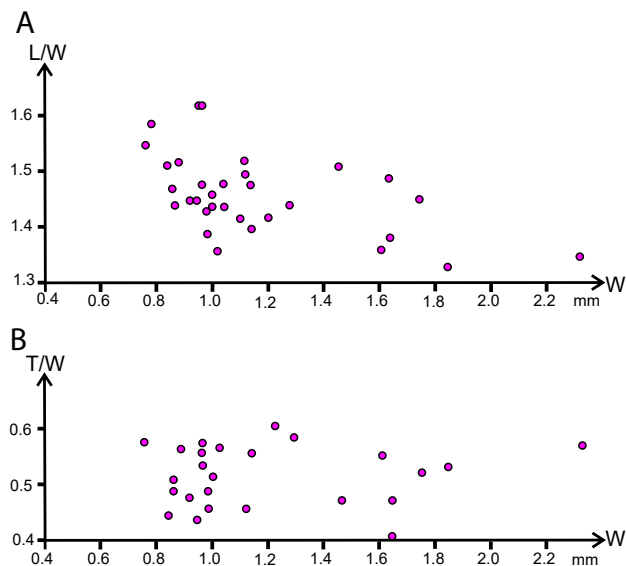


Fig. 64. *Rugia tenuicostata* Steinich, 1963. Scatter diagrams. L=length, W=width, T=thickness.

mm they start to grow in a ventro-lateral direction. At $W=0.7$ mm the direction of growth turns back to a medial direction. The foramen is triangular and hypothyrid. The hinge is very similar to that found in the species of *Terebratulina*. The posterior parts of the inner socket ridges are slightly curved laterally. The cardinal process is very poorly delimited or completely missing. The teeth are stump and rather delicate. The brachidium has long, thin crura, which converge strongly in an antero-ventral direction. The crural processes are short, spatulate and well-defined but do not meet at any time during growth. The descending branches are thin and converge to fuse in an acute angle. The mantle and arms have a well-developed spicular skeleton, which in most cases is strongly recrystallized, hindering preparation. The adult lophophore was a plectolophe.

R. tenuicostata differs from *Rugia acutirostris* in the more triangular outline, less pointed beak, smaller density of costellae and especially in their fretsaw-like morphology. Small species are difficult to distinguish from *Terebratulina subtilis* but this species have numerous, only weakly knobbed costellae compared to *R. tenuicostata* with the fretsaw-like costellae.

Material. Jylland. Nye Kløv: 4 (Johansen 1987); Rørdal-1: 62.

Møn. Hvide Klint: 54; Hvidskud 195; Hundefangsklint: 65; Store Taler: 39; Lille Taler: 12; Maglevands-pynt: 9; Nylands Nakke: 2.

Chronostratigraphy in Denmark. Lower Maastrichtian, *jasmundi-longicollis* to *pulchellus-tenuicostata* Zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark, the species is known from eastern Poland (Bitner &

Pisera 1979), Rügen (Steinich 1965) and Krons Moor in northern Germany (Surlyk 1982), Belgium (Simon 2000) and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1970, 1972, 1984), Johansen & Surlyk 1990), Simon (2000).

***Rugia acutirostris* Steinich, 1965**

Figs 65, 66, 67

R. acutirostris is micromorphic. The outline of small specimens is elongate subpentagonal but changes gradually to elongate pointed oval. Both valves are uniformly and gently inflated. The ears are small and mainly poorly delimited. About 6–8 radial costae are formed at $W=0.2\text{--}0.3\text{ mm}$ and new costellae are added by intercalation during growth to reach a number of about 40. The costellae are weakly knobbed or more rarely smooth and curve gently laterally in larger specimens. Growth lines are few in numbers and not very strong.

The beak is sharply pointed and suberect. The foramen is very small, subtriangular, hypothyrid and laterally delimited by elongate triangular, narrow

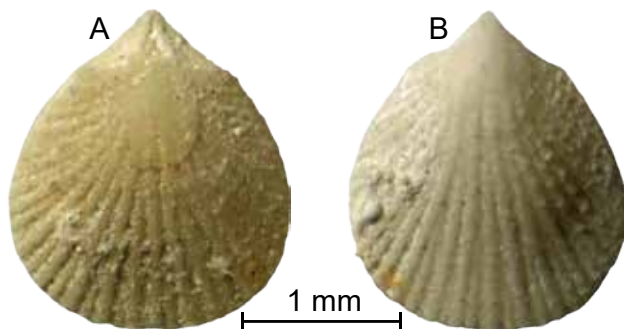


Fig. 65. *Rugia acutirostris* Steinich, 1965. A. Dorsal view. Note pointed rostrum and numerous, laterally curved, fairly smooth costellae. New costellae formed by intercalation. B. Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

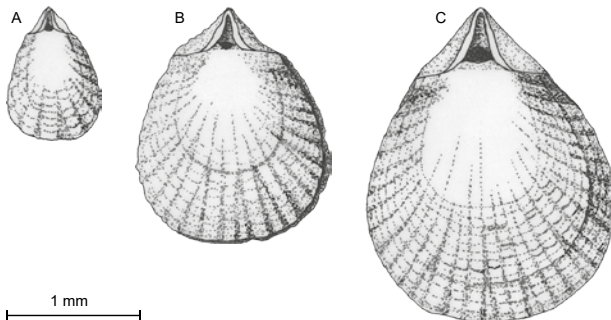


Fig. 66. *Rugia acutirostris* Steinich, 1965. A–C. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

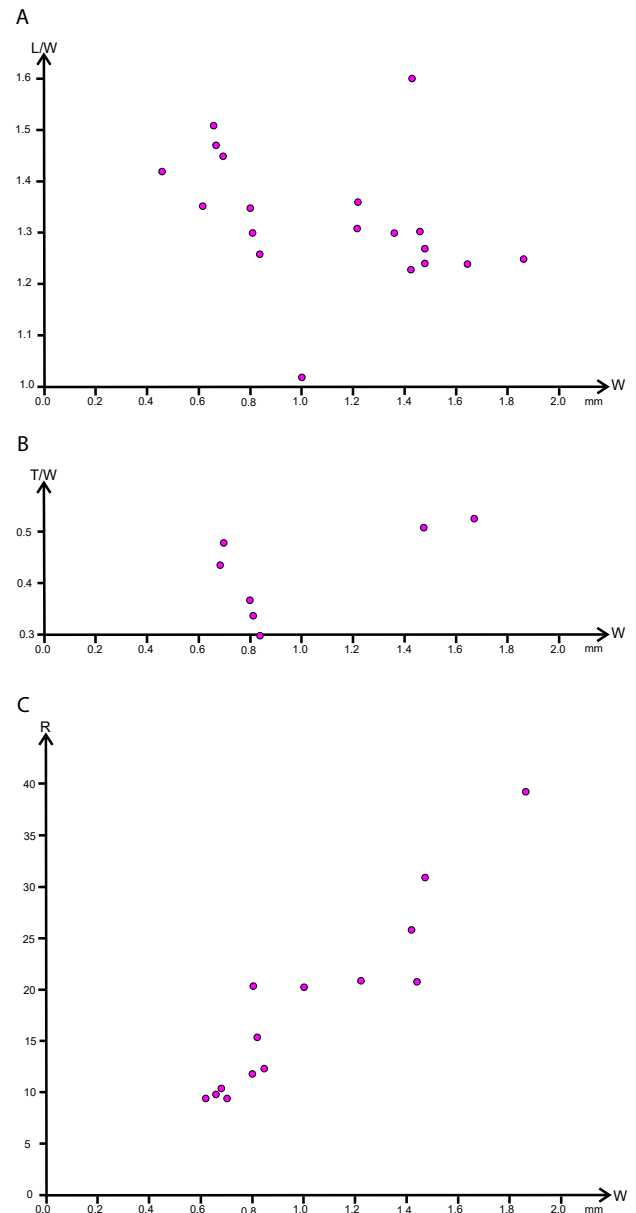


Fig. 67. *Rugia acutirostris* Steinich, 1965. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Upper lower Maastrichtian, Møns Klint (Fig. 2).

deltidial plates. The pedicle collar is very long. The hinge is similar to species of *Terebratulina* and to that of *Rugia tenuicostata*.

R. acutirostris has a well-developed spicular skeleton, which is mainly recrystallized. The adult lophophore is a plectolophe. The filaments also possess a strong spicular skeleton. The species is characterized by its pointed oval outline, the strongly pointed beak and the small foramen. It differs from *Rugia stenius* n. sp. by the significantly higher number of costellae.

Material. Falster. Gedser Fyr: 3; Gedser Odde: 4.

Jylland. Dania: 5; Nye Kløv: 5 (Johansen 1987).
Møn. Hvide klint: 27; Hvidskud: 292; Hundefangs-
klint: 99; Lille Bissinge: 4; Sommerspiret: 42.
Sjælland. Karlstrup: 15; Kongsted: 18; Stevns Klint: 8.

Chronostratigraphy in Denmark. Lower Maastrichtian, *acutirostris-spinosa* to *pulchellus-pulchellus* Zones. Outside Denmark it has been found in eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1965) and Krons Moor (Surlyk 1982, 1984) in northern Germany and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1970a, 1972, 1982, 1984), Johansen (1987), Johansen & Surlyk (1990).

***Rugia stenius* n. sp.**

Figs 68, 69

Derivation of name. After the eminent preparator and photographer of fossils Sten Lennart Jakobsen.
Type locality: Karlstrup (1 in Fig. 2).

Type horizon. Sample Karlstrup 2, about 4 m below the Maastrichtian–Danian boundary (Fig. 5B).

Stratigraphy. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone.

Holotype. Fig. 68A. Sample Karlstrup 2.

Paratypes: Fig. 68, B–D. Sample Karlstrup 2.

Measurements of the holotype. Length of ventral valve: 1.6 mm. Length of dorsal valve 1.3 mm. Width at midline: 1.3 mm. Width of hinge line: 0.71 mm. Thickness: less than 0.3 mm. Length of foramen: 0.19 mm. Width of foramen: 0.12 mm. Number of costae/costellae: 18

Diagnosis. A small *Rugia* (see Steinich, 1965, p. 115). Up to 19 costellae with a sculpture of small tubercles. Costellae wider during growth. Only few short new costellae formed by intercalation.

Description. This micromorphic species is one of the smallest brachiopods in the Maastrichtian chalk of Denmark. It rarely reaches a length of more than about 1.8 mm and a width of about 1.6 mm. The outline of small specimens is subpentagonal but changes gradually to pointed elongate ovate. It is longer than wide throughout growth, but this reflects the presence of the elongate pointed beak. The shell is thin and ventribiconvex, the dorsal valve being less inflated than the ventral valve. The ears are relatively small. About 8 costae are already formed at W=0.6 mm. New costae are added at the ears laterally to

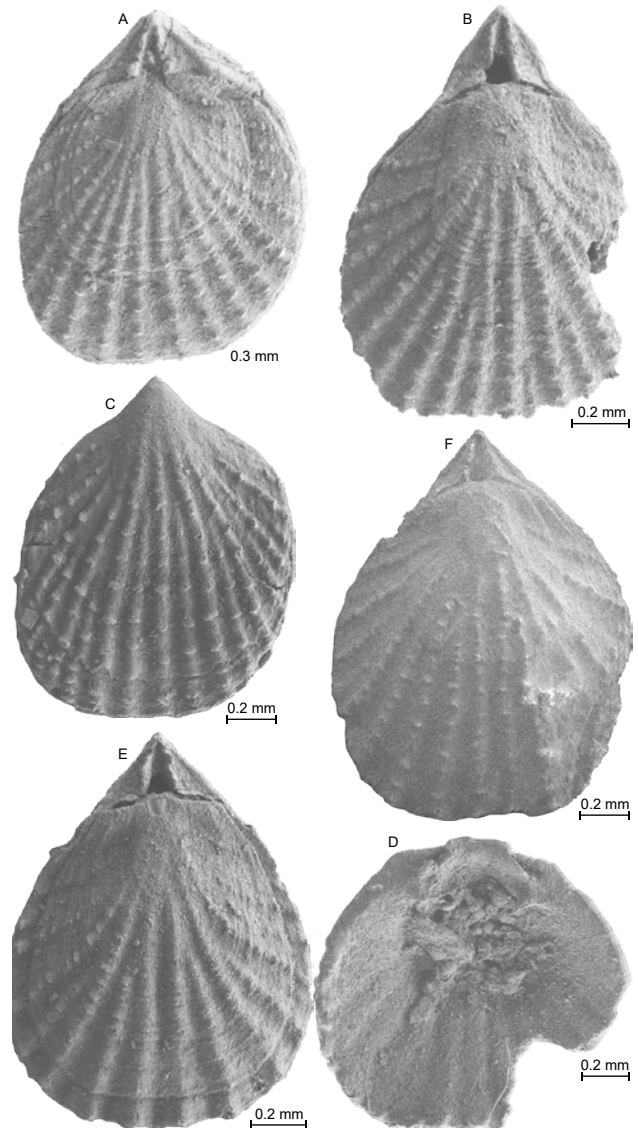


Fig. 68. *Rugia stenius* n. sp. A. Holotype. B, C, E, F. Paratypes. D. Dorsal valve, inside view. Sample Karlstrup 2. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. All specimens from sample Karlstrup 2, Karlstrup (Figs 2, 5B).

the first formed and only a few short new costellae are added by intercalation during growth. The highest observed number of costellae is 19 in the holotype. The costae do not branch but become gradually wider during growth. The costae are low, rounded in cross section and may have a sculpture of small tubercles. It is commonly difficult to distinguish between new costae or costellae and irregular short lines of tubercles. This is the case both for new costae formed at the ears and for new costellae formed by intercalation, and it is sometimes a matter of decision if such short rows of tubercles should be counted as costae or not. The morphology of the hinge and brachidium is similar to those seen in the other species

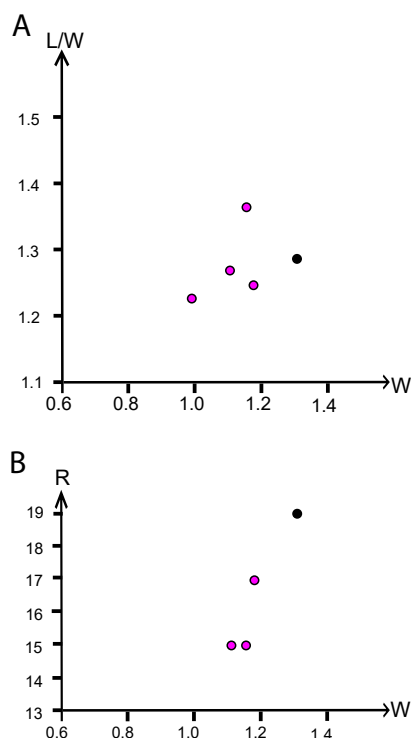


Fig. 69. *Rugia stenius* n. sp. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Sample Karlstrup 2. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Karlstrup (Figs 2, 5B).

of *Rugia*.

Rugia stenius n. sp. differs from its close relative and predecessor *Rugia acutirostris* Steinich, 1965 in the significantly lower number of costellae and its distinctive outline.

Material. Sjælland. Karlstrup: K 2: 12 ind.; K 4: 1 ind.; Karlstrup 'no number': 6 ind. Stevns Klint: S 1: 2 ind.; S 3: 6 ind. Jylland. Dania: D 5: 2 ind.; D 8: 2 ind.; D 12: 3 ind.

Chronostratigraphy in Denmark. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. The species has not been recorded outside Denmark. *Rugia acutirostris* had its last occurrence in the upper lower Maastrichtian *pulchellus-pulchellus* Zone and is missing in the *pulchellus-tenuicostata*, *tenuicostata-semiglobularis*, *semiglobularis-humboldtii* and *humboldtii-stevensis* Zones only to return as *Rugia stenius* n. sp. in the uppermost Maastrichtian *stevensis-chitoniformis* Zone. This is a nice example of phyletic speciation similar to what is seen the *Isocrania costata*–*Isocrania sendeni* lineage (Surlyk 1973; Simon 2007; this study).

Rugia tegulata Surlyk, 1970

Figs 70, 71, 72

R. tegulata is micromorphic. The outline is subtriangular to pointed oval. The maximum width lies anterior to the midline of the shell. The L/W varies between 1.28 and 1.63, decreasing rapidly with growth. Blunt ears are present. The shell is rather thick, slightly bi-convex and the dorsal valve is a little less convex than the ventral valve. Five costae are formed at W=0.5 mm and the number increases rapidly by intercalation to about 20. This takes place very irregularly so that the relation between number of costellae and width varies considerably. The costellae are very strongly sculptured with transverse plate-like scales arranged like roof tiles. They are as wide as the costellae, point anteriorly, and form an angle of about 50° with the shell surface. There are 3–4 growth lines.

The beak is suberect and the area is small. The foramen is triangular, hypothyrid and laterally limited by deltidial plates, which commonly take shape of two irregular ridges. There is, in addition, a constriction at the middle of each deltidial plate. The inner socket ridges are short but strong. Crura are long and thin like in the other species of *Rugia* and arise from the anterior edge of the ridges. A fully developed brachidium was found in only a few specimens due to the limited material. The descending branches converge rapidly to fuse into a strong bridge. The ascending branches are very short and blunt.

R. tegulata has a very strong spicular skeleton, which develops during ontogeny from a schizolophe to a zygalophe. The adult lophophore seems to have been a plectolophe. The spicular skeletons of the filaments are long and the brachial lip is strongly devel-

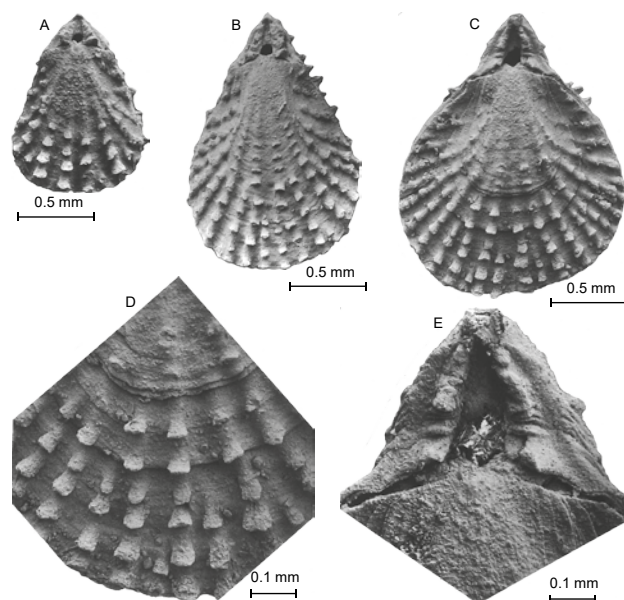


Fig. 70. *Rugia tegulata* Surlyk, 1970. A–C. Growth stages. C. Dorsal view of the holotype. D. Details of the scale-like tubercles of the costellae. E. Details of the foramen and deltidial plates. Lower upper Maastrichtian, *semiglobularis-humboldtii* Zone. Lindholm (19 in Fig. 2).

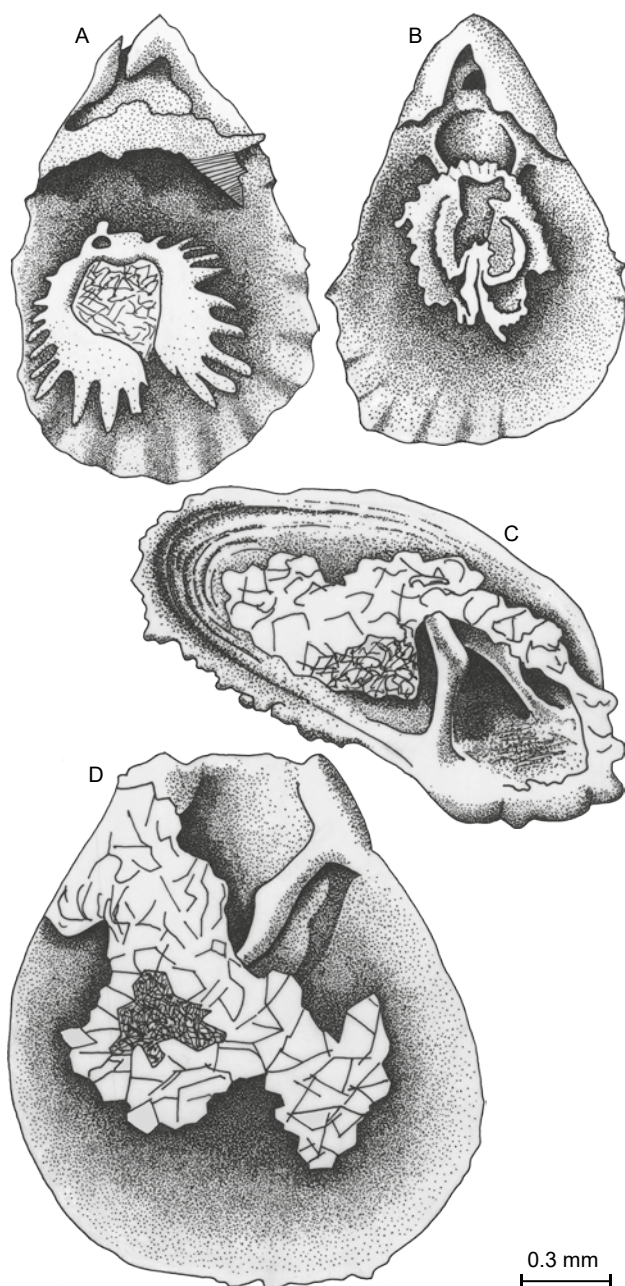


Fig. 71. *Rugia tegulata* Surlyk, 1970. **A, B.** Schizolophous lophophore in dorsal view. **C, D.** Brachidium and strongly recrystallized spicular skeleton of lophophore. Lindholm (16 in Fig. 2).

oped.

R. tegulata can be distinguished from other species of *Rugia* and *Terebratulina* by the sculpture of the costellae consisting of platy, transverse scales.

Material. Jylland. Danmark: 6; Lindholm: 35; Nørre Sundby: 2; Rørdal: 10 (Lauridsen & Surlyk 2008). Møn. Sættepileklint: 3.

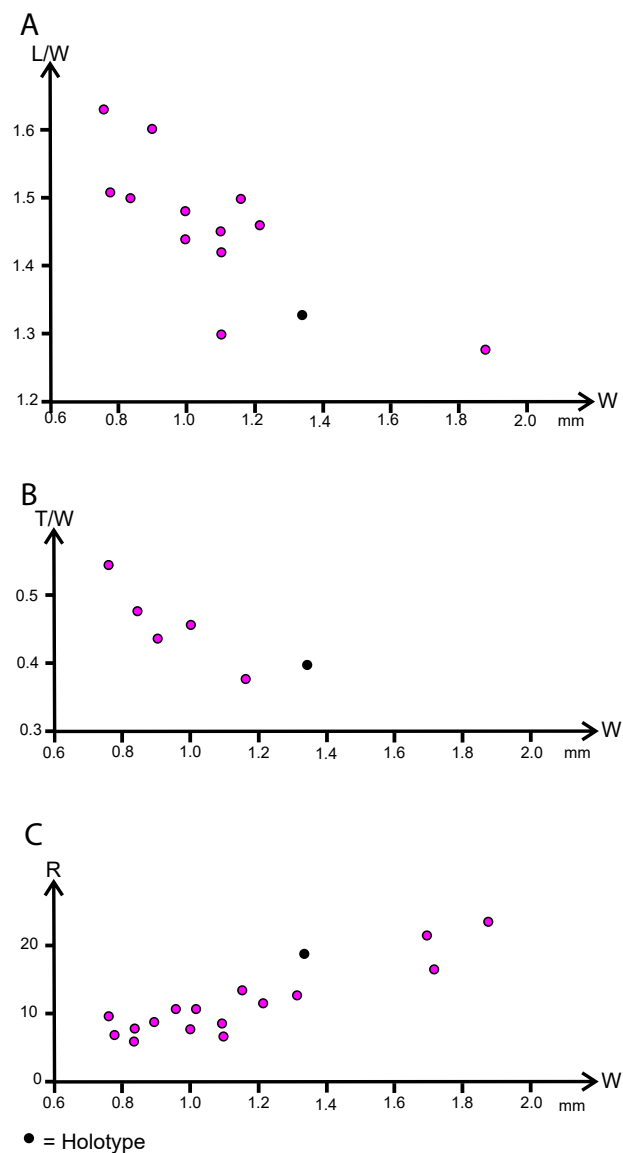


Fig. 72. *Rugia tegulata* Surlyk, 1970. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Lindholm (19 in Fig. 2).

Chronostratigraphy in Denmark. Upper lower Maas-trichtian – lower upper Maas-trichtian, corresponding to the upper part of the *pulchellus–tenuicostata* Zone and the *semiglobularis–humboldtii* Zone (Surlyk 1970b, 1984; Surlyk *et al.* 2013). Outside Denmark *R. tegulata* is known from Hemmoor (Sample Hemmoor 937, Surlyk & Schröder unpublished data) in northern Germany, and Norfolk in eastern England (Johansen & Surlyk 1990)

Pertinent references. Surlyk (1970b, 1984), Johansen & Surlyk (1990), Lauridsen & Surlyk (2008).

***Rugia spinosa* Surlyk, 1970**
Figs 73, 74, 75

R. spinosa is micromorphic. The outline is pointed ovate. The L/W varies between 1.04 and 1.33. The greatest width lies anterior to the midline of the shell. Stumpy, blunt ears are present. The shell is strongly biconvex. The anterior commissure is rectimarginate. The shell is thin. The characteristic sculpture consists of long, solid, cylindrical, pointed spines. They are irregularly distributed all over the surface of the shell and have variable form and size. On the posterior part of the shell the spines tend to stand at a right angle to the surface of the shell, while they are directed forwards and are larger on the anterior part. The large spines commonly begin as an irregular, plain rib, which later breaks away abruptly and extends as a spine. The spines may be arranged in rows as a sort of extended granules on an indistinct rib. The ribs are very few in numbers, mainly 1–8, are irregularly distributed and may be seen on the inside of the shell as strong, plain ribs.

The beak is very short and suberect and the area is narrow and indistinct. The deltidial plates are narrow and triangular and the foramen is very small and submesothyrid. The hinge is similar to the hinge in the other species of *Rugia*. The inner socket ridges are closely spaced and very short with an antero-lateral bend. A cardinal process is present only in the largest specimens and is small, rounded and does not extend as far as the posterior part of the inner socket ridges. The posterior part of the socket ridges and cardinal process together protrude beyond the posterior edge of the shell. The teeth are short, triangular, and pointed. The shape of the brachidium is similar to that of *Rugia tenuicostata*. Crura are long, thin and cylindrical, originating from a position anterior to the inner socket ridges. They are directed forward and medially at an angle of about 45° to the median plane of the shell. Spicules have not been observed.

Material. Falster. Gedser Odde: 7; Gedser Fyr: 17. Jylland. Rørdal-1, 85–96 m depth: 6. Møn. Hvide Klint: 3.

Chronostratigraphy in Denmark. Lowermost Maas-trichtian, *spinosa*–*subtilis* Zone. Outside Denmark *R. spinosa* is known from Krons Moor in northern Germany (Surlyk 1982) and from Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Surlyk (1970b, 1982, 1984); Johansen & Surlyk (1990).

Subfamily Draciinae Steinich, 1967

Genus *Dracius* Steinich, 1967

Type species *Dracius carnifex* Steinich, 1967

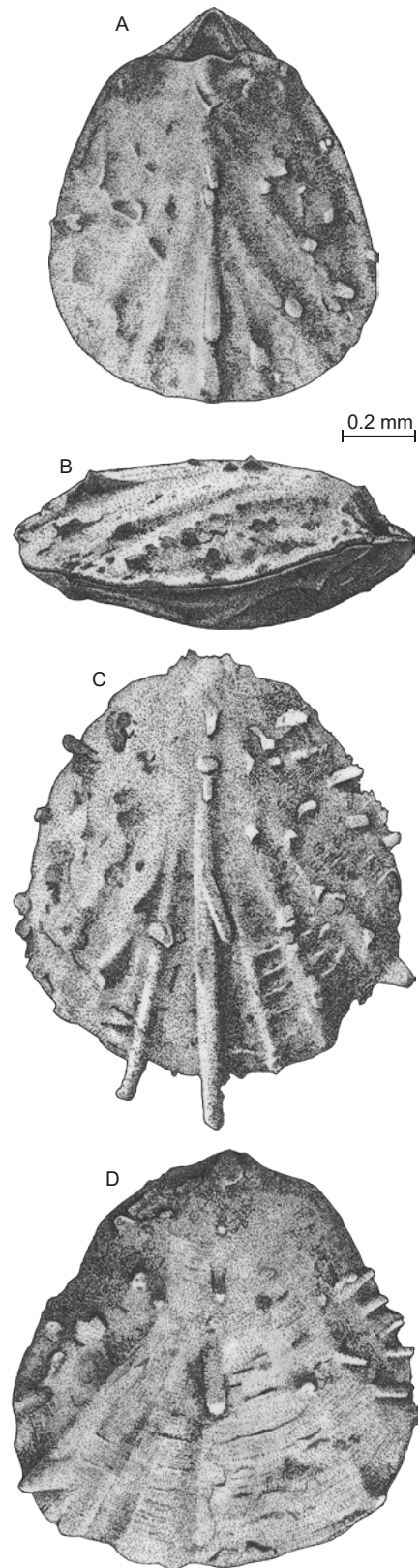


Fig. 73. *Rugia spinosa* Surlyk, 1970. **A, B.** Dorsal and slightly oblique lateral views of holotype, respectively. **C, D.** Dorsal valves. Lower lower Maastrichtian, *spinosa*–*subtilis* Zone, Gedser Fyr (Fig. 2).

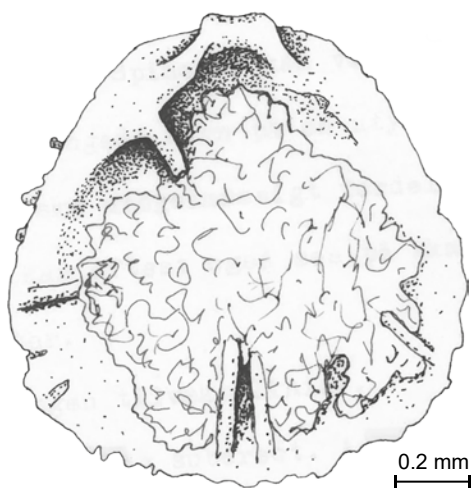


Fig. 74. *Rugia spinosa* Surlyk, 1970. Internal view of dorsal valve, showing internal ribs. Lower lower Maastrichtian, *spinosa-subtilis* Zone, Gedser Fyr (Fig. 2).

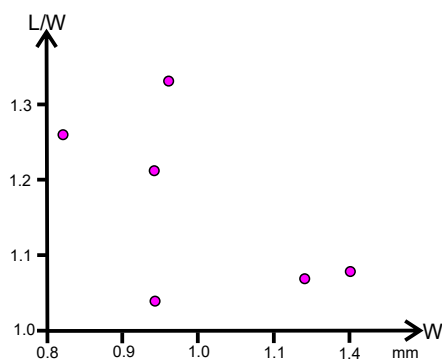


Fig. 75. *Rugia spinosa* Surlyk, 1970. Scatter diagram. L=length, W=width.

Dracius carnifex Steinich, 1967 Figs 76, 77, 78

D. carnifex is micromorphic. The outline is oval to subpentagonal, but all specimens show more or less strong irregularities in shape. Small specimens are always longer than wide but the shape changes during growth to become more circular. The shell is planoconvex to weakly concavoconvex. The anterior commissure is rectimarginate in the most regular forms. The dorsal valve is always smooth, whereas the ventral valve has numerous, rather strongly developed radial costellae. At $W=0.5$ mm 7–8 costae are formed, at the start as irregular rows of small tubercles. The number increases by intercalation during growth to about 35. The tubercles are irregularly grained, small, and commonly thorn-like. The areas between the costellae increases relatively during growth to become 2–3 times as wide as the costellae.

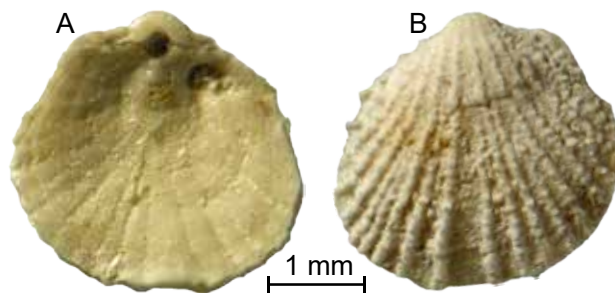


Fig. 76. *Dracius carnifex* Steinich, 1967. A. Dorsal view. Note the weak, irregular costellae. B. Same specimen in ventral view. Note the irregular, knobbed costae and intercalated costellae. Lower Maastrichtian. Møns Klint (Fig. 2).

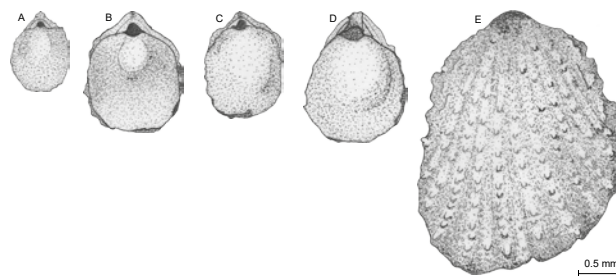


Fig. 77. *Dracius carnifex* Steinich, 1967. A–E. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

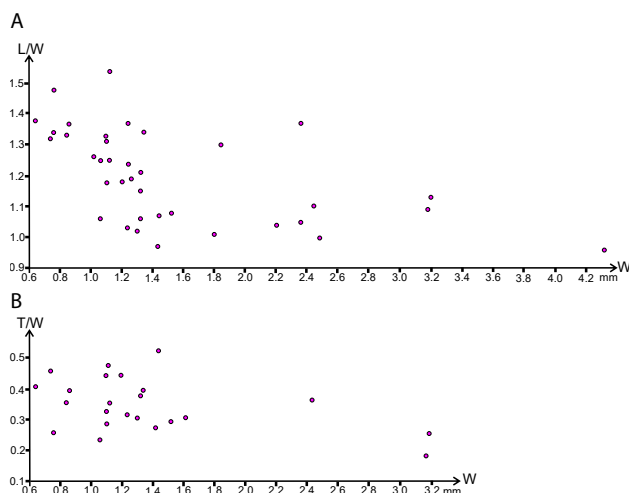


Fig. 78. *Dracius carnifex* Steinich, 1967. Scatter diagrams. L=length, W=width, T=thickness.

The beak is short and suberect and the area is small. The foramen is already in small forms delimited by a ridge formed where the two deltidial plates meet. During growth the foramen is indented into the dorsal valve but without any resorption of the valve. At $W>3.5$ –4 mm the part of the foramen located in the dorsal valve is larger than that in the ventral valve. The hinge is not strongly developed. The teeth are flattened and somewhat dorsally curved. An almost

fully developed brachidium is present already at $W=0.7$ mm. The crura are strong and extend from the bases of the inner socket furrows. They are directed antero-ventrally, have short ascending branches and a transverse band is developed at about $W=1.7$ mm. The internal part of the shell is smooth. The well-developed spicular skeleton is commonly recrystallized but the adult lophophore seems to have been an early plectolophe.

Material. Jylland. Eerslev: 2; Ferslev: 1; Rørdal: 4.
Møn. Hvide Klint: 2; Hvidskud: 110; Hundefangsklint: 10; Store Taler: 1.
Sjælland. Karlstrup: 2; Stevns Klint 2.

Chronostratigraphy in Denmark. Lower Maastrichtian, *spinosa-acutirostris* to *pulchellus-tenuicostata* Zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark, *D. carnifex* is known from Rügen (Steinich 1967) and Krons Moor (Surlyk 1982) in northern Germany and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1967), Surlyk (1982), Johansen & Surlyk (1990).

Superfamily Kingenoidea Elliott, 1948

Family Kingenidae Elliott, 1948

Subfamily Kingeninae Elliott, 1948

Genus *Kingena* Davidson, 1852

Type species *Kingena lima* Defrance, 1828

***Kingena pentangulata* (Woodward, 1833)**

Figs 79, 80, 81, 82

K. pentangulata is small to medium-sized. The outline at $W<1$ mm is pointed oval, during growth it changes to subtriangular, and becomes circular to subpentagonal at $W>3$ mm. It has a very thin shell and is accordingly almost always deformed. The L/W decreases rapidly during growth from 1.02–1.31 to 0.92–1.13. The largest width lies anterior to the shell midline in young specimens and close to the midline in adults. Small specimens are weakly biconvex to almost planoconvex. Specimens at $W>3$ mm are uniformly biconvex. The hinge margin is almost straight and passes evenly into the lateral shell margins. The anterior commissure is rectimarginate. The shell has an ornamentation of closely spaced, regular, cone-shaped to elongate tubercles with a length 2–3 times the diameter. The umbonal part of the dorsal valve is, however, always smooth. The beak is almost straight to suberect in small specimens but changes to suberect at $W>2$ mm and is almost erect in very large specimens. The area is wide and sharply delimited.

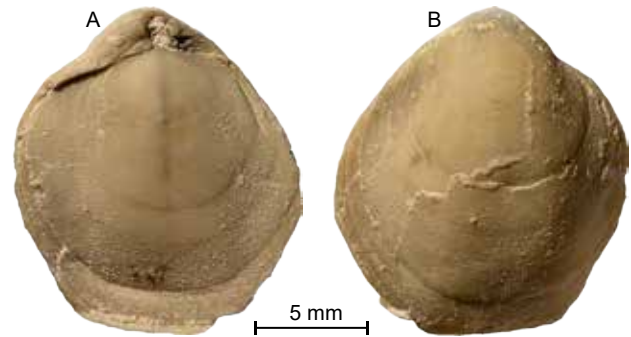


Fig. 79. *Kingena pentangulata* (Woodward, 1833). A. Dorsal view. B. Same specimen in ventral view. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

The foramen is large and trapezoidal at $W<4$ –6 mm and submesothyrid. At $W>6$ mm it becomes gradually more indented into the ventral valve and becomes permesothyrid associated with increasing incurving of the beak. The foramen is laterally delimited by relatively wide, triangular deltidial plates. The teeth are strong, pointed, and backwards curved. Larger specimens have a well-developed hinge plate that is connected to a median septum which begins to form at $W=0.8$ –1 mm. At $W=1.5$ mm two pointed, anteriorly directed branches are formed at the top of the anterior front of the septum. Simultaneously, two short crura are formed and the descending, strongly diverging branches extend at a marked break from the ends of the crura. In a deformed specimen with $W=1$ cm a posteriorly directed loop extends from the front of the septum (Fig. 81).

Fragments of *K. pentangulata* resembles fragments of *A. inusitata* Steinich, 1968, which is very common in the Danish Maastrichtian, and older records of *Kingena lima* (Defrance, 1828) by Posselt (1894, p. 47) and Nielsen (1909, p. 170) may actually be fragments of *A. inusitata*.

Material. Falster. Gedser Fyr: 2; Gedser Odde: 8.

Jylland: Ferslev: 2; Gudumholm: 1; Hillerslev 2; Lindholm: 4; Linds: 2; Rørdal: 8.

Møn. Hvide Klint: 12; Hvidskud: 27; Hundefangsklint: 6.

Sjælland. Stevns Klint: 1.

Outside Denmark *K. pentangulata* is known from eastern Poland (Popiel-Barczyk 1984), Belgium (Simon 2000), Norfolk in eastern England (Johansen & Surlyk 1990),

Chronostratigraphy in Denmark. Lower Maastrichtian, *longicollis-jasmundi* to *pulchellus-pulchellus* Zones and uppermost part of the lower Maastrichtian to the Cretaceous–Palaeogene boundary, *tenuicostata-semiglobularis* to *stevensi-chitoniformis* Zones (Surlyk 1984; Surlyk *et al.* 2013).

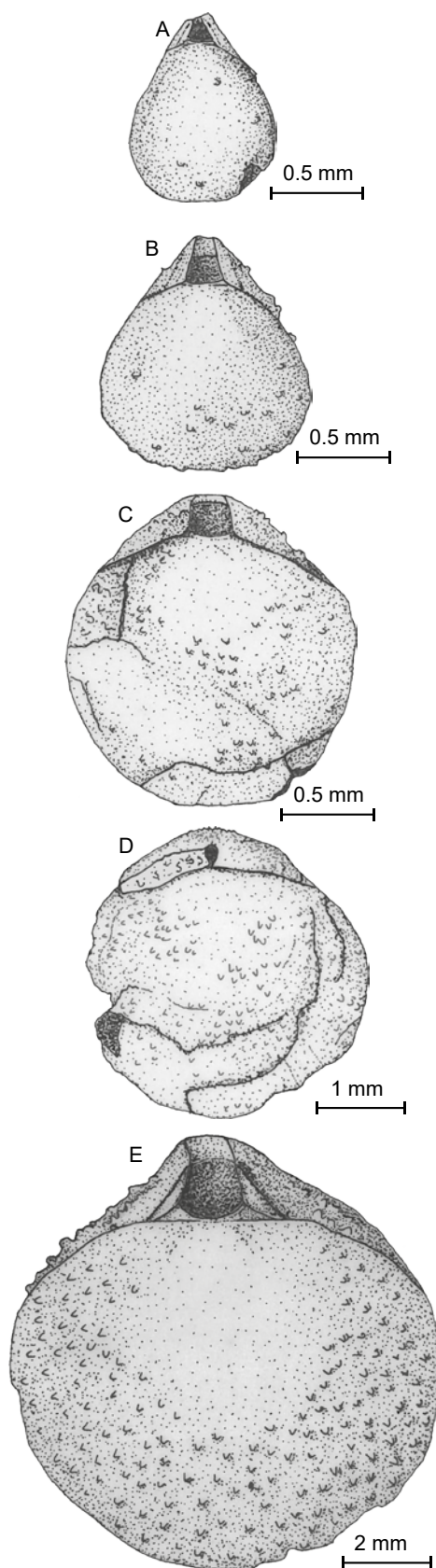


Fig. 80. *Kingena pentangulata* (Woodward, 1833). A–E. Growth stages. Lower Maastrichtian, Møns Klint (Fig. 2).

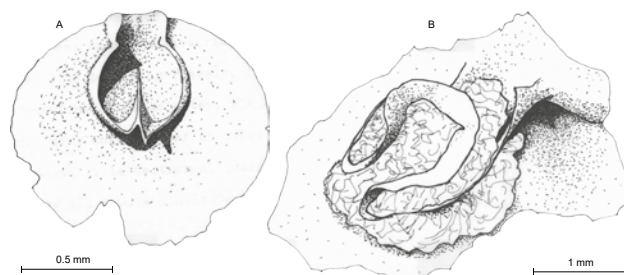


Fig. 81. *Kingena pentangulata* (Woodward, 1833). Details of septum and brachidium in juvenile (A) and adult (B) specimens. Lower upper Maastrichtian, Lindholm (Fig. 2).

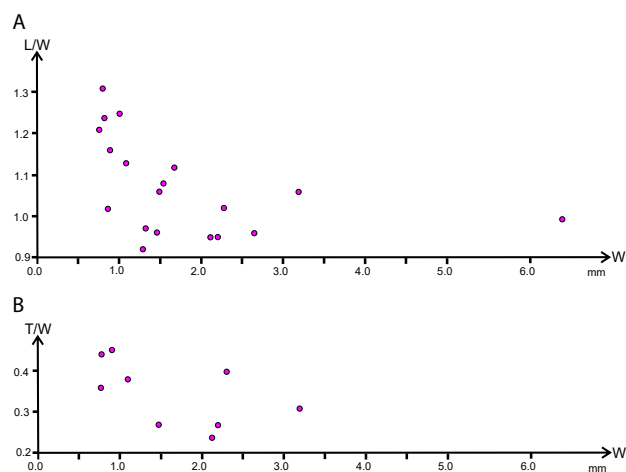


Fig. 82. *Kingena pentangulata* (Woodward, 1833). Scatter diagrams. L=length, W=width, T=thickness.

Pertinent references. Surlyk (1969, 1984), Owen (1970), Johansen & Surlyk (1990), Simon (2000).

Superfamily Laqueoidea Thomson, 1927

Subfamily Dalligadinae MacKinnon & Lee, 2006

Genus *Dalligas* Steinich, 1968

Type species *Dalligas nobilis* Steinich, 1968

***Dalligas nobilis* Steinich, 1968**

Figs 83, 84

D. nobilis is micromorphic. The investigated material comprises 10 dorsal valves, only three of which are undeformed. The outline of the shell is elongate ovate in small specimens but rapidly changes to subcircular. The greatest width lies at the midline of the shell in large specimens. The valve is weakly biconvex with an almost plane dorsal valve and a rectimarginate anterior commissure. The shell is thin. The greatest width is at the shell midline. Small

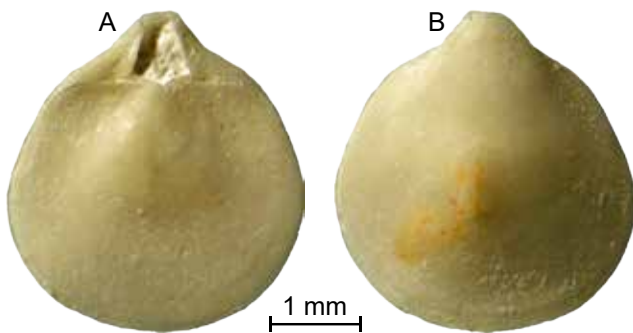


Fig. 83. *Dalligas nobilis* Steinich, 1968. A. Dorsal view. Note the straight hinge line and large truncated triangular foramen. B. Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

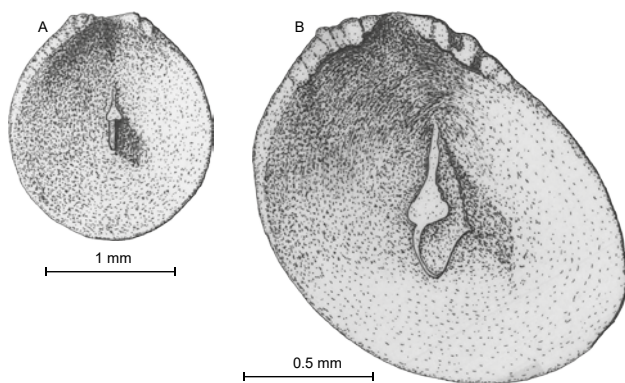


Fig. 84. *Dalligas nobilis* Steinich, 1968. A, B. Internal views of inner side of dorsal valve, showing details of the dorsal median septum. Lower upper Maastrichtian. Gudumholm (Fig. 2).

specimens have a smooth surface. The dorsal valves of specimens at $W > 3$ mm may possess weak radial ribs, whereas the ventral valve may have more than 40 flat, slightly tuberculate costellae. There are few but rather strong growth lines on large specimens. The beak is weakly suberect. The width of the area increases during growth. The foramen is relatively large, elongate triangular and hypothryid. It is delimited by deltidial plates and does not extend into the dorsal valve. The inner socket ridges are very short and there is no cardinal process. The median septum has a steep anterior margin and a slightly incurved posterior margin from where two short stump triangular ascending branches extend. Crura and descending branches are completely missing.

D. nobilis is very difficult to distinguish from juvenile specimens of *Magas chitoniformis* and *Scumulus inopinatus* Steinich, 1968. It differs from the former in having a poorly developed brachidium, and in the weak radial ribs developed at $W > 3$ mm. This is never the case at *M. chitoniformis* (von Schlotheim, 1813), which also differs in the strongly punctate shell. It differs from *S. inopinatus*, which commonly has a

more irregular outline than *D. nobilis* Steinich, 1968, and in having a hypothryid foramen.

Material. Jylland. Gudumholm: 5; Lindholm: 4; Nye Kløv: 20 (Johansen 1987); Rørdal: 1.

Outside Denmark, the species has been recorded from Rügen in northern Germany (Steinich 1968b) and Norfolk in eastern England (Johansen & Surlyk 1990).

Chronostratigraphy in Denmark. Uppermost lower Maastrichtian – lower upper Maastrichtian, *tenuicostata*–*semiglobularis* and *semiglobularis*–*humboldtii* brachiopod Zones (Surlyk 1984; Surlyk *et al.* 2013).

Pertinent references. Steinich (1968b), Johansen & Surlyk (1990).

Subfamily Gemmarculinae Elliott, 1947

Genus *Ruegenella* Owen, 1977

Type species *Ruegenella humboldtii* (von Hagenow, 1842)

Ruegenella humboldtii (von Hagenow, 1842)

Figs 85, 86, 87

This is one out of quite a few of the brachiopods in the Danish chalk which has been referred to a new genus (Owen 1977) since the works on the brachiopods from Rügen (Steinich 1965) and Denmark (Surlyk 1969, 1972) who referred the species to *Gemmarcula*. I do not consider the erection of a new genus for this species necessary but have followed it since the two genera show some easily recognizable, but not necessarily significant differences in external morphology.

R. humboldtii is medium-sized. The outline of the shell is triangular to subtriangular and specimens at $W = 1.00$ m are clearly elongate. The outline of the dorsal valve is trapezoidal. The greatest width lies at the anterior margin of the shell but moves closer to the shell midline during growth. Young specimens are

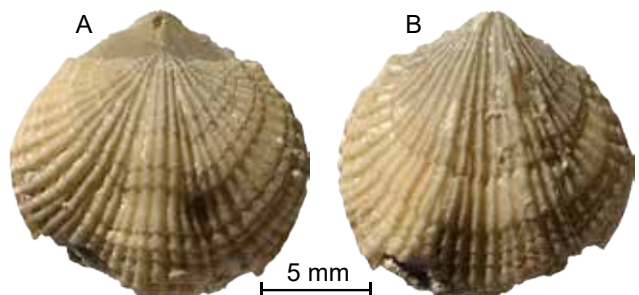


Fig. 85. *Ruegenella humboldtii* (von Hagenow, 1842). A. Dorsal view. B. Same specimen in ventral view. Upper upper Maastrichtian. Kulsti Rende, Stevns Klint (Figs 2, 6).

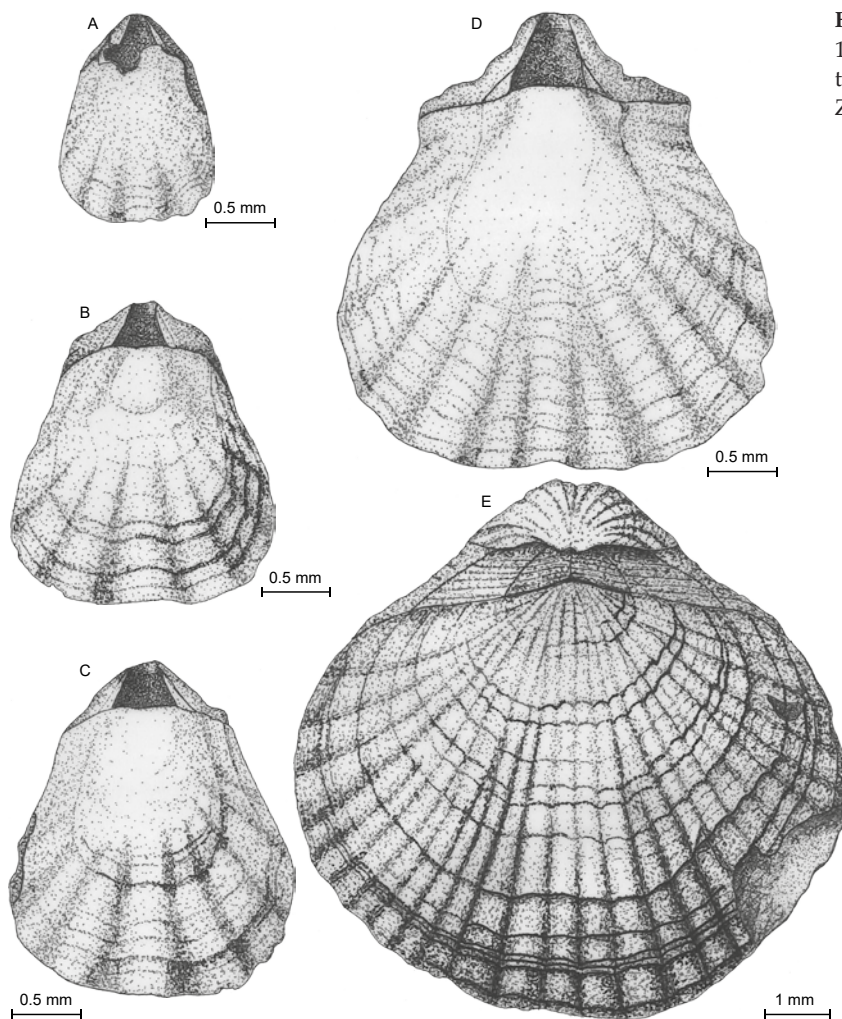


Fig. 86. *Ruedgenella humboldtii* (von Hagenow, 1842). **A–E.** Growth Stages. Upper upper Maas-trichtian, *stevensis*–*chitoniformis* brachiopod Zone. Stevns Klint (Fig. 2).

rather flat but changes to strongly biconvex during growth. The dorsal valve is always flatter than the ventral. Two diverging furrows appear in the dorsal valve at $W=2.5\text{--}3\text{ mm}$. They become deeper during growth and subdivides the valve into three equally inflated parts. In the ventral valve, the two furrows correspond to two folds. The anterior commissure is broadly biplicate. 4–7 costae are formed at $W=0.7\text{--}0.8\text{ mm}$. They are wide, flat and rapidly become stronger. The median costae start to split at $W=1.2\text{--}1.7\text{ mm}$. The costellae do not split dichotomously but start as subordinate lateral branches on the primary costae. The costellae are mainly straight and increase in numbers to 32–50. They are rounded in cross section and have a sculpture of very low transverse rings. There are numerous well-defined growth lines.

The beak is short and suberect in small specimens. The area is initially small, planar and sharply delimited and becomes relatively stronger and slightly concave during growth. The initially large, triangular foramen is delimited by two narrow deltidial plates below $W=3.0\text{ mm}$. these become collar-like during

growth and fuse medially. The pedicle collar is very long in small specimens. The foramen is submesothryd and circular in fully grown specimens. Development of the brachidium starts at $W=0.8\text{--}1.0\text{ mm}$ with the formation of a high median septum and ascending branches of the crura. The later ontogenetic development is well described by Steinich (1965, p. 163–169) to which the reader is referred as the present material mainly comprises young specimens below $W=2\text{ mm}$.

Material. Jylland. Nørre Flødal: 1; Linds: 1; Ellidshøj: 1.
Sjælland. Karlstrup: 8; Stevns Klint: 3.

Chronostratigraphy in Denmark. Upper Maastrichtian, *humboldtii*–*stevensis* and *stevensis*–*chitoniformis* Zones.

Pertinent references. Steinich (1965), Surlyk (1984).

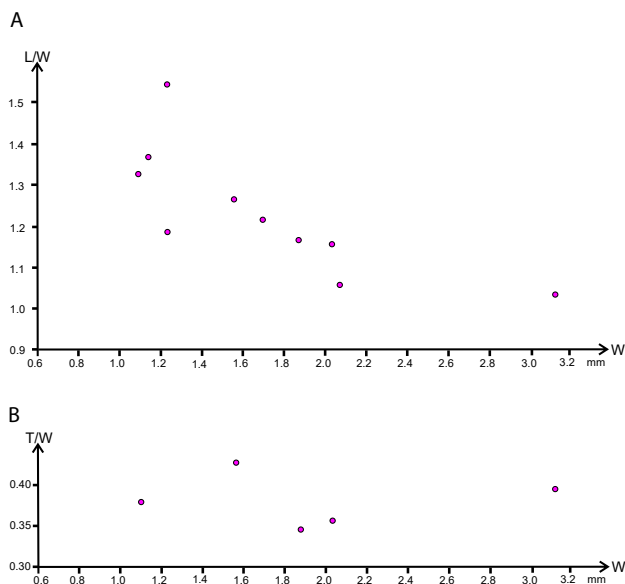


Fig. 87. *Ruegenella humboldtii* (von Hagenow, 1842). Scatter diagrams. L=length, W=width, T=thickness.

Ruegenella sp. Fig. 88

A single juvenile specimen referred to *Ruegenella* was found in Rørdal-1, core 70, depth 79.80–80.02 m. It has the following dimensions: L: 2.20 mm; LD: 1.80 mm; W: 2.08 mm; number of costae: 16. It deviates from *R. humboldtii* in its relatively larger L/W of 1.06, LD/W=0.75 (LD= length of dorsal valve), its relatively wider hinge line and in particular in the larger number of costae at this small stage. It may represent a new species of *Ruegenella*, but the material is too limited to allow this to be evaluated. However, its strati-

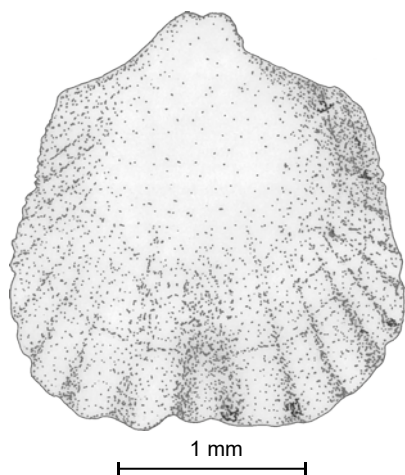


Fig. 88. *Ruegenella* sp. Rørdal-1, core 1. Ventral valve. Note the relatively large number of costae and greater width at hinge line compared to specimens of *Ruegenella humboldtii* of the same size. Rørdal (Fig. 2).

graphic occurrence in the lowermost Maastrichtian well below the upper Maastrichtian occurrence of *R. humboldtii* supports the hypothesis that it represents a new species and finds of *Ruegenella* elsewhere in the Campanian–Maastrichtian boundary strata should be carefully compared with *R. humboldtii* from the upper Maastrichtian.

Chronostratigraphy in Denmark. Lowermost Maastrichtian, *spinosa–subtilis* Zone (Surlyk 1984; Surlyk et al. 2013).

Pertinent references. Surlyk (1969, 1984).

Subfamily Trigonoseminae Elliott, 1965

Genus *Trigonosemus* König, 1825

Type species *Trigonosemus elegans* König, 1825

Trigonosemus pulchellus (Nilsson, 1827)

Figs 89, 90, 91

T. pulchellus is medium sized. The investigated material mainly comprises juvenile specimens $W < 2\text{--}3$ mm. The later ontogenetic evolution is well described by Steinich (1965) and the ontogenetic stages were illustrated by Surlyk (1972, fig. 10). The outline of very small specimens is strongly elongate and more or less pointed ovate but is circular to subpentagonal in adult forms. The shell is biconvex at $W = 0.6\text{--}0.8$ mm, where after it becomes planoconvex. A broad dorsal sinus is formed at $W = 2\text{--}3$ mm and is reflected in the ventral valve as a stump, median keel. However, the sinus is not formed in all specimens. The shell becomes rather thick during growth. The number of strong radial costellae increases by intercalation from 2–4 at $W = 0.6\text{--}0.7$ mm to 20–25 in large specimens. They are initially very irregular, but their width does not increase after $W = 3\text{--}5$ mm. There are numerous

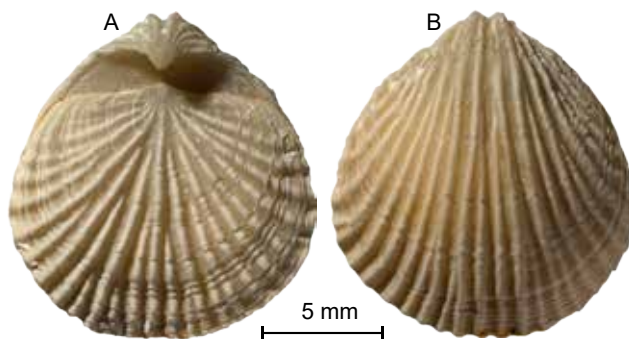


Fig. 89. *Trigonosemus pulchellus* (Nilsson, 1827). **A.** Dorsal view. Note the incurved rostrum, the closed foramen, and the strong, laterally curved costellae where new ones are added by intercalation. **B.** Same specimen in ventral view. Upper lower Maastrichtian, *pulchellus–pulchellus* Zone. Møns Klint (Fig. 2).

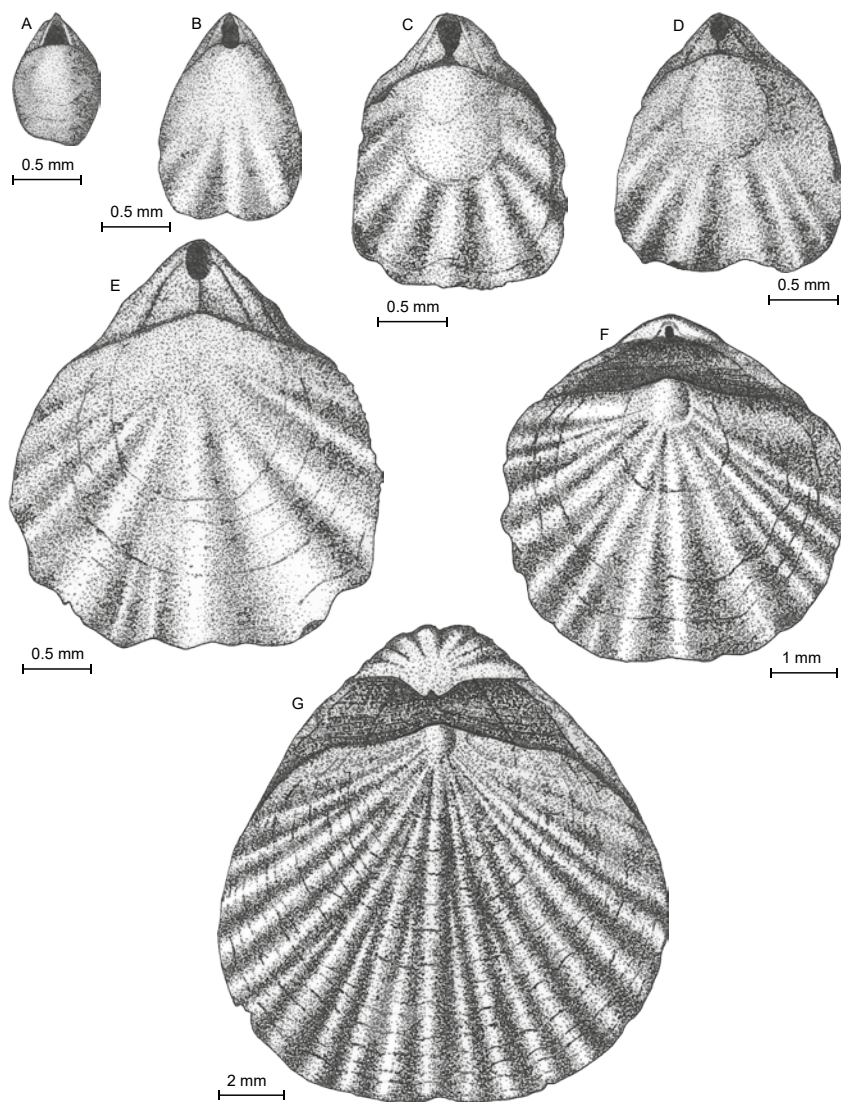


Fig. 90. *Trigonosemus pulchellus* (Nilsson, 1827). A–G. Growth stages. Upper lower Maastrichtian, *pulchellus*–*pulchellus* Zone. Hvidskud, Møns Klint (Figs 2, 4).

densely spaced growth lines. The beak is pointed and suberect in young specimens but becomes strongly incurved during growth. The area which in the early stages is very small and sharply delimited becomes concave following increasing curvature of the beak. The foramen is in very small specimens delimited by two narrow elongated triangular deltidial plates. They become fused at $W=2.0$ – 2.5 mm and the foramen becomes restricted to the ventral valve, which in adults is circular, and permesothyrid. The hinge is very strongly developed in adult specimens. The sockets are deep and the teeth are stump and already in early stages supported by strong tooth plates. A brachidium is not yet formed in specimens at $W<0.6$ – 0.7 mm. At $W=1$ mm two lamellae are formed laterally from a low median ridge. They become fused and forms a high, rectangular median septum. The descending branches are formed at $W=1.4$ – 1.5 mm and two lateral plates are at the same time developed on the posterior edge of the median septum. They form

a coherent oval plate at $W=2.0$ – 2.5 mm. The anterior margin of the septum is split into two flanges at $W=2$ mm and the descending branches fuse with the septum at $W=3$ mm. The crural processes are short, pointed and slightly posterior at this point. The foramen becomes completely filled with shell material during growth and thus did not support a functional pedicle. The later stages are described in detail by Steinich (1965).

Adult specimens of *T. pulchellus* have in some cases been confused with *Ruegenella humboldtii* but the resemblance is only superficial. *T. pulchellus* has a dorsal median sinus, whereas *R. humboldtii* has a median dorsal ridge laterally delimited by two furrows. Specimens $W<0.6$ mm where costellae have not yet been formed are difficult to distinguish from some species of *Argyrotheca* or *Bronnothyris* of the same size. *T. pulchellus* is, however, more elongate and is commonly somewhat asymmetrical.

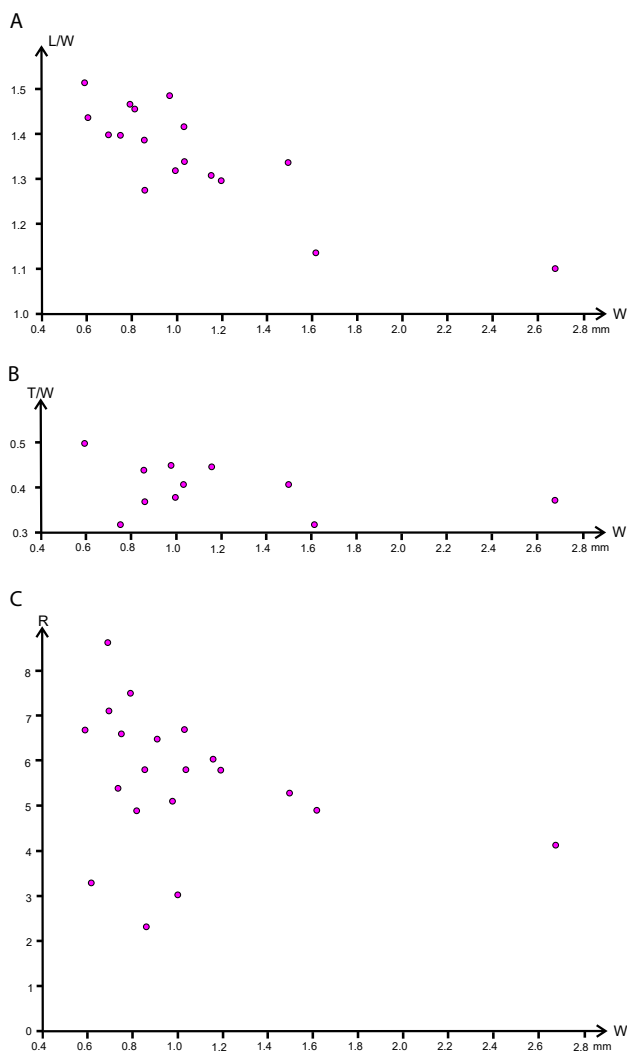


Fig. 91. *Trigonosemus pulchellus* (Nilsson, 1827). Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs/costellae. Upper lower Maastrichtian, *pulchellus*–*pulchellus* Zone.

Material. Jylland. Rørdal-1: 1.

Møn. Hundefangsklint: 3; Hvidskud: 68; Maglevands-pynt: 3; Nylands Nakke: 1; Sommerspiret: 3.

Chronostratigraphy in Denmark. Upper lower Maas-trichtian, *pulchellus*–*pulchellus* Zone (Surlyk 1970a, 1972, 1984; Surlyk & Birkelund 1977; Surlyk *et al.*

2013). Outside Denmark *T. pulchellus* is known from Rügen (Steinich 1965) and Krons Moor (Surlyk 1982) in northern Germany.

Pertinent references. Steinich (1965), Surlyk (1972).

Superfamily Megathyridoidea Dall, 1870

Family Megathyrididae Dall, 1870

Genus *Argyrotheca* Dall, 1900

Type species *Argyrotheca cuneata* Risso, 1826

Argyrotheca hirundo (von Hagenow, 1842)

Figs 92, 93, 94

A. hirundo is micromorphic. The outline subtriangular. The L/W varies between 0.90 and 1.24, but the shells are mainly clearly elongate. The largest width lies anterior to the shell midline. The shell is biconvex and the ventral valve is strongly convex, whereas the dorsal is rather flat. Poorly delimited ears are present and the shell margin may be extended laterally into two pointed wings, but this is uncommon. The anterior commissure is rectimarginate to slightly ventrally curved. Two costae are formed at W=1.0 mm, and two more are formed laterally to the two first at W=1.6 mm; the number may in this way increase to 6. The costae are arranged into two bundles separated by a median sinus and the costae of each bundle are close to parallel. A single costa is commonly formed in the sinus at W=1.6 mm or later. Up to 7–8 clear growth lines occur on large forms. The beak is pointed and suberect. The area is planar to slightly concave. The foramen is large, triangular and hypothyrid and limited laterally by narrow deltidial plates. A strongly developed pedicle collar has a posteriorly directed anterior margin. The dorsal median septum is high and touches the ventral valve.

Argyrotheca hirundo is a highly variable species, but still relatively easy to distinguish from species of *Bronnothyris* in the material. It is particularly characterized by the subtriangular outline and inflated ventral valve. It is possible that *Bronnothyris obstinata* (Steinich 1965) should be referred to *A. hirundo*. Steinich (1965) had relatively few specimens of *B. obstinata* at his disposal and his illustrated specimens

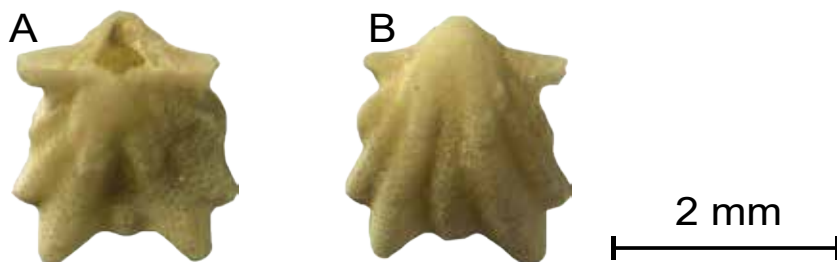


Fig. 92. *Argyrotheca hirundo* (von Hagenow, 1842). A. Dorsal view. Note the laterally diverging costae and the onset of a new one in the median sinus. B. Same specimen in ventral view. Lower Maas-trichtian. Møns Klint (Fig. 2).

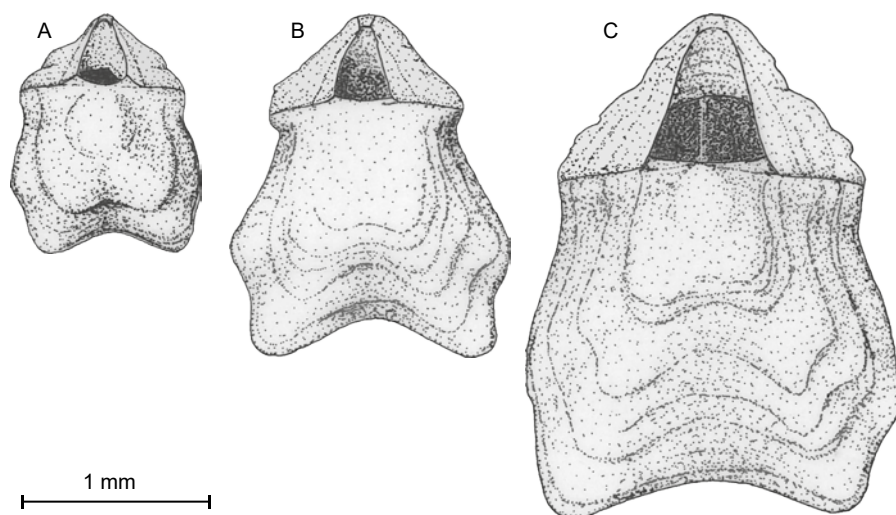


Fig. 93. *Argyrotheca hirundo* (von Hagenow, 1842). A–C. Growth stages. Lower upper Maastrichtian, *semiglobularis–humboldtii* Zone. Ferslev (Fig. 2).

fall within the variation of *A. hirundo*. In addition, most of the Danish material of *A. hirundo* falls between the two examples of *A. hirundo* and *B. obstinata* figured by Steinich (1965, Pl. 17, figs 3a–d and Pl. 18, figs 3a–d, respectively). Both types are connected by

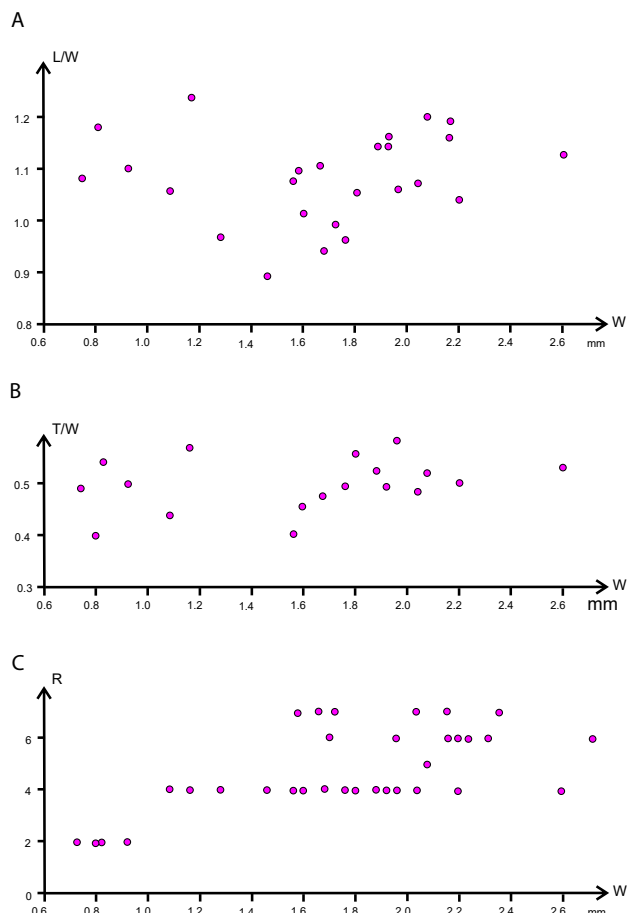


Fig. 94. *Argyrotheca hirundo* (von Hagenow, 1842). Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs/costae.

gradual, even transitions in the present material.

Material. Falster. Gedser Fyr: 3.

Jylland. Rørdal: 76; Danmark: 28; Eerslev: 3; Ferslev: 25; Gudumholm: 123; Hillerslev: 2; Kjølbygård: 2; Lindholm: 55; Linds: 9; Mjels: 1; Nye Kløv: 77 (Johansen 1987); Smidie: 2.

Møn. Hvidskud: 16; Store Taler: 12; Lille Taler: 6; Nylands Nakke: 8; Forchhammers Pynt: 2; Sættepileklint: 2.

Sjælland: Karlstrup: 3; Stevns Klint: 1.

Outside Denmark *A. hirundo* has been found in eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1982, 1984), Belgium (Simon 2000), and in Norfolk in eastern England (Johansen & Surlyk 1990).

Chronostratigraphy in Denmark. Maastrichtian. All brachiopod zones.

Pertinent references. Steinich (1965), Surlyk (1984), Johansen & Surlyk (1990) and Simon (2000).

Genus *Bronnothyris* Popiel-Barczyk & Smirnova, 1978

Type species *Bronnothyris bronnii* (Roemer, 1841)

Bronnothyris bronnii (Roemer, 1841)

Figs 95, 96, 97

The genus *Bronnothyris* with *Terebratula bronnii* Roemer 1841 as the type species was erected by Popiel-Barczyk & Smirnova (1978) for Late Cretaceous megathyridid species resembling *Argyrotheca* but with septal flanges extended ventrally from the dorsal valve. These flanges are very minor structures and I consider it an example of unnecessary over-splitting, but since it is accepted in the Treatise and we followed it in Schröder & Surlyk (2020) it is used

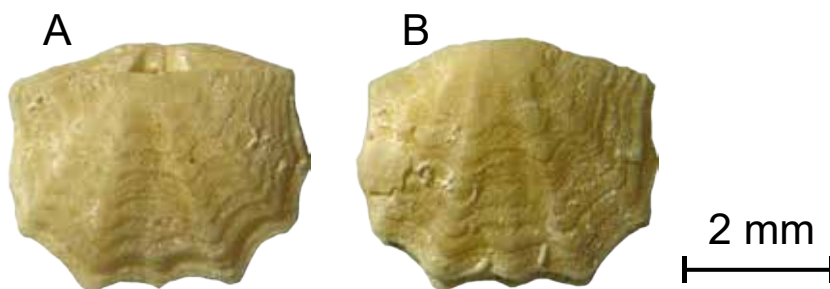


Fig. 95. *Bronnothyris bronnii* (Roemer, 1841). A. Dorsal view. B. Same specimen in ventral view, Uppermost Maastrichtian, *stevensis*-*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

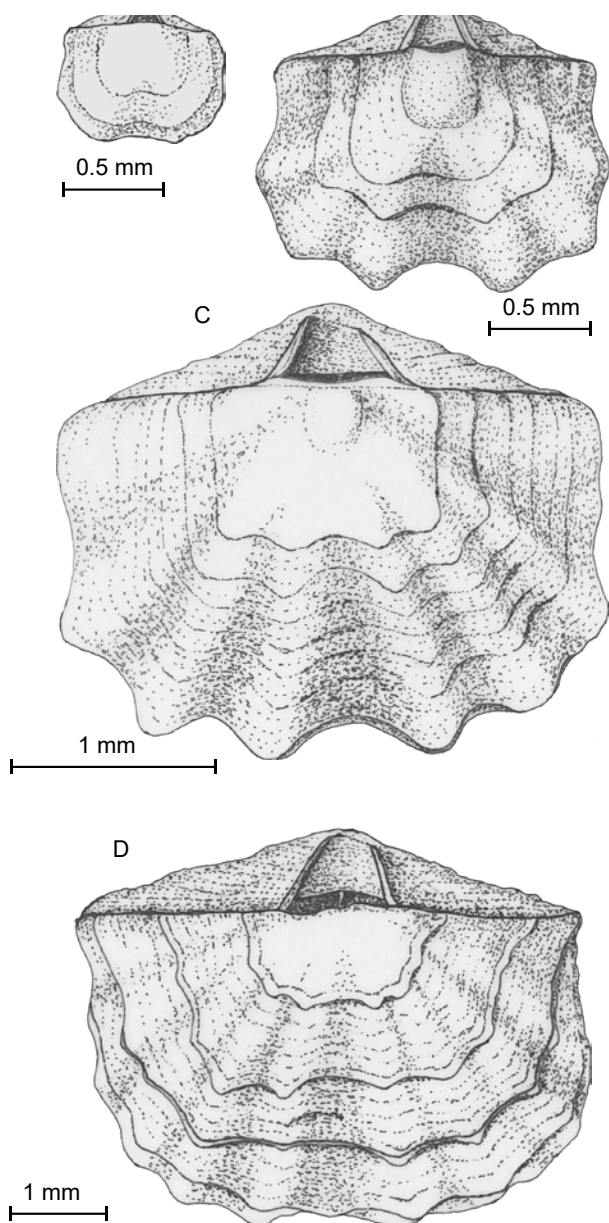


Fig. 96. *Bronnothyris bronnii* (Roemer, 1841). A–D. Growth stages. Upper lower Maastrichtian. Hundefangsklint, Møns Klint (Figs 2, 4).

here.

B. bronnii is micromorphic. The outline is semi-circular to subpentagonal, but quite variable. The largest width is along the hinge line. The L/W varies between 0.68 and 1.12. Small specimens are bi-convex but the dorsal valve becomes flat during growth. The ears are poorly defined. At $W=0.6$ mm a broad, median sinus is formed, resulting in a bilobate outline of the shell. A costa is intercalated on each lobe at $W=0.9$ mm and the number of costae has now increased to 4. New costae are formed laterally to the earlier at $W=1.6$ mm and again two additional at $W=3.0$ mm, reaching a total of 8 costae arranged into two bundles. The costae are flat and extend only slightly beyond the shell margin. There are up to 8 strong growth lines. The beak is pointed and erect to slightly suberect. The deltidial plates are narrow and the foramen is large and triangular. The pedicle collar is well developed. A ventral median septum is very thin and rather short.

The species has earlier been split into *A. bronnii* for hemispherical forms and *A. buchii* (von Hagenow, 1842) for subquadrangular forms. There is, however, a gradual transition between these two morphologies and the splitting probably reflects the limited number of specimens available of this small species to the earlier workers. There are also gradual transitions to *Bronnothyris coniuncta* Steinich, 1965, but the two species can always be distinguished on differences in inner morphology (Steinich 1965).

Material. Falster. Gedser Fyr: 12; Gedser Odde: 16. Jylland. Danmark: 19; Eerslev: 27; Gudumholm: 125; Lindholm 57; Mjels: 7; Nye Kløv: 39 (Johansen 1987); Nørre Flødal: 3; Linds: 21; Rørdal: 61; Spentrup: 3; Sønder Kongerslev: 2. Møn. Forchhammers Pynt: 8; Hundefangs Klint: 269; Hvide Klint: 54; Hvidskud: 2122; Lille Taler: 2; Maglevandspynt: 4; Nylands Nakke: 5; Sommerspiret: 25; Store Taler: 3; Sættepileklint: 7; Vitmunds Nakke: 46. Sjælland. Karlstrup: 190; Stevns Klint: 1.

Chronostratigraphy in Denmark. Maastrichtian. *B. bronnii* occurs in all the brachiopod zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark it has been found at Rügen (Steinich 1965), Hemmoor and Krons Moor in northern Germany (Surlyk 1984; Surlyk

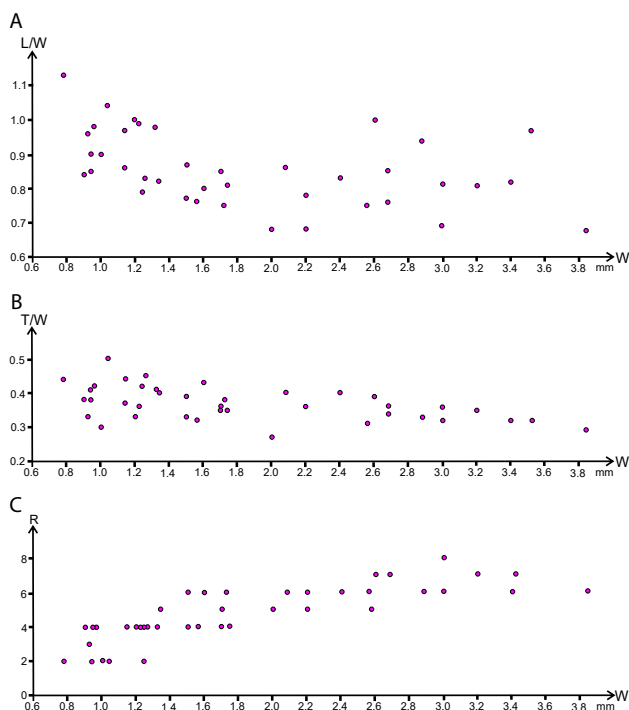


Fig. 97. *Bronnothyris brononii* (Roemer, 1841). Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae. Lower Maastrichtian. Møns Klint (Fig. 2).

& Schröder unpublished data) and in Norfolk in eastern England (Surlyk & Johansen 1990).

Pertinent references. Steinich (1965), Surlyk (1969, 1972, 1984), Johansen & Surlyk (1990).

***Bronnothyris coniuncta* Steinich, 1965**
Figs 98, 99, 100

Bronnothyris coniuncta is micromorphic. It has a hemicircular outline and the hinge line is normally extended into two wings. The largest width is always at the hinge line. The L/W varies between 0.55 and 0.71. The shell is flattened biconvex and the anterior commissure is rectimarginate. Four radial costae are formed at $W=1$ mm and two more are formed laterally to the first-formed at $W=1.6$ mm. The costae are arranged into two bundles separated by a median sinus. They diverge strongly and two more are formed laterally to the earlier ones at $W=2.8$ mm, but not al-

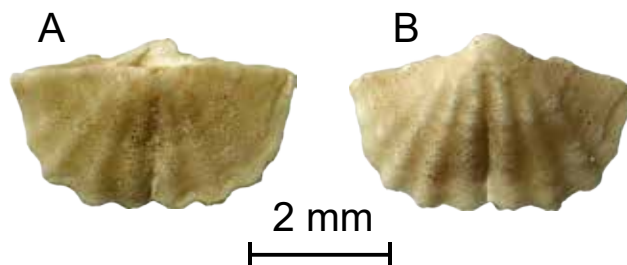


Fig. 98. *Bronnothyris coniuncta* Steinich, 1965. A. Dorsal view. B. Ventral view of same specimen. Upper lower Maastrichtian. Hvidskud Møns Klint (Figs 2, 4).

ways in both bundles, so the total number is normally at maximum 8. The costae are not very strong and extend only slightly beyond the shell margin. Large specimens have 4–5 clear growth lines. The beak is pointed or may be truncated. The area is broad and flat. The foramen is large, triangular, hypothryid and limited laterally by two narrow deltidial plates. The pedicle collar is strongly developed, planar with a straight anterior margin. The dorsal median septum is high, whereas the ventral septum is very thin. *B. coniuncta* is characterized by its very wide “*Spirifer*-like” outline.

Material. Jylland: Danmark: 4; Ferslev: 1; Gudumholm: 4; Nye Kløv: 5 (Johansen 1987). Møn. Forchhammers Pynt: 4; Hvide Klint: 6; Hvidskud: 45; Hundefangsklint: 19; Maglevandspynt: 1; Nylands Nakke: 1. Sjælland. Karlstrup: 1.

Chronostratigraphy in Denmark. Lowermost Maastrichtian to the middle part of the upper lower Maastrichtian and upper Maastrichtian; *spinosa-subtilis* to *pulchellus-pulchellus* Zones and *semiglobularis-humboldtii* to *stevensis-chitoniformis* brachiopod Zones (Surlyk 1984; Surlyk *et al.* 2013). Outside Denmark the species is known from eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1965) and Hemmoor in northern Germany (Surlyk & Schröder unpublished data), and Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1965), Surlyk (1969), Johansen & Surlyk (1990).

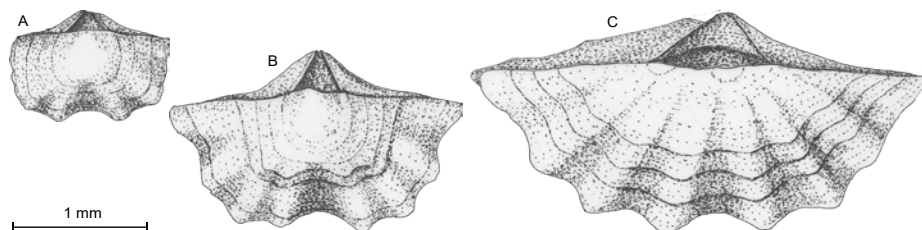


Fig. 99. *Bronnothyris coniuncta* Steinich, 1965. A–C. Growth stages. Upper lower Maastrichtian. Hvidskud Møns Klint (Figs 2, 4).

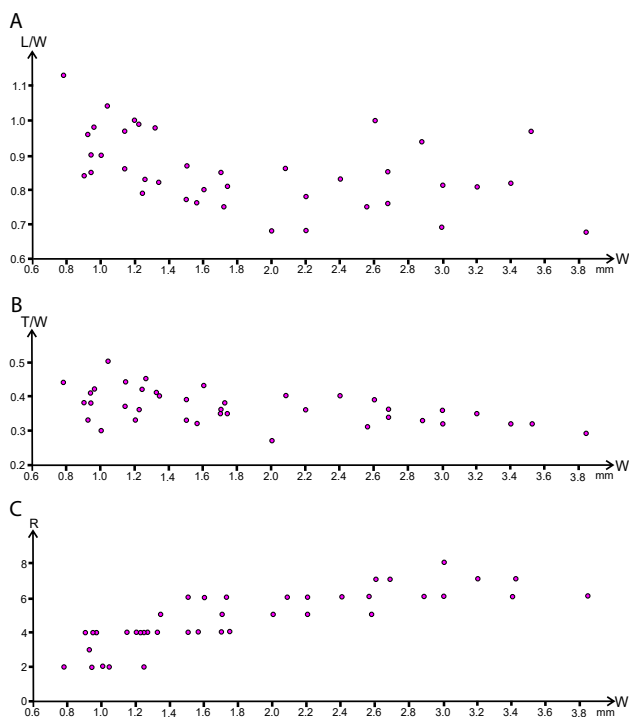


Fig. 100. *Bronnothyris coniuncta* Steinich, 1965. Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae.

***Bronnothyris stevensis* (Nielsen, 1928)**
Figs 101, 102, 103

B. stevensis is micromorphic. The outline is subpentagonal and the lateral shell margins are almost parallel. The shell is biconvex and both valves are equally inflated. The ears are poorly delimited. Four radial costae are formed at $W=0.5$ mm. Two additional costae are formed laterally to the first two at $W=0.8$ mm, and two additional costae are formed laterally to the first formed at $W=1.6$ mm, so that the number has increased to 8. The costae form two bundles separated

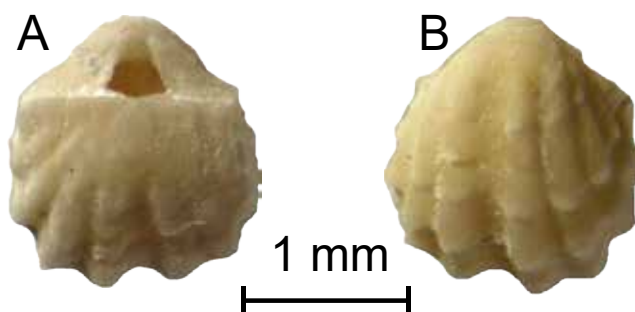


Fig. 101. *Bronnothyris stevensis* (Nielsen, 1928). A. Dorsal view. B. Same specimen in slightly oblique ventral view. Note the characteristic arrangement of two bundles each comprising three costae. Upper upper Maastrichtian, *stevensi*-*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

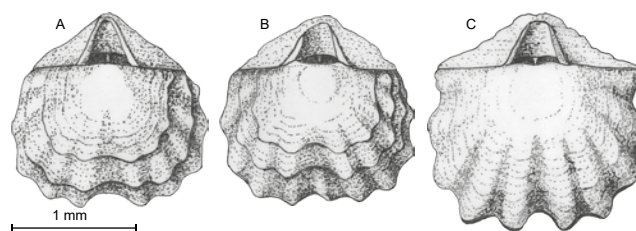


Fig. 102. *Bronnothyris stevensis* (Nielsen, 1928). A–C. Growth stages. Upper upper Maastrichtian, *stevensi*-*chitoniformis* brachiopod Zone. Stevns Klint (Fig. 2).

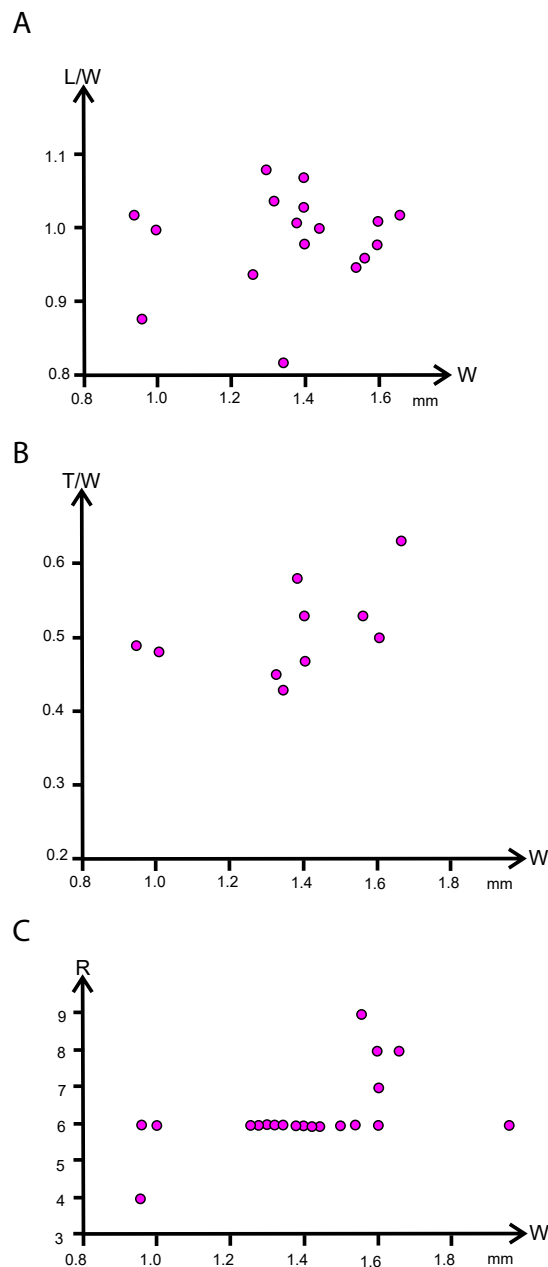


Fig. 103. *Bronnothyris stevensis* (Nielsen, 1928). Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae.

by a median sinus. The costae are closely spaced and normally close to parallel within each bundle.

The beak is large, weakly curved and sharply truncated posteriorly. It is delimited laterally by two narrow deltidial plates. The foramen is large, triangular and hypothyrid. The pedicle collar is very strongly developed. The hinge plate is well-developed and subdivided into two concave circular parts. The teeth are very small and stump. The brachidium is fully developed in all specimens investigated. Crura are essentially not developed. The crural processes are short, pointed and directed posterior-medially. The dorsal median septum is strongly developed and touches the inside of the ventral valve. Its anterior margin stands almost at a right angle to the inner side of the valve and its top is situated anterior to the midline of the valve. A short septum is situated in the ventral valve, running from the posterior end of the valve almost to the anterior margin.

Bronnothyris stevensis is easy to distinguish from the other species of *Bronnothyris* and *Argyrotheca* in the material. It is not very variable and is characterized by the strongly inflated valves, and the two bundles of parallel costae separated by a median sinus.

Material. Jylland: Eerslev: 11; Nye Kløv: 1061 (Johansen 1987).

Sjælland. Karlstrup: 6; Stevns Klint: 77.

Chronostratigraphy in Denmark. Upper upper Maastrichtian, *stevensis*–*chitoniformis* brachiopod Zone.

Pertinent references. Nielsen (1928), Steinich (1965), Surlyk (1984), Johansen (1987).

Superfamily Platidioidea Thomson, 1927

Family Platidiidae Thomson, 1927

Subfamily Platidiinae Thomson, 1927

Genus *Aemula* Steinich, 1968

Type species *Aemula inusitata* Steinich, 1968

***Aemula inusitata* Steinich, 1968**

Figs 104, 105, 106

A. inusitata is micromorphic and the shell is relatively thin. The outline is oval to circular, but commonly highly irregular, and the margin may have strong indentations. The shell may thus be highly asymmetric with antero-lateral extensions. This asymmetry may also be reflected in the shape of the foramen. The L/W is highly variable due to the irregular shape of many shells, but there is a tendency to an increase in relative width during growth. L/W is generally between 0.8 and 1.0 in specimens with W>1.8 mm, while it varies between 0.95 and 1.2 in smaller specimens. The shell is planoconvex to slightly concavoconvex, and the anterior commissure is rectimarginate in specimens with a regular shape. The dorsal valve is almost always smooth, with faint growth lines, while the ventral valve has small, short cone-shaped tubercles and no visible growth lines. Tubercles are rarely seen in specimens with W<1 mm. There is no correlation between density of tubercles and shell size.

The beak is short and suberect and the area is small and sharply delimited. The hinge line is almost straight. The foramen is rather large and amphithyrid. A triangular delthyrium occurs in the ventral valve, and the dorsal valve has a semicircular indentation formed by resorption of the dorsal umbo. The foramen diameter varies between 0.18 and 0.72 mm and it is relatively larger in smaller specimens. It is limited laterally by narrow deltidial plates. The short and slightly elevated pedicle collar is delimited from the deltidial plates by a furrow. The teeth are very short and blunt. The inner socket ridges are strong and extend somewhat at the posterior shell margin. Steinich (1968a, p. 198) described the hinge plates as rather strongly developed. This is in contrast to the specimens in the present material, which rarely possess hinge plates, and these are only present in specimens with a convex dorsal valve.

The brachidium is poorly developed and consists of two small wing-like ascending branches sitting on a low triangular-shaped septum, which is situated anterior to the shell midline and almost touches the ventral valve. The branches are strong and blunt but can also be developed as thin triangular plates. The inner side of the shell is smooth. Poorly defined mus-

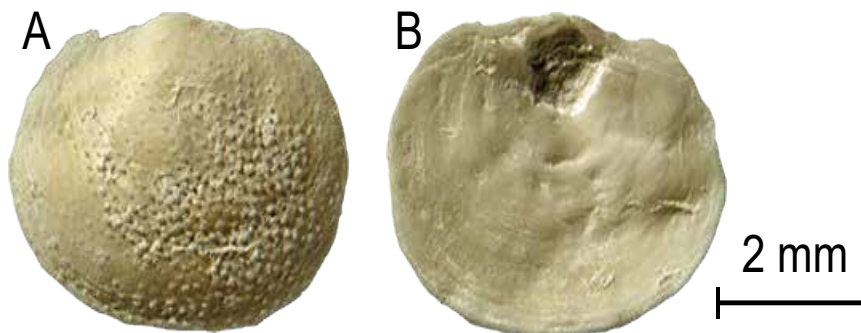


Fig. 104. *Aemula inusitata* Steinich, 1967. A. Ventral view of an unusually regular specimen, showing the sculpture comprising densely spaced tubercles. B. Dorsal valve of the same specimen showing the characteristic amphithyrid foramen. Lower Maastrichtian. Møns Klint (Fig. 2).

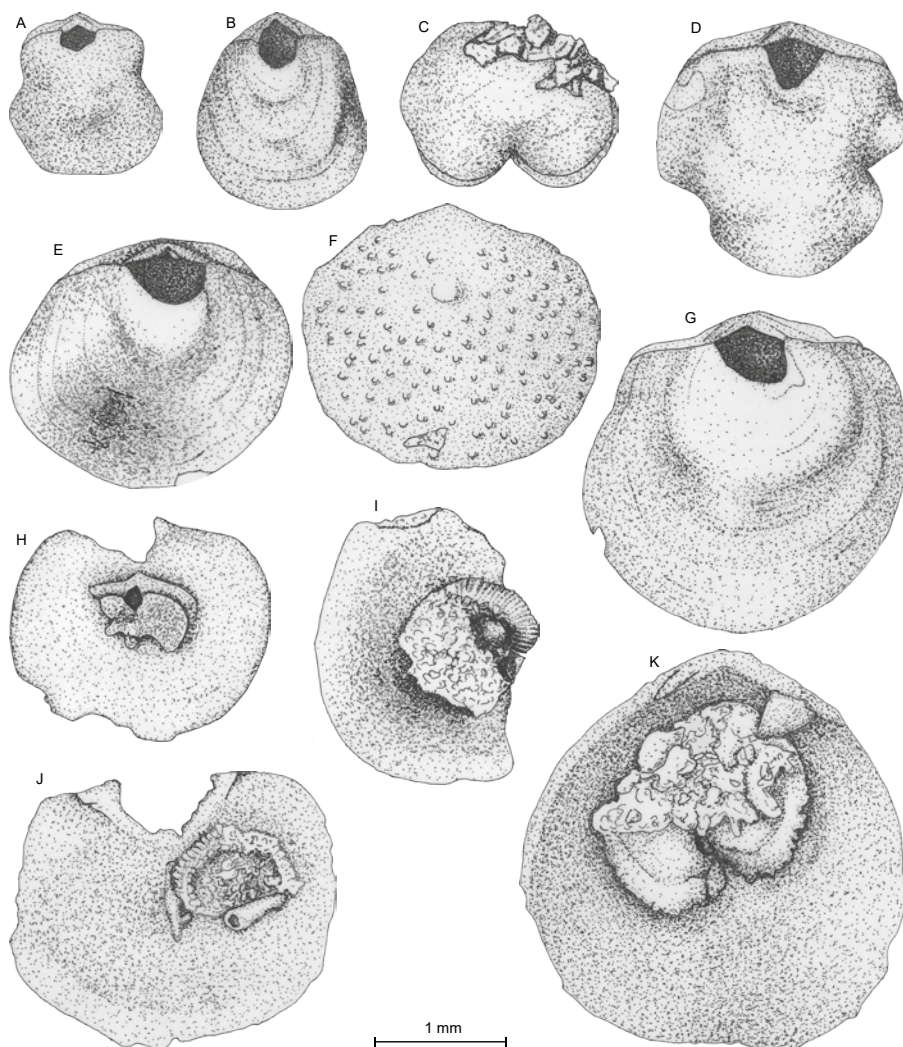


Fig. 105. *Aemula inusitata* Steinich, 1967. **A, B, D, E, G.** Growth stages in dorsal view, showing the characteristic outline of the shell with irregular indentations of anterior margin. **C.** Ventral view. **F.** Ventral valve showing the sculpture comprising small tubercles. **H.** Spicular skeleton, showing circular mouth opening and brachial furrow. **I, J, K.** Spicular skeleton of the lophophore which was a schizolophe as there is no median spiral. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

cle scars occur in the ventral valve. They are separated by a low ridge, which extends to the posterior valve margin where it fuses with the pedicle collar.

Aemula inusitata has a strongly developed spicular skeleton, showing that the lophophore was a schizolophe. The brachial furrow is 0.1 mm wide and delimited by a single filament row and a very strongly developed brachial lip. There are 20 filaments/mm of lophophore arm. The mouth penetration is about 0.1 mm wide in large specimens.

A. inusitata can be difficult to separate from juvenile specimens of *Scumulus inopinatus* Steinich, 1968 and *Dalligas nobilis* Steinich, 1968. *A. inusitata*, however, is distinguished by the presence of tubercles on the ventral valves.

It was noted by Surlyk (1974) that a related smooth form listed as *Aemula* sp. with a relatively regular outline common in the Maastrichtian chalk of Hemmoor in northern Germany represents a new species. It is intended to be described as a new species in a paper on the brachiopods from Hemmoor in NW

Germany (Surlyk & Schröder unpublished data).

Material. Falster. Gedser Fyr: 3.

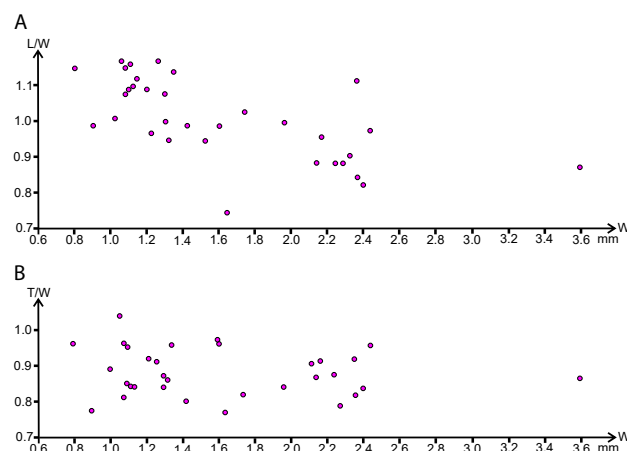


Fig. 106. *Aemula inusitata* Steinich, 1967. Scatter diagrams. L=length, W=width, T=thickness.

Jylland: Danmark: 15; Eerslev: 2; Ferslev: 40; Gudumholm: 100; Hillerslev: 1; Kjølbygård: 3; Lindholm: 32; Mjels: 36; Nye Kløv: 47 (incl. a few specimens from one sample in the lowermost Danian; Johansen 1987); Nørre Flødal: 12; Smidie: 3; Spentrup: 16; Rørdal: 20. Møn. Hvide Klint: 9; Hvidskud: 223; Hundefangsklint: 23; Sættepileklint: 1. Sjælland: Karlstrup: 132; Stevns Klint: 163.

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones. A few specimens from the lowermost Danian at Nye Kløv are listed as belonging to *A. inusitata* (Johansen 1987). Outside Denmark *A. inusitata* has been recorded in eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1968a), Hemmoor and Krons-moor in northern Germany (Surlyk 1972, 1982, 1984; Surlyk & Schröder unpublished data) and in Norfolk in eastern England (Johansen & Surlyk 1990).

Pertinent references. Steinich (1968a), Surlyk (1972, 1984), Johansen & Surlyk (1990), Surlyk & Schröder (unpublished data).

Genus *Scumulus* Steinich, 1968

Type species *Scumulus inopinatus* Steinich, 1968

Scumulus inopinatus Steinich, 1968

Figs 107, 108, 109

Scumulus inopinatus is micromorphic. The outline is elongate ovate, but commonly rather irregular. The L/W varies between 1.00 and 1.38. The largest width lies at or immediately anterior to the shell midline. The transition from the lateral shell margins to the hinge line is even and rounded. The shell is ventribi-convex. However, the anterior part of the ventral valve is rather flat and the anterior half is planar or even slightly concave in some specimens. The anterior commissure is rectimarginate to incipiently sulcate. The surface of the shell is smooth without ornamentation. The beak is short, straight and stump. The

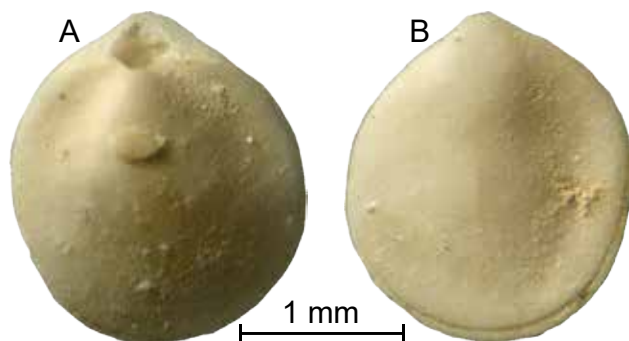


Fig. 107. *Scumulus inopinatus* Steinich, 1968. A. dorsal view. Note the amphithyrid foramen. B. same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

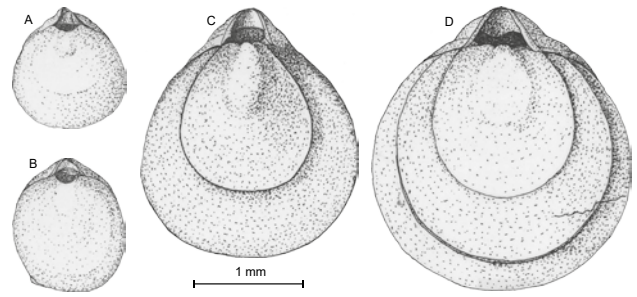


Fig. 108. *Scumulus inopinatus* Steinich, 1968. A–D. Growth stages. Note that the foramen changes during growth from amphithyrid to hypothyrid in adult forms. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 7).

area is broad and triangular. The deltidial plates are very narrow. The foramen is large and amphithyrid and extends into the dorsal valve. The pedicle collar is strongly developed as is also the hinge. The teeth are small, pointed and parallel or slightly diverging. Crura are formed at $W=1$ mm and are parallel in the early stages. A dorsal median septum is well developed and reaches the ventral valve at $W=1$ mm. The ends of the crural arms converge rapidly and fuse with the median septum at $W=1.6$ mm. *S. inopinatus*

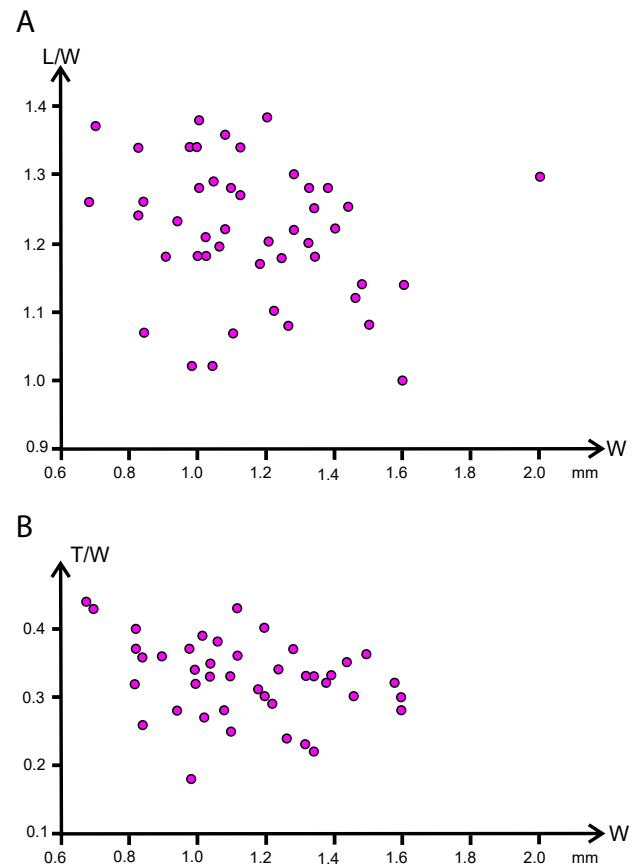


Fig. 109. *Scumulus inopinatus* Steinich, 1968. Scatter diagrams. L=length, W=width, T=thickness

possesses a very strongly developed spicular skeleton and the lophophore was a zygolophe. The filaments had short spicular skeletons.

Juvenile specimens of *S. inopinatus* resemble *M. chitoniformis* (von Schlotheim, 1813) of the same size but can be distinguished by their amphithyrid foramen and by the strongly punctate shell of *M. chitoniformis*.

Material. Falster. Gedser Fyr: 2.

Jylland. Bjerre: 2; Dania: 9; Danmark: 92; Eerslev: 19; Ferslev: 47; Gudumholm: 520; Hillerslev: 13; Kjølbjergård: 14; Lindholm: 281; Linds: 53; Mjels: 20; Nørre Flødal: 85; Rørdal: 63; Smidie: 8; Spentrup: 17; Sønder Kongerslev: 1.

Møn. Forchhammers Pynt: 6; Hundefangsklint: 618; Hvide Klint: 23; Hvidskud: 2470. Maglevandspynt: 6; Nylands Nakke: 3; Sandpynten: 65; Sommerspiret: 12; Store Taler: 2; Vitmunds Nakke: 60.

Sjælland: Karlstrup: 558; Stevns Klint: 795. Outside Denmark it is known from Rügen (Steinich 1968a), Hemmoor and Krons Moor (Surlyk 1982; Surlyk & Schröder unpublished data) in northern Germany, Norfolk in eastern England – specimen marked with a question mark in Johansen & Surlyk (1990).

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones (Surlyk *et al.* 2013).

Pertinent references. Steinich (1968a), Johansen & Surlyk (1990).

Suborder Terebratulidina Muir-Wood, 1955

Superfamily Uncertain

Family Terebratulidae King, 1850

Subfamily Magasinae Dall, 1870

Genus *Magas* J. Sowerby, 1816 in 1815-1818

Type species *Magas chitoniformis* (von Schlotheim, 1813)

***Magas chitoniformis* (von Schlotheim, 1813)**

Figs 110, 111, 112

The lack of recognition of the higher taxonomic position of *M. chitoniformis* presented in Lee *et al.* (2007) is somewhat surprising, considering that it is one of the most common and characteristic species in the Upper Cretaceous chalk of northern Europe. I follow the most commonly used taxonomic assignment (e.g. Steinich, 1965).

M. chitoniformis is small to medium-sized. The outline in small specimens is elongate ovate but changes to circular during growth. Young specimens are

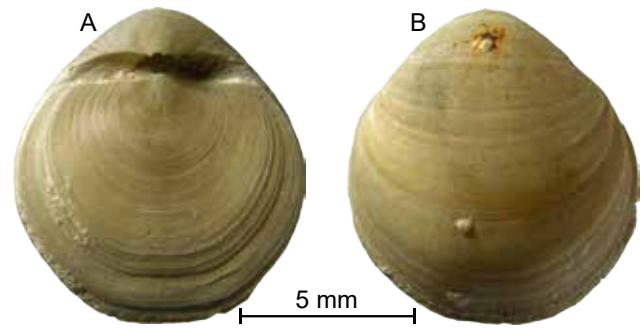


Fig. 110. *Magas chitoniformis* (von Schlotheim, 1813). A. Dorsal view. Note the strongly incurved rostrum, which almost closes the foramen; Adult *M. chitoniformis* thus belongs to the highly characteristic group of hemispherical species in the Maastrichtian chalk (Surlyk 1972). B. Same specimen in ventral view. Lower Maastrichtian. Møn's Klint (Fig. 2).

thin shelled but the shell become very thick during growth, especially in the posterior part. The shell is strongly punctate. The L/W decreases from 1.45 at W=0.7 mm to values between 0.8 and 1.1 at W=3.5 mm. The greatest width is at or immediately anterior to the shell midline. Small specimens <2 mm are uniformly biconvex but the ventral valve becomes strongly inflated during ontogeny, while the dorsal valve becomes gradually less inflated. Large specimens are always nearly planoconvex. A broad, rather flat median sinus is formed at W>5–6 mm and the anterior commissure becomes slightly unisulcate. Large specimens have 6–9 well-defined growth lines. The surface of the shell is smooth. The beak is almost erect in small specimens but becomes strongly incurved during growth, whereby the small, sharply delimited area becomes concave. The triangular foramen is laterally limited by narrow, well-defined deltidial plates. It becomes extended somewhat into the ventral valve during growth and rapidly becomes submesothyrid. It is essentially hidden by the incurved beak in large specimens. The pedicle collar is well developed. The hinge margin rapidly becomes straight during ontogeny. The hinge is rather strong. The brachidium begins to form at W=0.6 mm and is first marked by the formation of a strong, high median septum that touches the dorsal valve. The crura are formed at W=1.1–1.2 mm. They are short and diverge strongly and two ascending branches are formed at W=1.7–1.8 mm as two elongate triangular plates at the posterior margin of the septum. At the same time two thin descending branches are formed and fuse with the ascending branches at W=2.6–2.8 mm. The main morphology of the brachidium did not undergo significant changes during further growth. A low, median keel is situated in the ventral valve and extends from the posterior margin and somewhat anterior to the shell midline. A co-

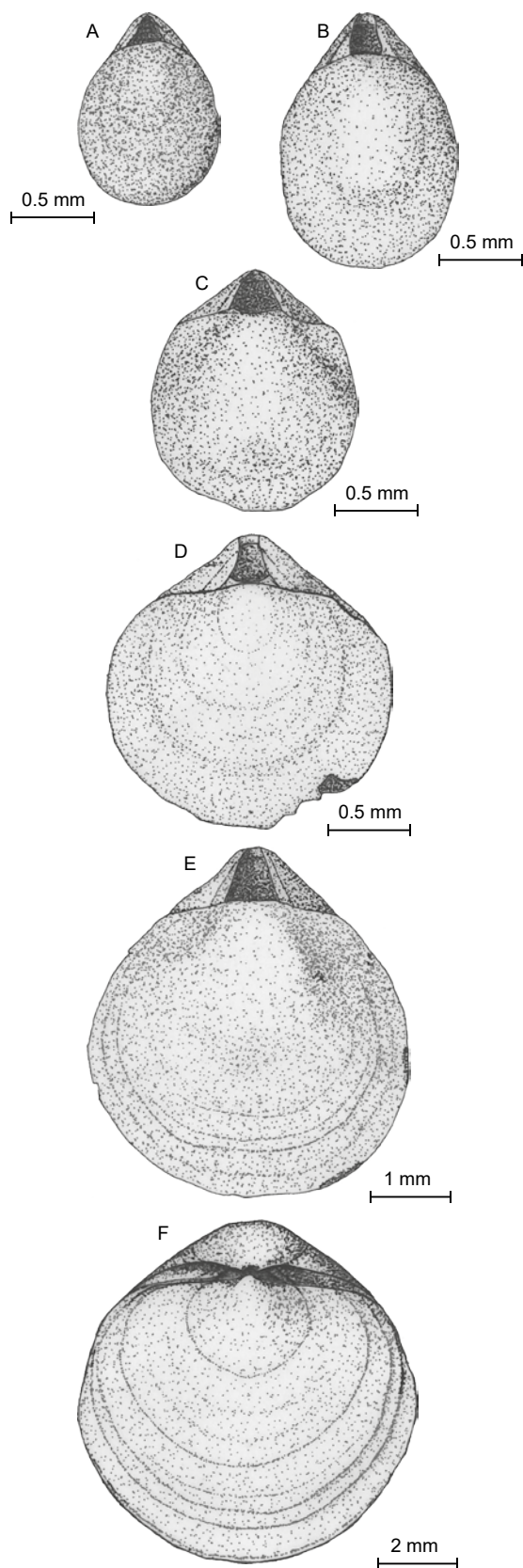


Fig. 111. *Magas chitoniformis* (von Schlotheim, 1813). A–F. Growth stages. A–D. Nørre Flødal and E. Gudumholm. Lower upper Maastrichtian. F. Møns Klint, upper lower Maastrichtian (Fig. 2).

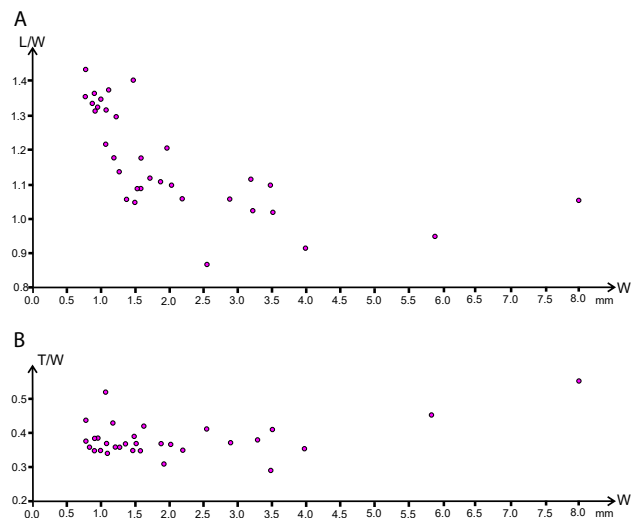


Fig. 112. *Magas chitoniformis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width, T=thickness.

herent spicular skeleton has not been observed but single spicules occur laterally to the posterior part of the median septum and on the brachidium. They are platy with irregular indentations commonly resulting in a star-shaped form.

Small specimens of *M. chitoniformis* are difficult to distinguish from *Dalligas nobilis* and *Scumulus inopinatus* of the same size. *S. inopinatus* differs in its amphithyrid foramen, and the commonly rather irregular outline. *D. nobilis* has faint radial costellae from $W=3$ mm, but smaller specimens can only be distinguished by the very simple morphology of the brachidium and by the lack of the strongly punctate shell characterizing *M. chitoniformis*.

Material. Falster. Gedser Fyr: 4.

Jylland: Danmark: 32; Ferslev: 49; Gudumholm: 480; Kjølbygård: 12; Lindholm: 234; Linds: 67; Mjels: 51; Nye Kløv: 12 (Johansen 1987); Nørre Flødal: 183; Rørdal: 144; Smidie: 9; Spentrup: 13.

Møn. Forchhammers Pynt: 6; Hundefangsklint: 648; Hvide Klint: 48; Hvidskud: 2724; Lille Taler: 1; Maglevandspynt: 13; Nylands Nakke: 3; Sommerspiret: 2; Store Taler: 5.

Sjælland. Karlstrup: 539; Stevns Klint: 178.

Outside Denmark, *M. chitoniformis* is known from eastern Poland (Bitner & Pisera 1979), Rügen (Steinich 1965), Hemmoor and Krons Moor (Surlyk 1982; Surlyk & Schröder unpublished data) in northern Germany, Norfolk in England (Johansen & Surlyk 1990).

Chronostratigraphy in Denmark. Maastrichtian, all brachiopod zones (Surlyk 1972, 1984; Surlyk *et al.* 2013).

Pertinent references. Steinich (1965), Surlyk (1972, 1984, 2025), Johansen & Surlyk (1990), Hansen & Sur-

Palaeoecology

The morphological adaptations, modes-of-life and population structures of the brachiopods of the Danish chalk were studied by Surlyk (1972, 1973, 1974) and Schröder & Surlyk (2020). The most characteristic ecological group is Group Ia of Surlyk (1972, fig. 5), 'Minute forms able to use very small substrates', comprising close to 20 micromorphic species, *Terebratulina faujasii*, *T. longicollis*, *T. subtilis*, *Rugia tenuicostata*, *R. acutirostris*, *R. stenius* n. sp., *R. tegulata*, *R. spinosa*, *Gisilina gisii*, *G. jasmundi*, *Dracius carnifex*, *Aemula inusitata*, *Scumulus inopinatus*, *Bronnothyris brononii*, *B. coniuncta*, *B. stevensis*, *Argyrotheca hirundo* and *Dalligas nobilis*. It is clearly reflected by the genus names that this adaptation to a life on the chalk ooze was developed in a variety of mainly unrelated taxonomic groups. The chalk contained only very small hard potential substrates such as fragments of fossils, notably bryozoans and other small shelly fossils, larger fossils being rare and scattered. This unusual adaptation evolved gradually in the Late Cretaceous Chalk Sea to culminate in the late Campanian – Maastrichtian. The occurrence and especially the abundance of this group of micromorphic species was more or less unknown before the work of Steinich (1965). Scattered specimens of adult micromorphic species were commonly misinterpreted as juveniles or as paedomorphic, i.e. retention of juvenile traits into adulthood. This is clearly not the case as shown by the complete absence of medium- or larger sized specimens, growth line studies and by the presence of fully developed adult plectolophous lophophores in species of *Terebratulina*, *Rugia* and *Gisilina* (Surlyk 1969, 1972).

In 1972 little was known about substrate preferences of brachiopods in general and more specifically about the great variability of the brachiopod pedicle in terms of morphology and function. However, Surlyk (1972) inferred a number of different adaptations to the life on the soft chalk ooze in some cases involving ontogenetic changes from larval attachment to small hard substrates to a free-living mode-of-life when the substrate was outgrown. In addition, *Terebratulina chrysalis* was interpreted to have had a root-like pedicle allowing attachment to a great variety of substrates.

Group Ib of Surlyk (1972), 'Medium to very large sized forms confined to large, hard substrates' includes only two species, *Neoliothyris obesa* and *N. fittoni*. Their rarity clearly reflects the rarity of appropriate large, hard substrates. This lifestyle is reflected in the large pedicle opening although this feature cannot be directly equated with attachment to large,

hard substrates such as shells or rock walls.

Group Ic, attached directly to the sediment comprised only one species, the medium-sized *Terebratulina chrysalis* although this ability was probably shared with several other species in the chalk. It was interpreted to have had a root-like pedicle, which allowed attachment to a great variety of substrates, ranging from direct attachment to the fine-grained chalk ooze of the seafloor over bryozoan debris, soft sponges and larger shelly invertebrates, to submarine rock walls (Surlyk 1972; Schröder & Surlyk 2020; Curry 1981, 1982). *Terebratulina chrysalis* belongs to a large group of closely related generalists, which were able to live on a great variety of substrates. This interpretation was based on examination of the similar modern species *Terebratulina retusa* (Linnaeus, 1758) which possesses a highly variable root-like pedicle (collections of the Natural History Museum of Denmark; Surlyk 1972, fig. 8). Its shape does not show any special morphological adaptations, which together with the nature of the pedicle may explain its remarkable evolutionary success. It was thus one of the few brachiopods, which successfully survived the K–Pg boundary and it has recently been documented from the lower Selandian, Palaeogene Kerteminde Marl Formation in Denmark (Schröder & Surlyk 2024).

Group II of Surlyk (1972), 'Secondarily free-living forms, medium to large sized' comprises 10 species, 6 of which are hemispherical, a shape highly characteristic in the brachiopod fauna of the chalk. A hemispherical shell commonly associated with a gradual closure of the foramen was developed in a number of mainly unrelated groups reflecting a transition to a free-living lifestyle. The more-or-less hemispherical species include *Thecidea papillata*, *Meonia semiglobularis*, *Gyrosoria gracilis*, *Magas chitoniformis*, *Trigonosemus pulchellus*, and to some extent, *Ruegenella humboldtii*. The only brachiopods of the chalk where the foramen became completely closed during growth are *Cretirhynchia retracta* and *T. pulchellus* and they were thus without doubt free-living as adults. Most of the other species in group II of Surlyk (1972) had a very small foramen and they were in effect also free-living, but with a thin, long pedicle which could serve as a sort of anchor in the chalk ooze or as a means of movement of the shell with respect to water currents (see Richardson 1997). The hemispherical *M. chitoniformis* has been found in a monospecific cluster at Stevns Klint, counting as much as 53 specimens in otherwise very pure chalk, which showed numerous body fossils and imprints of large sponges (Surlyk 2025). The cluster is interpreted as representing a single spatfall, which settled on a large soft sponge. At the death of the sponge probably by a muddy chalk ooze debris flow they were instantaneously buried together with the sponge without being scattered and mixed with

other fossils. So, in spite of the hemispherical valve and the strongly incurved umbo it was not necessarily free-living as adult. This serves to illustrate the great variability of the pedicle and the nature of attachment or a free-living lifestyle.

Group III, 'Burrowing forms' contains only one species, "*Lingula*" *cretacea* and the interpretation of a burrowing mode-of-life is only based on analogy with modern relatives. It is mainly very well preserved in spite of its thin and delicate nature, lending some support to this interpretation. Fractures and breakage thus seem in all cases to result from compaction of the chalk.

Group IV, 'Attached to substrate by cementation' has two subgroups. Group IVa, 'Attached to very small substrates' includes the inarticulate *Isocrania costata*, *I. barbata* and *I. sendeni*, each with a minute attachment surface which became redundant during growth. These species thus became secondarily free-living.

Group IVb, 'Confined to large, hard substrates' includes *Crania craniolaris*, *C. antiqua*, *Ancistrocrania parisiensis*, *Thecidea recurvirostra*, *Vermiculothecidea vermicularis* and *Praelacazella wetherelli*. These are all very rare reflecting the rarity of available substrates, and are only very rarely, or not at all found in the washing residues

The brachiopods of the Danish Maastrichtian chalk thus represent close to all possible types of specializations to the available substrates. Some of these morphological adaptations were developed in taxonomically quite unrelated groups probably over long periods of time. However, the chalk represents one of the most long-lived and uniform marine sea floor habitats known, having existed in the same area for about 30 million years without interruptions. The interpretations of Surlyk (1972) are supported by the review of the lifestyles of modern brachiopods by Richardson (1997), highlighting the great variability of shape and function of the brachiopod pedicle.

Summary

A total of 44 brachiopod species represented by more than 35,000 individuals from 42 localities exposing the Maastrichtian chalk of Denmark is described. Almost all specimens are obtained from bulk samples of chalk washed by a method involving heating in a supersaturated Glauber's Salt solution followed by freezing repeated for about 15 times (Surlyk 1972). The sample weight is typically 5–10 kg, except for much smaller samples taken from cored boreholes. This material is supplemented with larger, centimetre-sized specimens hand-picked in outcrop. The retrieved brachiopod fauna is dominated by large numbers of juvenile specimens. The brachiopods are

described with emphasis on the ontogenetic evolution of most of the species in order to ease determination of juvenile specimens and interpretation of changes in lifestyle during growth. Illustrations of growth stages are supported by scatter plots showing lengths (L), widths (W) and number of ribs – costae and costellae (R) for the common species.

The stratigraphic distribution of the species allows definition of 12 brachiopod zones in the uppermost Campanian – Maastrichtian chalk of northern Europe (Surlyk 1984; Surlyk *et al.* 2013). The zones are given binomial names after the lowest and highest occurrence, respectively of the species defining the zonal boundaries (e.g. *tenuicostata*–*pulchellus* Zone). The Maastrichtian part corresponds to the upper eight zones. The zonal subdivision has been applied in southern Sweden, Poland, northern Germany, Belgium and eastern England. The material formed the basis for a palaeoecological synthesis (Surlyk 1972), for palaeoecological studies of selected species (Surlyk 1973, 1974) and in a comparative study of the morphological adaptations in the main depositional environments of the Chalk Sea (Schröder & Surlyk 2020). It has more recently been used in holostratigraphic syntheses of the Danish upper Campanian – Maastrichtian chalk (Surlyk *et al.* 2013; Thibault *et al.* 2024b).

The nomenclatural acts of this paper are registered on ZooBank. LSID of the new species *Rugia stenius* <https://zoobank.org/NomenclaturalActs/4D20B0FE-DB09-4BDB-B938-31D7E47732E8>

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Notes on Late Cretaceous – earliest Paleocene xenophorid gastropods from Denmark, Belgium and the Netherlands

KAI INGEMANN SCHNETLER, JOHN W.M. JAGT, PAUL H.M. VAN KNIPPENBERG, HENRIK MADSEN & JAN AUDUN RASMUSSEN



Geological Society of Denmark
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In Late Cretaceous and earliest Paleocene gastropod assemblages from Denmark, north-east Belgium and the south-east Netherlands, originating from white chalk and biocalcarenic facies alike, xenophorids or ‘carrier shells’ constitute merely a minor component. The main interest of these marine gastropods lies in the fact that they attach foreign objects, such as bivalve shells, serpulid worm tubes, bryozoans, fragments of echinoid tests and spines, as well as gastropod shells to their conchs. The first specimens of xenophorid shells, with attached foreign objects, from the lower upper Maastrichtian white chalk of Hillerslev (Jylland) are here presented, assigned to *Xenophora nilssoni* for the time being and compared with coeval and younger material from Belgium and the Netherlands. It appears that more than one species is represented in the latter lot, but this requires more detailed assessment of larger populations. *Xenophora nilssoni* is here recorded to range from the lower Campanian to upper Maastrichtian in the Netherlands-Belgium border region, while *Xenophora* sp. 1 refers to a population from the Meerssen Member, subunit IVf-7 (lowermost Paleocene) in southern Limburg, the Netherlands. Wherever possible, attached foreign objects are identified to genus and/or species.

Keywords: Gastropoda, Stromboidea, Xenophoridae, carrier shells, attachments, taxonomy, palaeoecology.

Kai Ingemann Schnetler [ingemann@schnetler.dk], Fuglebakken 14, Stevnstrup, DK-8870 Langå, Denmark. John W.M. Jagt [john.jagt@maastricht.nl], Natuurhistorisch Museum Maastricht, De Bosquetplein 6–7, NL-6211 KJ Maastricht, the Netherlands. Paul H.M. Van Knippenberg [pavak@home.nl], Gelrestraat 10, NL-5995 XH Kessel, the Netherlands. Henrik Madsen [henrik.madsen@museummors.dk], Fossil and Mo-clay Museum, Museum Mors, Skarrehagevej 8, DK-7900, Nykøbing Mors, Denmark. Jan Audun Rasmussen [jan.rasmussen@museummors.dk], Fossil and Mo-clay Museum, Museum Mors, Skarrehagevej 8, DK-7900 Nykøbing Mors, Denmark.

In north-west Europe, the small- to medium-sized, low conical, trochospiral shells of ‘carrier shells’, or xenophorids, constitute only a minor component of Late Cretaceous and early Paleocene gastropod assemblages. Although more than one species appears to be represented, the name *Xenophora onusta* (Nilsson, 1827) has been used by nearly all previous authors for forms of Santonian(?), Campanian and Maastrichtian age. Pacaud (2016, p. 50) has recently noted that the name *Trochus onusta* Nilsson, 1827 is invalid, being preoccupied by *Trochus onusta* Lightfoot, 1786, an extant species, and itself a junior synonym of *Trochus conchyliophora* von Born, 1780, and suggested *Xenophora nilssoni* Pacaud, 2016 as a replacement name. Nilsson’s (1827) original material came from the coarse-grained, calcarenitic Köpings Sandstone (“calcarenosa” of Nilsson 1827) in south-

ern Sweden, which equates with the *basiplana-roemeri* Zone (*sensu germanico*) in the lower upper Campanian (Kennedy & Christensen 1997).

Here, we present the first Danish examples of xenophorid shells, with attached foreign objects such as gastropods, bivalves and a primary spine of a cidaroid echinoid, from white chalk facies at Hillerslev, northern Jylland (Fig. 1), dated as late early to early late Maastrichtian (*tenuicostata-semiglobularis* and *semiglobularis-humboldtii* brachiopod zones; Møns Klint Formation) (Fig. 2). In the extended type area of the Maastrichtian Stage (Fig. 3) in the south-east Netherlands and north-east Belgium, xenophorids have been recorded from the mid-nineteenth century onwards, mostly in faunal lists and invariably referred to as *Xenophora onusta* (Nilsson, 1827). Bosquet (1860, 1868) noted this form from strata dated as

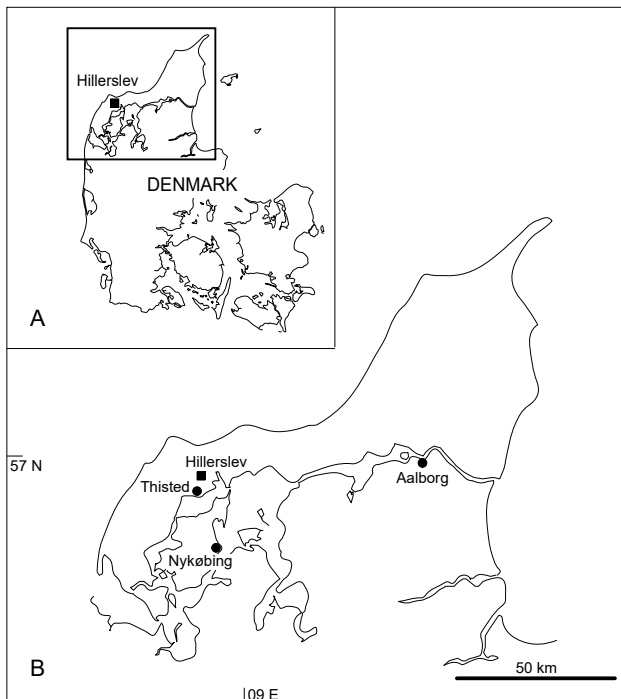


Fig. 1. Map of Denmark, showing the locality of Hillerslev in northern Jylland.

‘Hervien’ (= Vaals Formation in current terminology; lower Campanian) and ‘Maastrichtien’ (= Maastricht and Kunrade formations in current terminology; upper Maastrichtian). Binkhorst van den Binkhorst (1861-1862) was the first to illustrate a specimen in internal mould preservation from the ‘calcaire de Kunraed’ (= Kunrade Formation, in current terminology), while his material was subsequently revised by Kaunhowen (1898), who also provided details of the stratigraphical provenance, recording specimens from the Nekum Member (Maastricht Formation; Fig. 4). In both papers, the name *Xenophora onusta* is used.

It is highly likely that more than one species is involved in the material studied herein. Specimens from indurated levels, such as the top of the Emael Member and the overlying base of the Nekum Member (Maastricht Formation) in the Maastricht area (the Netherlands) are more or less three-dimensionally preserved, so that the apical angles may be measured.

For the time being, we use the name *Xenophora nilssonii* for the Danish specimens and for two composite moulds from the Vijlen Member (interval 6) and numerous silicified shells as well as external and internal moulds from the Gronsveld, Emael, Nekum and Meerssen (subunits IVf-1 to IVf-6) members (Fig. 4). Under the name of *Xenophora* sp. 1, an earliest Paleocene population (Meerssen Member, subunit IVf-7) from the Geulhem area (the Netherlands) is listed here. These forms are distinguished on overall shell

proportions, apical angle and ornament, where preserved.

Below, a brief overview of the stratigraphy of the levels that have yielded the present xenophorid material is given, first for Denmark, and secondly, for the Liège-Limburg area (Belgium, the Netherlands).

Localities and stratigraphy

Denmark

The Hillerslev chalk quarry is situated in north-west Jylland, north of Limfjorden (Fig. 1), c. 5 km north of Thisted (co-ordinates: 57.008°N, 8.72°E); it covers an area of approximately 600 × 700 metres.

This locality is situated in the Danish Basin, immediately south of the tectonically significant Tornquist Zone, more precisely on the Thisted Dome, a salt-influenced structure extending between Thisted and Hanstholm (Hansen & Håkansson 1980). Fracturing is widespread at the site and quarry faces reach over 10 metres in height, although most are less high. The non-indurated chalk excavated is assigned to

Ma	Thibault <i>et al.</i> (2025)		Surlyk <i>et al.</i> (2013)	Birkelund (1957)	Surlyk (1984, 2025)	
	Stages	Boreal sub-stages	Litho-stratigraphy	Belemnite zones	Brachiopod zones	
66.0	Maastrichtian	upper upper	Høj. Mb.	<i>Bln. casimirovensis</i>	10	<i>stevens-chitoniformis</i>
			Sigerslev Member		9	<i>humboldtii-stevens</i>
67.0			Rørdal Mb.	<i>Blt. junior</i>	8	<i>semiglobularis-humboldtii</i>
68.0		lower upper	Møns Klint Formation		7	<i>tenuicostata-semiglobularis</i>
69.0					6	<i>pulchellus-tenuicostata</i>
70.0	Camp.	upper lower		<i>Bln. occidentalis</i>	5	<i>pulchellus-pulchellus</i>
71.0					4	<i>subtilis-pulchellus</i>
72.0					3	<i>spinosa-subtilis</i>
		lower lower	Mandehoved Formation	<i>Bln. lanceolata</i>	2	<i>acutirostris-spinosa</i>
73.0			Boesdal Mb.		1	<i>jasmundi-acutirostris</i>

Fig. 2. Lithostratigraphy (formations, members and horizons; Surlyk *et al.* 2013; Thibault *et al.* 2025) and belemnite and brachiopod zonation (Birkelund 1957; Surlyk 1984, 2025) of uppermost Campanian and Maastrichtian strata in Denmark.

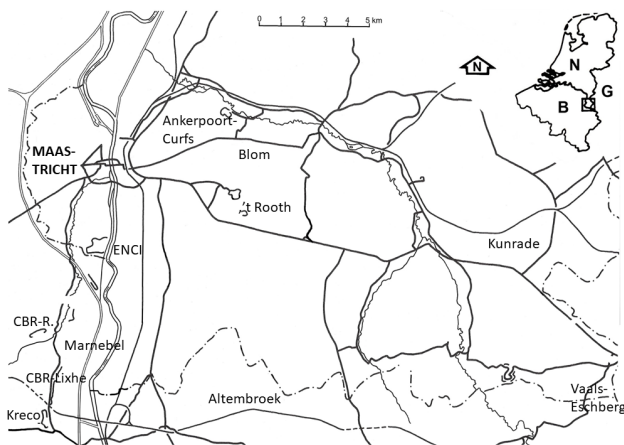


Fig. 3. Map of the extended type area of the Maastrichtian Stage (southern Limburg, the Netherlands, and contiguous areas in Belgium and Germany), showing localities that have yielded xenophorid material described herein.

the Møns Klint Formation (Surlyk *et al.* 2013) and is light grey to white in colour, being almost entirely composed of biogenic material, primarily abundant calcareous coccolith remains interspersed with skeletal fragments of bryozoans, brachiopods, bivalves, sponges and echinoderms. The dominant lithofacies is bioturbated pelagic chalk mudstone.

Macrofossil and ichnofossil assemblages from Hillerslev have received attention in numerous papers, including Birkelund (1979, 1993), Surlyk (1970, 1984), Jagt *et al.* (1999), Machalski (2005) and Vallon *et al.* (2020). Surlyk (1984, 2025) correlated strata exposed at Hillerslev quarry with the *tenuicostata*-*semiglobularis* and *semiglobularis*-*humboldtii* brachiopod zones, dated as latest early to earliest late Maastrichtian. Associated ammonites include *Hoploscaphites constrictus constrictus* (J. Sowerby, 1817), *H. tenuistriatus* (Kner, 1848), *Saghalinites wrighti* Birkelund, 1965 and *Pachydiscus neubergicus* (von Hauer, 1858), support this dating (Birkelund 1993; Machalski 1996, 2005). Even if dating of strata exposed at Hillerslev quarry awaits to be determined in detail, currently an age of between 69 and 67 Ma may be proposed (see Thibault *et al.* 2025).

North-east Belgium and south-east Netherlands

In the extended type area of the Maastrichtian Stage (Fig. 3), the Upper Cretaceous succession has been subdivided into five formations, with numerous members and horizons (omission surfaces, hardground, fossil hash levels; see Jagt 1999), only few of which have yielded xenophorid gastropods in various states of preservation (*i.e.* composite moulds, internal/external moulds and silicified shells). These units are as follows:

Vaals Formation (Fig. 4). Within the lower part of this glauconitic, sandy/silty unit, the so-called 'Müller's Bed' (Gemmenich Member) has yielded a highly diverse silicified macrofauna, including numerous molluscs, in particular near Vaals-Eschberg (W.M. Felder & Bosch 2000). This bed is named after a local headmaster, Johannes Müller, who collected such silicified macrofossils and described and named these (Müller 1847, 1851, 1859). This fauna was subsequently revised by Holzapfel (1884, 1885, 1887–1888, 1889). Albers & Felder (1979) showed 'Müller's Bed' to have been situated within their 'sandy silt biotope' of silty, glauconitic, extensively bioturbated, fine-grained sands, with the bed itself representing an original biocoenosis of high diversity, including many gastropod species suggestive of rich thallopiphyte growth. Xenophorids, here assigned to *Xenophora nilssoni*, are rare in these assemblages (Table 1).

Within the Vaals Formation important index biota such as inoceramid bivalves and ammonoid and coleoid cephalopods are comparatively rare.

Houthem Formation

	Meerssen Mb, IVf-7	Vroenhoven Hz	
	Meerssen Mb, IVf-1/-6	Berg en Terblijt Hz	66.02 Ma (K/Pg)
Maastricht Formation	Nekum Mb, IVe-3/4-4	Caster Hz	66.13 Ma
	Nekum Mb, IVe-1/2-2	Kanne Hz	66.25 Ma
	Emael Mb	Laumont Hz	66.35 Ma
	Schiepersberg Mb	Romontbos Hz	66.55 Ma
	Gronsveld Mb	Schiepersberg Hz	66.60 Ma
	Valkenburg Mb	St. Pieter Hz	66.90 Ma
	Lanaye Mb	Lichtenberg Hz	67.00 Ma
	Lixhe 3 Mb	Nivelle Hz	67.80 Ma
Gulpen Formation	Lixhe 2 Mb	Boirs Hz	68.60 Ma
	Lixhe 1 Mb	Halembaye 1 Hz	69.20 Ma
	Vijlen Mb, interval 6	Wahlwiller Hz	69.70 Ma
	Vijlen Mb, interval 5	Zonneberg Hz	
	Vijlen Mb, intervals 0-4	Böckler Hz	70.40 Ma
	Beutenaken Mb	Bovenste Bos Hz	(Camp/Mstr)
	Zeven Wegen Mb	Froidmont Hz	72.60 Ma
		Zeven Wegen Hz	

Vaals Formation

Fig. 4. Lithostratigraphy (formations, members and horizons) of Upper Cretaceous-lowermost Paleocene strata in the type area of the Maastrichtian Stage, and dating of horizons (after Vellekoop *et al.* 2022; see also Keutgen 2018). The Kunrade Formation (not shown) is considered to be the lateral, near-shore equivalent of the upper Gulpen Formation (Lanaye Member) to the Emael Member of the Maastricht Formation (P.J. Felder & Bless 1989; Jagt 1999).



Fig. 5. *Xenophora nilssoni* Pacaud, 2016 (DK 1076), upper lower to lower upper Maastrichtian, Hillerslev (northern Jylland, Denmark). **A:** Entire slab with the two parts of DK 1076 and *Saghalinites* sp. (bottom left-hand side). **B:** Base of DK 1076 with attached molluscs: indeterminate gastropod (a), indeterminate bivalve with adnate juvenile oyster (b), smooth pectinid valve (c), large specimen of *Amaea aliciae* T. Hansen, 2019 (d), *?Serrifusus binkhorsti* (Kaunhowen, 1898) (e), *?Pseudotoma danica* T. Hansen, 2019 (f). **C:** Apex of DK 1076 with attached molluscs: *?Dolicholatus* sp. (a), *?volutid* (b, c), *?fasciolarid* (d), indeterminate gastropod (e), fragment of oyster? (f). Microconch of *Hoploscaphites constrictus constrictus*, associated, but apparently not attached (g), and spine of cidaroid echinoid (h).

Albers (1976) recorded the belemnitelids *Gonioteuthis granulataquadrata* (Stolley, 1897), *G. quadrata* (de Blainville, 1827) and *Belemnitella praecursor* Stolley, 1897 and, on this basis, favoured correlation with the North German *granulataquadrata*, *lingualquadrata* and *pilula* zones (lower lower Campanian; see Niebuhr 2006). The base of the *granulataquadrata* Zone had previously been shown to correspond to the United States Western Interior *Scaphites leei* III Zone, dated at 83.5 ± 0.5 Ma (McArthur *et al.* 1993). Ammonite taxa particularly suited for both trans-Atlantic and European correlations include *Scaphites hippocrepsis* II-III (*sensu* Cobban 1969) and *Baculites vaalsensis* Kennedy & Jagt, 1995. In the Western Interior, the *Scaphites hippocrepsis* II Zone has been dated at 81 Ma (McArthur *et al.* 1994). Other, non-heteromorph ammonites from the Vaals Formation corroborate such an age assignment for the lower part of this unit (Jagt & Jagt-Yazykova 2019). However, the upper part has yielded a different ammonite assemblage, typical of the lower upper Campanian, the most important index being

Hoplitoplacenticeras marroti (Coquand, 1859). Other macrofaunal groups that may be used as proxies comprise inoceramid bivalves (Sornay 1982), with direct links to assemblages from the Münsterland Basin in north-west Germany (Walaszczyk 1997).

Gulpen Formation, Vijlen Member (Fig. 4). This highly complex unit of glauconitic limestone has been subdivided into intervals 0 to 6 (P.J. Felder & Bless 1994; P.J. Felder 1997), with correlations relying on benthic foraminifera and bioclast-based ecozones, as well as inoceramid bivalves, ammonites and belemnites. Only from the Haccourt-Lixhe area (Fig. 3) are xenophorids known to date. Amongst the rich macrofaunal assemblages from the Altembroek section, described in detail by Jagt *et al.* (1995), there are none. At that locality, various belemnite-rich levels within interval 4 were distinguished, but repeated reworking across a channelised sea floor must have occurred to explain associations of various taxa of early (*obtusum*, *sumensis* and *cimbrica* zones) and early

Table 1. Xenophorid records from the Campanian to lowermost Danian of the extended type area of the Maastrichtian Stage (north-east Belgium, south-east Netherlands), with indications of attached foreign objects.

Formation	Member	Age	Locality	Registration number (MHMM-)	Preservation style	Attachments	Illustration	Taxon
Vaals	Gemmenich	early Campanian	Vaals-Eschberg	899	silicified	fragments of irregular echinoid tests, bivalves		<i>Xenophora nilssonii</i>
Gulpen	Vijlen, interval 6	late early Maastrichtian	CBR-Lixhe quarry	M2146	composite mould	scars of bivalves, single gastropod spire	Fig. 7	<i>Xenophora nilssonii</i>
Gulpen	Vijlen, interval 6	late early Maastrichtian	Kreco quarry (formerly CPL SA)	M2343	composite mould	scars of bivalves		<i>Xenophora nilssonii</i>
Gulpen	Vijlen, interval 6	late early Maastrichtian	Kreco quarry (formerly CPL SA)	JJ 7301	composite mould	fragments of irregular echinoid test, pectinoid bivalves and brachiopods	Fig. 19	<i>Xenophora nilssonii</i>
Maastricht	Gronsveld	late Maastrichtian	ENCI quarry	M180	silicified	fragments of irregular echinoid test, cheilostome bryozoans		<i>Xenophora nilssonii</i>
Maastricht	Gronsveld	late Maastrichtian	ENCI quarry	M196	silicified	scars only		<i>Xenophora nilssonii</i>
Maastricht	Gronsveld	late Maastrichtian	ENCI quarry	M1509	silicified	faint scars only	Fig. 14	<i>Xenophora nilssonii</i>
Maastricht	Gronsveld	late Maastrichtian	ENCI quarry	M1524	silicified	scars only		<i>Xenophora nilssonii</i>
Maastricht	Gronsveld	late Maastrichtian	ENCI quarry	M1606	silicified	fragment of cheilostome bryozoan		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M186	silicified	fragments of serpulids and bivalves	Fig. 14	<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M187	silicified	fragments of irregular echinoid test, serpulids and decapod crustaceans		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M1436	silicified	vague scars only		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	ENCI quarry	M1533	silicified	fragments of serpulids and irregular echinoid tests		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M1798	silicified	fragments of serpulids and bivalves		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M2077	silicified	scars, mostly of bivalves	Fig. 14	<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M2094	silicified	fragment of irregular echinoid test		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M2158	silicified	fragments of serpulids and bivalves		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M2251	silicified	fragments of ostreid bivalves, serpulids, ?decapod crustaceans		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	Marnebel quarry, Eben Emael	M2386	internal mould	vague scars only		<i>Xenophora nilssonii</i>
Maastricht	Emael	late Maastrichtian	CBR-Romontbos quarry, Eben Emael	M2538	silicified	vague scars only		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M129	silicified	fragment of bivalve, scars		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M130	silicified	fragments of bivalves and irregular echinoid test, cyclostome bryozoan		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M308	silicified	fragments of serpulids and ostreid bivalves		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M476	ext + int moulds	fragments of irregular echinoid test, bivalves and serpulids		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M545	external mould	fragments of irregular echinoid test		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M609	ext + int moulds	fragments of irregular echinoid test, ostreid bivalves and serpulids		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M610	ext + int moulds	fragments of echinoid test, bivalves and serpulids	Fig. 12	<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M611	ext mould	fragments of echinoid test, pectinoid bivalves, single gastropod		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M1200	ext + int moulds	fragments of ostreid, ?cardiid and veneroid bivalves	Fig. 13	<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M1473	ext + int moulds	fragments of decapod crustaceans, single turritellid gastropod		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	ENCI quarry	M1705	ext + int moulds	fragments of bivalves and serpulids		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	Blom quarry, Berg en Terblijt	M1753	ext + int moulds	fragments of irregular echinoid test, astarid bivalves and cheilostome bryozoans, single gastropod		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	t Rooth quarry, Bemelen	M1969	ext mould	fragments of irregular echinoid test and bivalves		<i>Xenophora nilssonii</i>

Table 1. Continued

Formation	Member	Age	Locality	Registration number (MHMM-)	Preservation style	Attachments	Illustration	Taxon
Maastricht	Nekum	late Maastrichtian	Marnebel quarry, Eben Emael	M1986	ext + int moulds	fragments of irregular echinoid test, bivalves and serpulids		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	CBR-Romonbos quarry, Eben Emael	M2940	silicified	fragments of bivalves, serpulids and cheilostome bryozoans		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	CBR-Romonbos quarry, Eben Emael	M3347	silicified	fragments of astarid bivalves and serpulids		<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	ENCI quarry	JJ 15993	ext and int moulds	fragments of serpulids, astarid bivalve, irregular echinoid test	Fig. 16	<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	ENCI quarry	JJ 15832	ext + int moulds	fragments of bivalves and irregular echinoid test, cyclostome bryozoan	Fig. 17	<i>Xenophora nilssonii</i>
Maastricht	Nekum	late Maastrichtian	ENCI quarry	JJ 14685	ext + int moulds	fragments of bivalves and irregular echinoid test	Fig. 18	<i>Xenophora nilssonii</i>
Maastricht	Meerssen	late Maastrichtian	Blom quarry, Berg en Terblijt	M595	ext + int moulds	fragments of irregular echinoid test, bivalves, cheilostome bryozoan; single gastropod	Fig. 11	<i>Xenophora nilssonii</i>
Maastricht	Meerssen	late Maastrichtian	Ankerpoort-Curfs, Geulhem	M2967	ext + int moulds	fragments of irregular echinoid test and veneroid bivalves		<i>Xenophora nilssonii</i>
Maastricht	Meerssen	late Maastrichtian	Ankerpoort-Curfs quarry, Geulhem	M3345		fragments of irregular echinoid test and pectinoid bivalves		<i>Xenophora nilssonii</i>
Maastricht	Meerssen	latest Maastrichtian	Ankerpoort-Curfs quarry, Geulhem	JJ 13048	internal mould	scars only		<i>Xenophora nilssonii</i>
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M1715	ext + int moulds	fragments of cheilostome (lunuliform) bryozoans, arid and veneroid bivalves and echinoid test	Fig. 8	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M1723	ext mould	fragment of bivalves	Fig. 8	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M1730	ext + int moulds	fragments of irregular echinoid test, ostreid bivalves and ?gastropods		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M1924	ext + int moulds	fragments of cheilostome bryozoans, nuculanid bivalves and echinoid test; single gastropod	Fig. 9	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M1925	ext + int moulds	fragments of irregular echinoid test, cheilostome bryozoans, bivalves and ?serpulid		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M2280	ext + int moulds	fragments of echinoid test, cheilostome bryozoans, ostreid and pectinoid bivalves	Fig. 10	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M3058	ext + int moulds	fragments of irregular echinoid test, cheilostome bryozoans and arid bivalves		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Berg en Terblijt	M3059	ext + int moulds	fragments of irregular echinoid test, cheilostome bryozoans and bivalves		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 025	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 060	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 078	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 087	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 091	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 099	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 103	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 104	internal moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 128	ext + int moulds	fragments of bivalves and irregular echinoid test	Jagt <i>et al.</i> , 2013, fig. 7-1/O	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 131	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 189	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 193	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 197	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 247	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1

Table 1. Continued

Formation	Member	Age	Locality	Registration number (MHMM-)	Preservation style	Attachments	Illustration	Taxon
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 052	ext + int moulds	fragments of bivalves and irregular echinoid test	Jagt <i>et al.</i> 2013, fig. 7-1/N	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 266	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 286	external mould	fragments of bivalves and two gastropods		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2002 317	ext + int moulds	fragments of bivalves and irregular echinoid test	Fig. 15	<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2003 143	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2003 151	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2003 155	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2004 122	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2004 124	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2004 137	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	2004 138	ext + int moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	JJ 14030	external mould	base		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	early Danian	Ankerpoort-Curfs quarry, Geulhem	KUL2006 001	internal moulds	fragments of bivalves and irregular echinoid test		<i>Xenophora</i> sp. 1
Maastricht	Meerssen, IVf-7	late Maastrichtian	Ankerpoort-Curfs quarry, Geulhem	KK 16-	internal mould	scars only		<i>Xenophora nilssoni</i>
Kunrade			Kunrade area	Renkens-Zijlstra				

late Maastrichtian age. The sections exposed in the Haccourt-Lixhe area (Kreco [formerly CPL SA] and CBR-Lixhe quarries) are referred to the uppermost part of interval 5 and the entire interval 6 (Keutgen *et al.* 2010). The prime index fossils in this part of the succession are scaphitid ammonites, belemnite shells and inoceramid bivalves, including 'tegulated' species (Jagt *et al.* 1999; Walaszczyk *et al.* 2010). Overall, intervals 0–6 of the Vijlen Member correlate with the *obtusa* to *tegulatus/junior* zones of the North German subdivision (Niebuhr 2006). Xenophorid material is currently known only from interval 6 of this member and is here assigned to *X. nilssoni* (Table 1).

Maastricht Formation, Gronsveld to Meerssen members (Fig. 4). The Gronsveld Member comprises poorly indurated, fine- to coarse-grained biocalcarenes, with two horizons (St. Pieter and ENCI) clearly distinguishable in the basal portion, in particular at the former ENCI-Heidelberg Cement Group quarry. Storm-generated echinoderm Lagerstätten have been described from this level, as have silicified macrofaunal elements in proximity of crumbly flint bodies with a dark-coloured core. These faunules comprise scaphitid and baculitid ammonites, serpulid polychaetes, a sepiid, various species of gastropods and bivalves, as well as teleost otoliths and sea grass stems and roots (Hewitt & Jagt 1999; Van der Ham *et al.* 2017; Schwarzhans & Jagt 2021). Keutgen (2018) dated the St. Pieter Horizon at 66.7 Ma; Vellekoop *et al.* (2022) noted 66.9 Ma.

The Emael Member is a poorly indurated, fine-to coarse-grained, homogeneous biocalcarene, typically with large, regular flat and pipe-shaped flint bodies near the base. For the lower part of the Maastricht Formation (*i.e.* the Valkenburg, Gronsveld, Schiepersberg and Emael members), Villain (1977) assumed regional currents constant enough to transport sediment particles over the entire platform, at shallow palaeodepths of 20 to 40 metres, without oceanic influence and a relatively firm sea floor and clear waters. On microfossil evidence, Liebau (1978) and Sprechmann (1981) characterised this setting as fully marine (middle sublittoral, lagoon-like with near flat coastline and low hinterland), invariably above wave base in the euphotic zone, under subtropical temperatures, with seagrass communities and rich thallopiphyte assemblages, inclusive of washed-in terrestrial plants. The Lava Horizon within the upper Emael Member was dated at 66.5 Ma by Keutgen (2018). We follow P.J. Felder & Bless (1989) in considering the 'Kunrade Chalk' (now Kunrade Formation) to be the nearshore lateral equivalent of the Lanaye Member (uppermost Gulpen Formation) up to, at least, the base of the Emael Member (Maastricht Formation), to the west of the River Maas (Meuse; Fig. 3).

The Nekum Member comprises a poorly indurated

ed (except for a strongly cemented level above the Laumont Horizon, dated at 66.35 Ma by Vellekoop *et al.* (2022), coarse-grained, homogeneous limestone. Both the indurated uppermost portion of the Emael Member and the overlying 20 to 30 centimetres of the Nekum Member are replete with internal and external moulds of molluscs (bivalves, gastropods, scaphopods, nautiloids and heteromorph and non-heteromorph ammonites), as well as two species of serpulid polychaetes. These levels may be considered current-winnowed, time-averaged lumachelle or coquina beds. Locally coarse-grained fossil hash lenses and beds occur in the middle and upper part of this member, while the top corresponds to an omission surface (hardground), the Caster Horizon, dated at 66.2 Ma by Keutgen (2018) and at 66.13 Ma by Vellekoop *et al.* (2022).

The Meerssen Member consists of poorly indurated, coarse- to very coarse-grained limestones with clearly developed hardgrounds and fossil hash lay-

ers, with bryozoan remains and large benthic foraminifera. Liebau (1978) characterised these strata as high-energy deposits, with a marked production of carbonate detritus leading to the establishment of a broad, shallow, well-lit, warm carbonate platform with rich phytal association, and water temperatures of 20 to 25°C, allowing the growth of scleractinian corals and hippuritid/radiolitid rudists. The uppermost portion of subunit IVf-6 of the Meerssen Member is replete with external and internal moulds of molluscs, testifying to current winnowing leading to chaotic concentrations of empty shells (Vellekoop *et al.* 2020). The top of IVf-6 equates with the Bergen Terblijt Horizon, which coincides with the Cretaceous–Paleogene (K/Pg) boundary. Xenophorid material, both silicified and in external/internal mould preservation, is known, with the largest individuals recorded from the basal Nekum Member. For the time being, all specimens, except those from Meerssen Member subunit IVf-7 (see below), are here as-

Table 2. Late Cretaceous xenophorid records on the basis of literature sources, and indications of the nature of attached foreign objects.

Species name used	Reference	Country	Attachments <i>in situ</i>
Maastrichtian			
<i>Xenophora nilssoni</i> Pacaud, 2016	This study	Denmark	Gastropods, bivalves, echinoids
<i>Xenophora nilssoni</i> Pacaud, 2016	This study	Netherlands	Gastropods, bivalves, echinoids, serpulids, decapod crustaceans, bryozoans
<i>Xenophora onusta</i> (Nilsson, 1827)	Blank (1974)	Ukraine	
<i>Xenophora onusta</i> (Nilsson, 1827)	Bakayeva (2011)	Ukraine	
<i>Xenophora onusta</i> (Nilsson, 1827)	Kutscher & Kullessa (2010)	Germany	Bivalves, echinoids
<i>Xenophora onusta</i> (Nilsson, 1827)	Kaunhowen (1898)	Netherlands	
<i>Xenophora onusta</i> (nobis)	Binkhorst van den Binkhorst (1861-1862)	Netherlands	
<i>Xenophora onusta</i> (Nilsson, 1827)	Abdel-Gawad (1986)	Poland	
<i>Xenophora onusta</i> (Nilsson, 1827)	Tzankov & Motekova (1981)	Bulgaria	
<i>Xenophora hermax</i> Squires & Saul, 2001	Squires & Saul (2001)	USA	
<i>Xenophora leprosa</i> (Morton, 1834)	Richards (1962)	USA	
<i>Acanthoxenophora sinuosa</i> Perrilliat & Vega, 2001	Kiel & Perrilliat (2001)	Mexico	Gastropod
<i>Xenophora vasconcellosi</i> Oliveira, 1957	Ponder (1983)	Brazil	
<i>Xenophora</i> sp.	Darragh & Kendrick (1994)	Australia	Bivalves
<i>Xenophora trangahinsis</i> Basse, 1931	Ponder (1983)	Malagasy Republic	
<i>Xenophora madagascariensis</i> Collignon, 1951	Ponder (1983)	Malagasy Republic	
Campanian			
<i>Trochus onustus</i> Nilsson, 1827	Nilsson (1827)	Sweden	
<i>Xenophora nilssoni</i> Pacaud, 2016	This study	Netherlands	Bivalves, echinoids
<i>Trochus onustus</i> Nilsson, 1827	Goldfuss (1841, in 1826-1844)	Germany	
<i>Xenophora onusta</i> Nilsson sp.	Andert (1934)	Czech Republic	
<i>Xenophora onusta</i> (Nilsson, 1827)	Arnold (1968)	Germany	
<i>Xenophora onusta</i> (Nilsson, 1827)	O. Schneider (2007)	Germany	
<i>Xenophora onusta</i> (Nilsson, 1827)	Kollmann & Odin (2001)	France	
<i>Endoptygma umbilicata</i> Tuomey, 1854	Richards (1962)	USA	
<i>Xenophora carnatica</i> Stoliczka, 1868	Stoliczka (1868)	India	
<i>Xenophora leprosa</i> (Morton, 1834)	Dockery (1993)	USA	Gastropods, bivalves
<i>Xenophora canaliculata</i> (d'Orbigny, 1842)	Ponder (1983)	France	
<i>Xenophora willisi</i> Webster, 1983	Webster (1983)	Mexico	
Coniacian			
<i>Xenophora onusta</i> Nilsson sp.	Andert (1934)	Czech Republic	
Turonian			
<i>Xenophora grasi</i> Roman & Mazeran, 1920	Ponder (1983)	France	
<i>Xenophora simpsoni</i> Stanton, 1894	Perrilliat & Vega (2001)	USA	
Cenomanian			
<i>Xenophora</i> sp.	Stephenson (1952)	USA	

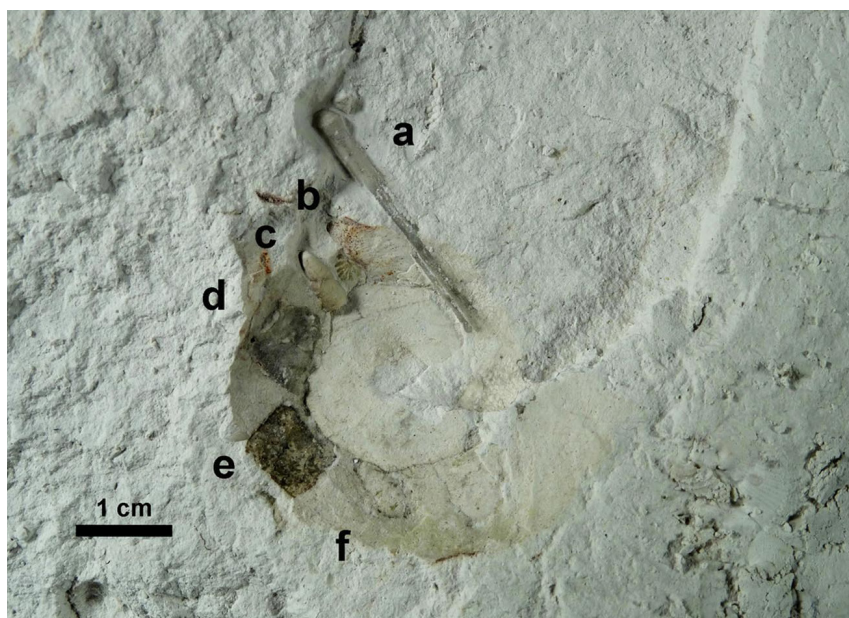


Fig. 6. *Xenophora nilssoni* Pacaud, 2016, upper lower to lower upper Maastrichtian, Hillerslev (northern Jylland, Denmark). Potential Danekræ PD66 (currently under evaluation by the Danekræ committee), with attached foreign objects: cidaroid spine (a), bryozoan? (b), sponge (c), fragment of bivalve (d), indeterminate fragment (e) and indeterminate gastropod (f).

signed to *X. nilssoni* (Table 1).

On palynological and molluscan evidence, the entire Maastricht Formation has been dated as late Maastrichtian, with the exception of the highest subunit (IVf-7) of the Meerssen Member, between the Bergen Terblijt and Vroenhoven horizons (Fig. 4), which is of earliest Danian age (Jagt & Jagt-Yazykova 2012; Jagt *et al.* 2013; Vellekoop *et al.* 2020). Principal index macrofossils of correlative value include various heteromorph and non-heteromorph ammonites, belemnitellid coleoids and ‘tegulated’ inoceramid bivalves (Keutgen *et al.* 2017; Jagt & Jagt-Yazykova 2018, 2019). These allow correlations with both Boreal and Tethyan sections in northern/north-eastern and southern Europe, respectively. Smit & Brinkhuis

(1996) integrated sedimentological, biostratigraphical, geochemical and palaeomagnetic analyses of the marginal-marine boundary section in the Geulhemmerberg underground quarries, close to Geulhem (Fig. 3). The base of subunit IVf-7 of the Meerssen Member is an undulating hardground (palaeorelief), with depressions up to 1.5 m deep, in heavily bioturbated calcarenites of subunit IVf-6, marking a brief period of non-deposition. Above this, initially coarse-grained sediments filling the depressions of palaeorelief represent a thinning-up and fining-up sequence, culminating in the 10–15 cm thick E clay. This would correspond to the Fiskeler Member (Rødvig Member; Surlyk *et al.* 2006).

On the basis of microfossils, in particular dinoflagellates and benthic foraminifera, and to a lesser de-



Fig. 7. *Xenophora nilssoni* Pacaud, 2016, with attached ?fusiform gastropod; NHMM M2146, CBR-Lixhe quarry, Lixhe (Liège, north-east Belgium), Gulpen Formation, Vijlen Member, interval 6 (upper lower Maastrichtian). Scale bar equals 10 mm.



Fig. 8. *Xenophora* sp. 1, with pieces of irregular echinoid test, cheilostome bryozoans and bivalves attached, former Ankerpoort-Curfs quarry, Geulhem (A: NHMM M1715) and veneroid and arcid bivalves (B: NHMM M1723), Maastricht Formation, Meerssen Member, subunit IVf-7 (lowermost Danian). Scale bars equal 10 mm.

gree sporomorphs, the K/Pg boundary equates with the Berg en Terblijt Horizon and not, as traditionally thought, with the overlying Vroenhoven Horizon, which separates the Maastricht and Houthem formations and would seem to be correlatable with the top of the Cerithium Limestone Member (Rødvig Formation) in eastern Denmark (Surlyk *et al.* 2006). Just below the Berg en Terblijt Horizon, very low, yet relatively slightly elevated Ir-contents have been observed. According to Smit & Brinkhuis (1996), the time span between the IVf-6 and IVf-7 strata, separated by the Berg en Terblijt Horizon, involved deposition of uppermost Maastrichtian calcarenites, followed by K/Pg storm or hypercane-related ‘washing’ of the palaeoshelf and erosion of uppermost Maastrichtian and lowermost Danian deposits, inclusive of an Ir-bearing layer. The xenophorid ‘population’ (some 50 specimens) from subunit IVf-7 of the Meerssen Member at Geulhem comprises merely small-sized specimens, here referred to as *Xenophora* sp. 1 (Table 1).

Material and methods

Danish material

Currently, the two specimens of xenophorid from Hillerslev quarry are the only ones on record from the white chalk facies in Denmark. One of these has

been declared Danekræ, namely DK 1076 (Fig. 5) and is housed in the collections of the Natural History Museum Denmark at Copenhagen. A second specimen, collected in 2021 (Fig. 6), awaits formal Danekræ evaluation and numbering.

Dutch–Belgian material

All material was collected over recent years either by splitting rocks, taken directly from quarry faces or from scree slopes after quarry blasting, or by wet sieving of matrix samples (up to several kilogrammes in weight). Only from subunit IVf-7 of the Meerssen Member have xenophorids been recovered that may be considered preserved *in situ*. This is indicated clearly by the fact this unit has also yielded co-occurring articulated bivalves, those preserved in butterfly position, as well as those documented undoubtedly *in situ*, such as poromyids and clavagellids (Jagt *et al.* 2013). Other occurrences reflect deposition in current-winnowed levels, resulting in coquina- or lumachelle-like levels, with rather chaotic structures and no real size sorting.

Wet sieving was favoured for samples from ‘early’ flint nodules in the Gronsveld and Emael members; only tap water was used.

Institutional abbreviations. NHMD, Natural History Museum Denmark, Copenhagen (with DK, Danekræ material); NHMM, Natuurhistorisch Museum Maas-



Fig. 9. *Xenophora* sp. 1, with nuculanid and indeterminate gastropod attached, former Ankerpoort-Curfs quarry, Geulhem; NHMM M1924), Maastricht Formation, Meerssen Member, subunit IVf-7 (lowermost Danian). Scale bar equals 10 mm



Fig. 10. *Xenophora* sp. 1, with fragments of irregular echinoid test, bryozoans and bivalves attached, former Ankerpoort-Curfs quarry, Geulhem; NHMM M2280, Maastricht Formation, Meerssen Member, subunit IVf-7 (lowermost Danian). Scale bar equals 10 mm.

tricht, Maastricht, the Netherlands (with several prefixes: JJ – J.W.M. Jagt Collection; KUL – Katholieke Universiteit Leuven Collection; see Vellekoop *et al.* (2020); M – P.H.M. van Knippenberg Collection; RZ – S. Renkens and J.J.P. Zijlstra Collection).

Systematic part

Remarks. The higher-level classification adopted here follows Ponder (1983), Bandel (2007) and Irwin *et al.* (2024).

Superfamily Stromboidea Rafinesque, 1815

Family Xenophoridae Troschel, 1852

Genus *Xenophora* Fischer von Waldheim, 1807

Type species. *Xenophora laevigata* Fischer von Waldheim, 1807 (= *Trochus conchyliophora* von Born, 1780) (ICZN Opinion 715, 1964).

***Xenophora nilssoni* Pacaud, 2016**

Figs. 5–7, 11–19

Selected synonyms (exclusively Danish, Belgian and Dutch records)

1851 *Trochus onustus* Nilsson; Müller, p. 44.

1860 *Xenophora onusta* Bosquet †; Bosquet, p. 376.

1861 *Xenophora onusta*, Nobis; Binkhorst van den Binkhorst, p. 38, pl. 3, fig. 14a–c.

1868 *Xenophora onusta*, Nilsson; Bosquet, p. 8.

1888 *Xenophora onusta* Nilss. sp.; Holzapfel, p. 152, pl. 14, fig. 28.

1898 *Xenophora onusta* Nilsson sp.; Kaunhowen, p. 50, pl. 3, fig. 15.

1943 *Xenophora onusta* (Nilsson); Van der Weijden, p. 107.

*2016 *Xenophora nilssoni* Pacaud, p. 50, fig. 5.

Material. See Tables 1 and 2.

Description of Danish specimens. DK 1076 (Fig. 5A–C): fairly large, low conical, width 85 mm and estimated height 80 mm; apical angle c. 85°; specimen consisting of two parts, presumably representing predator- or scavenger-cut shell; base, with lobed marginal flange and indistinct curved growth lines, lying with concave side up. Whorls medium convex, separated by distinct suture; low and with irregular surface. Aper-

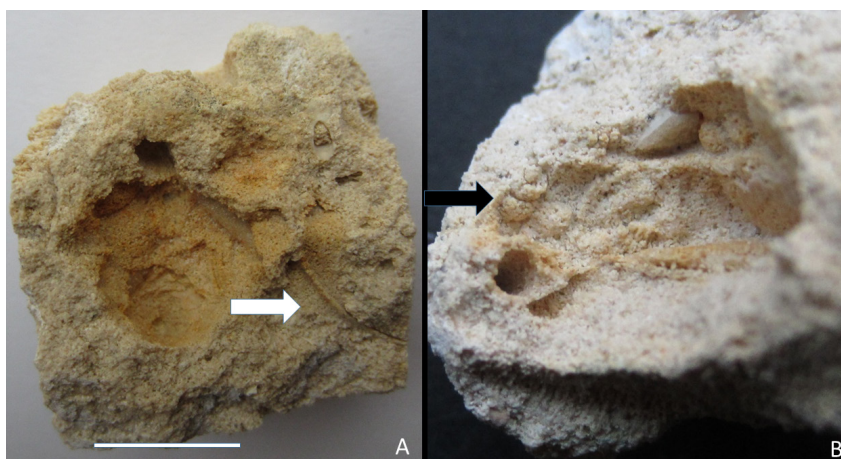


Fig. 11. *Xenophora nilssoni* Pacaud, 2016, with gastropod spire attached (black arrow: turritellid or aporrhaid?), NHMM M595, former Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (IVf-1 to -6). Scale bar equals 10 mm. The white arrow in A points to part of an aporrhaid digitation, in close proximity, but not attached to the xenophorid shell.

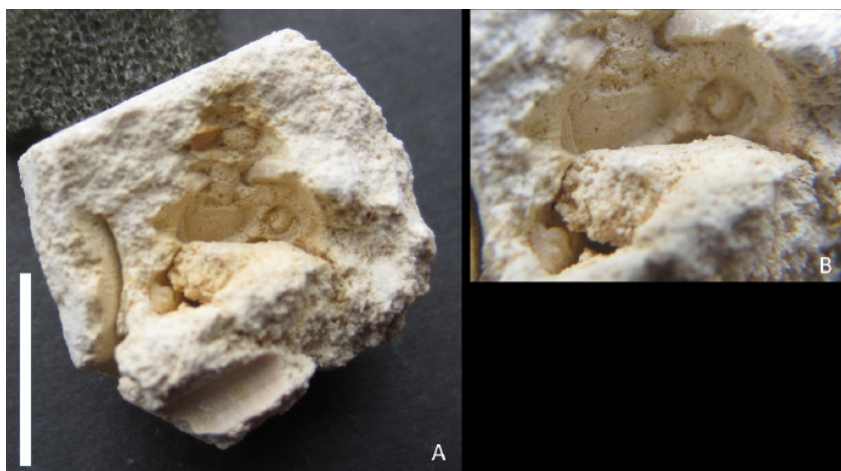


Fig. 12. *Xenophora nilssoni* Pacaud, 2016, with gastropod spire, as well as fragments of echinoid test and bivalves, NHMM M611, former Blom quarry, Berg en Terblijt, Maastricht Formation, Meerssen Member (IVf-1 to -6). Scale bar equals 10 mm.

ture not visible; umbilicus apparently absent; some weak spirals on adaxial part of base. Small cheilostome bryozoan colony on base. On visible portions of two last whorls are attached shells, preserved *in situ*. In all, nine gastropods and two bivalves recognised. Identifications of gastropods tentative because of state of preservation.

On base (Fig. 5B) attachments as follows: a juvenile indeterminate gastropod (letter **a**), attached by apex and preserved as composite mould). Indeterminate bivalve with adnate juvenile oyster (letter **b**), with quite prominent ribbing, attached by tip with convex side down. Left valve of smooth pectinid (letter **c**), attached by hinge margin, convex side down. Large (length >30 mm) specimen of *Amaea aliciae* T. Hansen, 2019 (letter **d**), preserved as composite mould, obliquely attached by apex but also reminiscent of '*Cerithium*' *imbricatum* Münster in Goldfuss, 1842 (see Säbele & Krupp 2013). Another gastropod (letter **e**), preserved as external mould and attached by periphery of two last whorls, tentatively assigned to *Serrifusus binkhorsti* (Kaunhowen, 1898), based on shell outline, similar position of spirals and rather similar axial ribs. External impression (letter **f**) of gastropod,

obliquely attached by apex and with sculpture similar to that of *Pseudotoma danica* T. Hansen, 2019.

Apex (Fig. 5C) with attached molluscs, as follows: poorly preserved external gastropod mould (letter **a**), tentatively assigned to *Dolicholaturus* sp., attached by periphery of all whorls. Another poorly preserved impression of gastropod attached by apex (letter **b**), tentatively interpreted as volutid based on outline and weak axial ribs, as another poorly preserved possible volutid (letter **c**). A possible fascioliid (letter **d**), preserved as impression and attached by apex, and indeterminate gastropod, attached by periphery of all whorls (letter **e**). Also attached fragment of oyster(?) (letter **f**) and cidaroid spine (letter **h**). A microconch scaphitid, preserved as external mould (letter **g**) is associated, but apparently not attached.

The potential danekræ PD66, currently under evaluation (Fig. 6), is preserved as an impression of apex and seen from below, with attached cidaroid spine (letter **a**), ?bryozoan (letter **b**), sponge (letter **c**), bivalve fragment (letter **d**), indeterminate fragment (letter **e**) and indeterminate gastropod (letter **f**). The specimen awaits formal Danekræ evaluation and numbering.

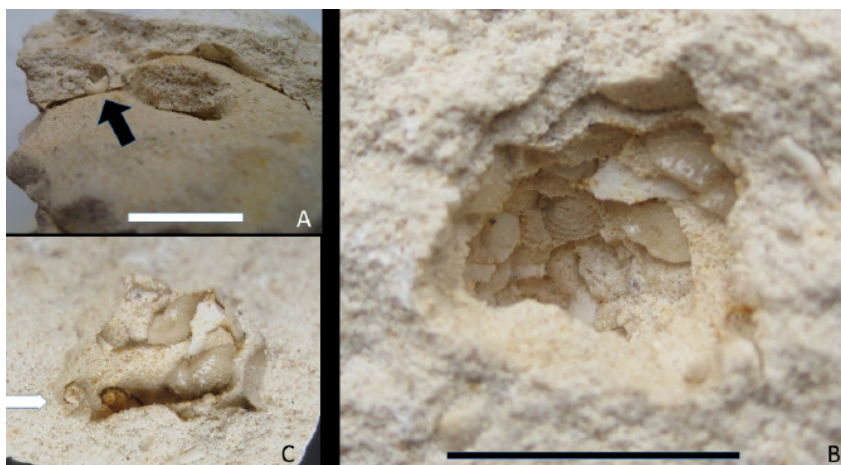


Fig. 13. *Xenophora nilssoni* Pacaud, 2016, with indeterminate gastropod attached, NHMM M1753, former Blom quarry, Berg en Terblijt, Maastricht Formation, Nekum Member (IVe-1/2-2). Scale bar equals 10 mm. **A:** NHMM M1473; **B:** NHMM M1753.

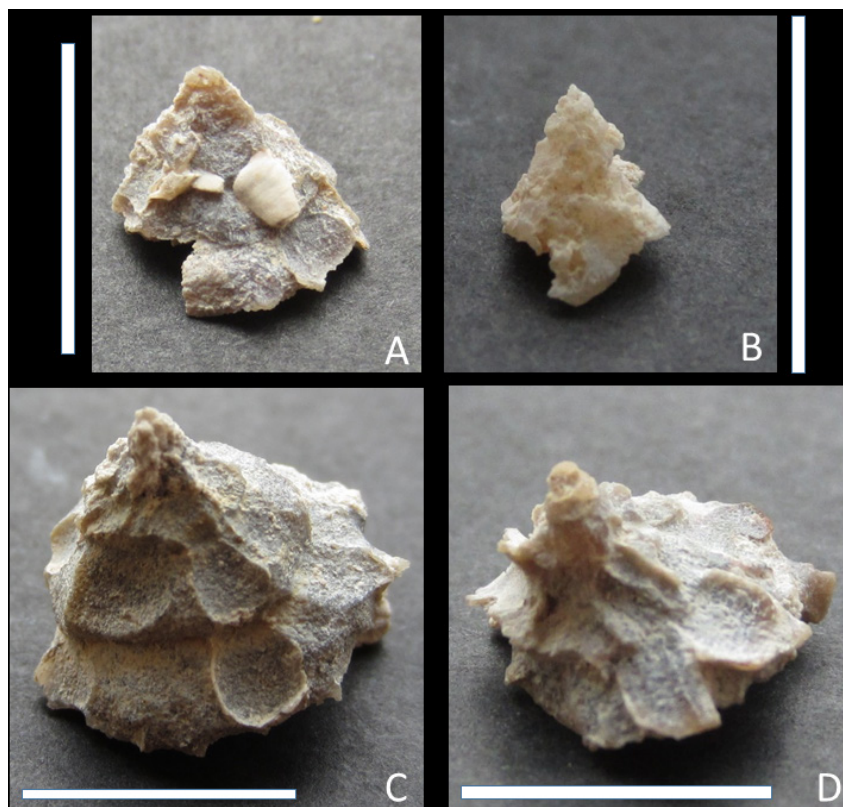


Fig. 14. *Xenophora nilssoni* Pacaud, 2016, silicified shells: **A:** NHMM M186A; **B:** NHMM M1509; **C:** NHMM M2077; **D:** NHMM M186C. Marnebel quarry, Eben Emael, Emael Member (**A, C, D**) and Gronsvelt Member, former ENCI quarry, Maastricht (**B**). Scale bars equal 10 mm.

Description of Dutch and Belgian material. Shells of small to medium size, ranging from a few millimetres in diameter, to around 50 mm; up to five whorls, but top part of shell preserved only in silicified material. Shell low, trochospiral; whorls flattened, sutures clearly impressed. Base apparently smooth, or with weak, curved spirals. Apical angle 76–100°, in most specimens around 90°. Attached foreign objects including serpulid polychaetes, mostly *Pyrgopolon mosae* (de Montfort, 1808), a common constituent in macrofossil assemblages of the middle and upper portions of the Maastricht Formation (Jäger 2005, 2012), as well as pectinoid, arcid, nuculanid, ?limopoid and ostreid bivalves, plus fragments of irregular echinoid tests (holasteroids; see Jagt 2000).

Single composite mould (NHMM JJ 7301) large sized, low and trochospiral, greatest diameter, as preserved c. 80 mm, apical angle c. 120°, also referred here, for now. Recognisable attached objects includ-

valves and brachiopod shell; close to shell margin on final whorl wrinkled ornament visible in places.

Discussion. Binkhorst van den Binkhorst (1861, p. 39) indicated an apical angle of 110° and his illustration of a large-sized internal mould shows curved growth lines on the base and even a furrow close to the umbilicus. Whether or not these features are indeed this clearly developed can only be judged on the basis of the original specimen.

For now, we use the name *Xenophora nilssoni* Pacaud, 2016 for this form, although the absence of shell material in the Maastricht Formation makes it impossible to assess the ornament, if any, of these particular specimens. In silicified specimens (NHMM Van Knippenberg Collection) traces of ornament, comparable to that seen in NHMM JJ 7301, are occasionally seen, both on whorls and on the base of the shell. Janssen (1984, pp. 188–190, pl. 53, fig. 5; pl. 54, fig. 1)

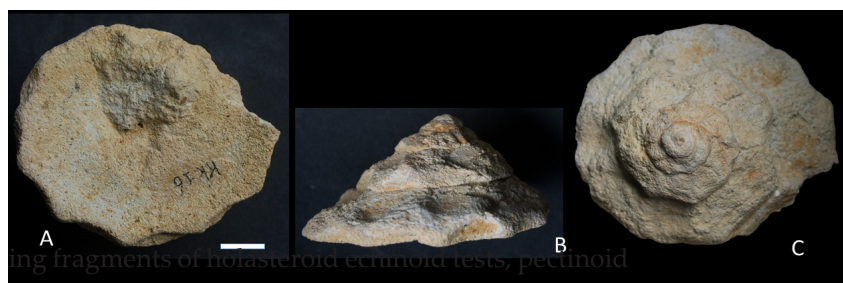


Fig. 15. *Xenophora nilssoni* Pacaud, 2016, internal mould, NHMM KK 16 (Renkens-Zijlstra Collection), Kunrade area, Kunrade Formation, upper part. Scale bar equals 10 mm.

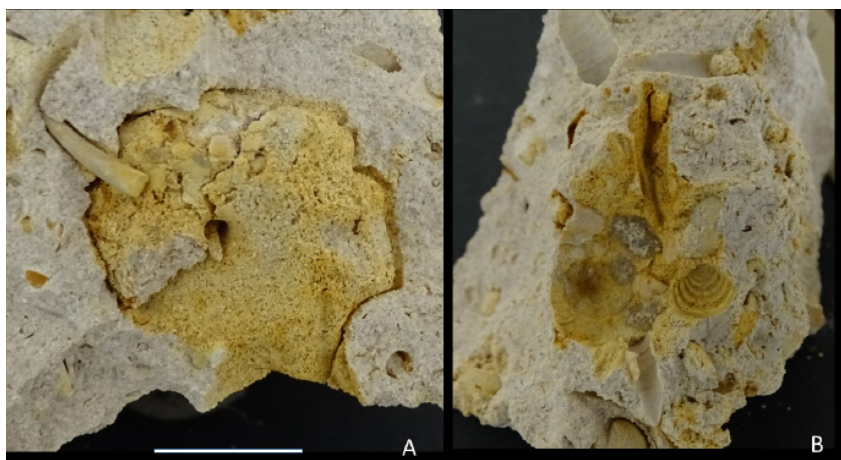


Fig. 16. *Xenophora nilssoni* Pacaud, 2016, internal and external moulds, NHMM JJ 15993; former ENCI quarry, Maastricht, Maastricht Formation, basal Nekum Member. Attached foreign objects include serpulid polychaetes, a fragmentary ostreid shell, an astartid bivalve and pieces of irregular echinoid test. Scale bar equals 10 mm.

demonstrated that two co-occurring Middle Miocene species, *Xenophora burdigalensis* (de Grateloup, 1847) and *X. deshayesi* (Michelotti, 1847) from the Winterswijk area (eastern Netherlands), could only be distinguished on the basis of shell ornament, in particular on the base.

Stratigraphical range. Vaals Formation (Gemmenich Member); Gulpen Formation (Vijlen Member, interval 6), Gronsveld, Emael, Nekum and Meerssen (up to IVf-6) members of the Maastricht Formation and Kunrade Formation in the south-east Netherlands and north-east Belgium; Møns Klint Formation in northern Jylland, Denmark, and elsewhere in Europe (Table 2).

***Xenophora* sp. 1**
Figs. 8–10

2013 *Xenophora onusta* auct. (? non Nilsson, 1827); Jagt *et al.*, p. 202, fig. 7-1/N, O.

2020 *Xenophora nilssoni*; Vellekoop *et al.*, p. 7, fig. 8L.

Material. Around 50 specimens in external and internal mould preservation, all from the Geulhem area, southern Limburg, the Netherlands (NHMM collections; Table 1).

Description. Small sized, not exceeding 20 mm in greatest diameter; low, trochospiral. Attached foreign objects include serpulid polychaetes, pectinoid, arcid and ostreid bivalves, plus fragments of irregular echinoid test and cheilostome bryozoans.

Discussion. For the time being, this is considered different from ‘populations’ from the Gronsveld, Emael and Nekum members (Maastricht Formation) and the Kunrade Formation, mostly on the basis of smaller size and base with close-set, curved growth lines.

Stratigraphical range. Lowermost Paleocene (lower Danian), Maastricht Formation, Meerssen Member, subunit IVf-7.

Records of Late Cretaceous xenophorids with attached gastropods

In contrast to other attached foreign objects, such as pieces of echinoid test, bivalve shells (entire or partial), serpulid worm tubes and cheilostome bryozoans, xenophorid shells with attached gastropod shells appear to be very rare. In the literature, only a handful of finds from the lower Campanian of the Hannover area (northern Germany; C. Schneider



Fig. 17. *Xenophora nilssoni* Pacaud, 2016, partial external and entire internal moulds, NHMM JJ 15832; former ENCI quarry, Maastricht, Maastricht Formation, basal Nekum Member. Merely scars of attached foreign objects left. Scale bar equals 10 mm.



Fig. 18. *Xenophora nilssoni* Pacaud, 2016, external and internal moulds, NHMM JJ 14865; former ENCI quarry, Maastricht, Maastricht Formation, basal Nekum Member. Attached foreign objects include larger bivalves (aragonitic) and flat pieces of irregular echinoid test. Scale bar in centimetres and millimetres.

2024), the Campanian of Mississippi, southern USA (Dockery 1993) and the Maastrichtian of Mexico (Kiel & Perrilliat 2001) have been recorded (Table 2).

Palaeoecological interpretations

Darragh & Kendrick (1994, p. 5, table 3), who recorded comparatively large-sized internal moulds of xenophorids from the upper Maastrichtian Miria Formation in the Carnarvon Basin (north-west Australia), considered *Xenophora* to be an ‘unspecialised

omnivore’ and pointed out that extant xenophorids were cryptic (Ponder 1983), preferring either grazing on fine algae, or microfauna collected from the substrate beneath the widened shell periphery. As far as attached foreign objects on xenophorid shells are concerned, phosphatic particles and inoceramid shell fragments were recorded by Darragh & Kendrick (1994, fig. 6).

Of note in the Meerssen Member, subunit IVf-7, is the fact that the commonest gastropod taxa are aporhaides and xenophorids. Shells of both families are found ‘floating’ in the biocalcarenitic matrix, in con-

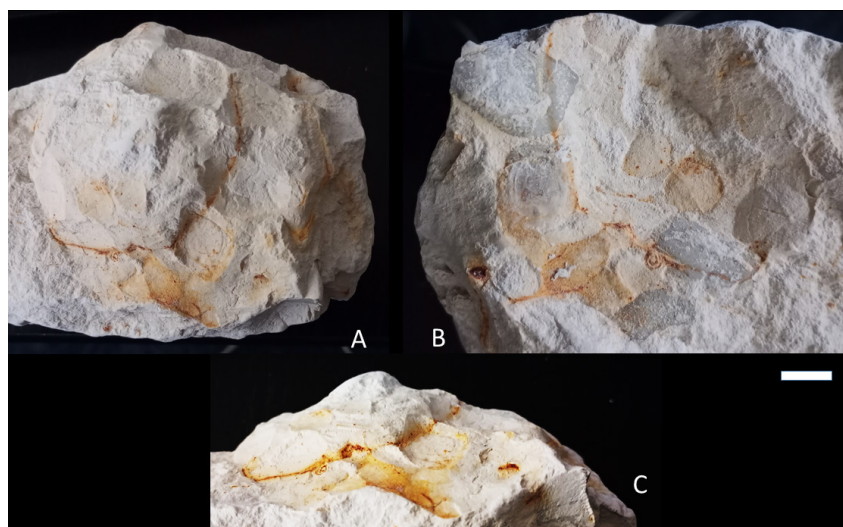


Fig. 19. *Xenophora nilssoni* Pacaud, 2016, composite mould, NHMM JJ 7301; Kreco (formerly CPL SA) quarry, Haccourt, Vijlen Member, interval 6, base + c. 4.5 m, with echinoid test fragments, a pectinoid bivalve and a brachiopod shell attached. Scale bar equals 10 mm.

trast to material from the underlying subunit IVf-6, and are considered to be preserved *in situ* (see also Jagt *et al.* 2013; Vellekoop *et al.* 2020).

Significance of the Danish gastropod fauna

In view of the fact that they possess aragonitic shells, the great majority of gastropods generally are very rare and/or poorly preserved in the Danish white chalk, comparable to other white chalk occurrences throughout Europe, with few exceptions (Kollmann & Odin 2001; Kutscher & Kullessa 2010). The best material is either that which became silicified early during diagenesis or 3D-preserved material from hardgrounds, with both internal and external moulds available. Gravesen & Jakobsen (2013) presented an overview of gastropod faunas from the upper Maastichtian white chalk in eastern Denmark, while T. Hansen (2019) described and illustrated gastropod assemblages from a hardground in the uppermost Maastichtian white chalk (zone 10, *stevensis-chitoniformis* brachiopod zone) and the lower Danian Cerithium Kalk facies along Stevns Klint (Sjælland, eastern Denmark).

The two specimens from Hillerslev are the only xenophorids known to date from the Danish white chalk. Specimen DK 1076 in particular provides an important contribution to our knowledge of gastropod faunas from the Maastichtian of Denmark in brachiopod zones 8 (*semiglobularis-humboldtii* Zone) and 9 (*humboldtii-stevensis* Zone), represented in the Hillerslev quarry succession.

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A brachiopod boring on a belemnite from the Santonian Bavnodde Greensand Formation of Bornholm, Denmark

FINN SURLYK, JESPER MILÀN & MARIANNE FALBE NATTESTAD



Geological Society of Denmark
<https://2dgm.dk>

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We report the first record of a brachiopod boring from the Santonian Bavnodde Greensand Formation on the south coast of the island Bornholm in the Baltic Sea. The minute, but highly characteristic boring is referred to the ichnospecies *Podichnus centrifugalis* Bromley & Surlyk, 1973. It occurs on a small, belemnite guard tentatively identified as *Goniocamax lundgreni lundgreni* (Stolley). The boring is composed of a number of small pits each formed by etching of one of the brachiopod pedicle rootlets or filaments. The pits are arranged in a small highly characteristic circle and their size increase gradually away from the centre of the circle. The Bavnodde Greensand contains a rich fauna, including five brachiopod species. *Terebratulula ciplensis* von Hanstein is interpreted as the most likely originator of the described specimen of *Podichnus centrifugalis*.

Keywords: *Podichnus centrifugalis*, Upper Cretaceous, pedicle trace, brachiopods, Bornholm, Denmark.

Finn Surlyk [finns@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen. Øster Voldgade 10, DK-1350 Copenhagen K, Denmark. Jesper Milàn [jesperm@oesm.dk], Kalk/Østsjælland Museer, Østervej 2, DK-4640 Faxe, Denmark. Marianne Falbe Nattestad [mfnattestad@gmail.com], Mulebyvej 43, 3700 Rønne, Denmark.

Borings made by brachiopod pedicles were identified during the study of Recent brachiopods in the collection of the Natural History Museum of Denmark (Surlyk 1972, fig. 8). It was noted that the pedicle of the brachiopod *Terebratulina retusa* Linnaeus, 1758 was split into rootlets which were able to etch holes in carbonate shell fragments. Subsequently a search by Richard Bromley of shelly fossils from the British Upper Cretaceous chalk housed at the Natural History Museum of England resulted in the finding of borings which were attributed to brachiopod pedicles. These borings were described as a new ichnogenus *Podichnus* Bromley & Surlyk, 1973 with the type species *Podichnus centrifugalis* Bromley & Surlyk, 1973.

The aim of the study is to describe the first find on the island of Bornholm in the Baltic Sea of the brachiopod boring *Podichnus centrifugalis* Bromley & Surlyk, 1973 from the Santonian Bavnodde Greensand Formation and to interpret the possible originator of the boring. The specimen is stored in the collection of the Natural History Museum of Denmark (MGUH 35001 & 35002).

Geological setting and stratigraphy

The island of Bornholm in the Baltic Sea is part of a fault block mosaic situated in a N–S oriented dog leg on the NW–SE-trending fundamental tectonic lineament, the Sorgenfrei-Tornquist Zone (Fig. 1). The zone forms the northern border of the Danish Basin and continues SE-wards into Poland (e.g. Liboriusen et al. 1987; Mogensen & Korstgård 2003; Surlyk & Lykke-Andersen 2007). The south coast of Bornholm exposes Palaeozoic, Triassic, Jurassic and Cretaceous sediments in small fault blocks (Gry 1969a,b; Graversen 2009). The Upper Cretaceous succession in this area comprises the Cenomanian Arnager Greensand, the Coniacian Arnager Limestone and the Santonian Bavnodde Greensand at the top. These formations are separated by major unconformities and the faunas of the Bavnodde Greensand are described by Ravn (1921, 1946), Douglas & Rankin (1969), Solakius (1989), Kennedy & Christensen (1991), Tröger & Christensen (1991), Packer & Hart (1994), Christensen & Schulz (1997) and Nattestad & Milàn (2021).

The age of the Bavnodde Greensand has been much debated as the different fossil groups seem to indicate different ages. The belemnites were interpreted as indicating a late Coniacian – early Santonian age (Christensen & Schulz 1997), whereas the foraminifers indicate a Santonian age (Douglas & Rankin 1969; Solakius 1989; Packer 1991; Packer et al. 1989). The inoceramid bivalves likewise indicate a Santonian age Tröger & Christensen (1991). Ammonites are rather rare in the formation and indicate a Santonian age (Kennedy & Christensen (1991). The different ages given in the literature to some extent reflect that different levels of the formation are exposed in the low coastal cliff due to a north-ward dip and the irregular shape of the coastline seen in map view. Detailed reference to the different fossil sites are given in Christensen & Schulz (1997) but these are not at all easy to follow. Another locality map was presented by Brüsich (1984). Christensen & Schulz (1997) assign the lower part of the formation where the belemnite with the *Podichnus* boring was found to the upper Coniacian, but a definitive age cannot be

ascertained for the time being. Thus, a Santonian age is given conforming with the bulk of the literature.

Geological age of the belemnite

The studied specimen of *Podichnus centrifugalis* Bromley & Surlyk, 1973 was found on a belemnite from the Bavnodde Greensand close to a locality named Sengedynen, roughly in the middle part of the long stretch of exposure (Figs 1, 2). The locality map of Christensen and Schulz (1987, fig. 4) is not easy to compare with official topographic maps. Place names are few and poorly defined, reflecting the nature of the exposure of the formation, an about 4 km long, low coastal cliff with very few hall marks. The main fix points are Bavnodde and Horsemeye Odde, two promontories in the middle and eastern end of the cliff, respectively (Fig. 2). A commonly used unofficial place name is Forchhammers Odde a very minor feature which by most authors are placed as indicated in Fig. 2. According to the third

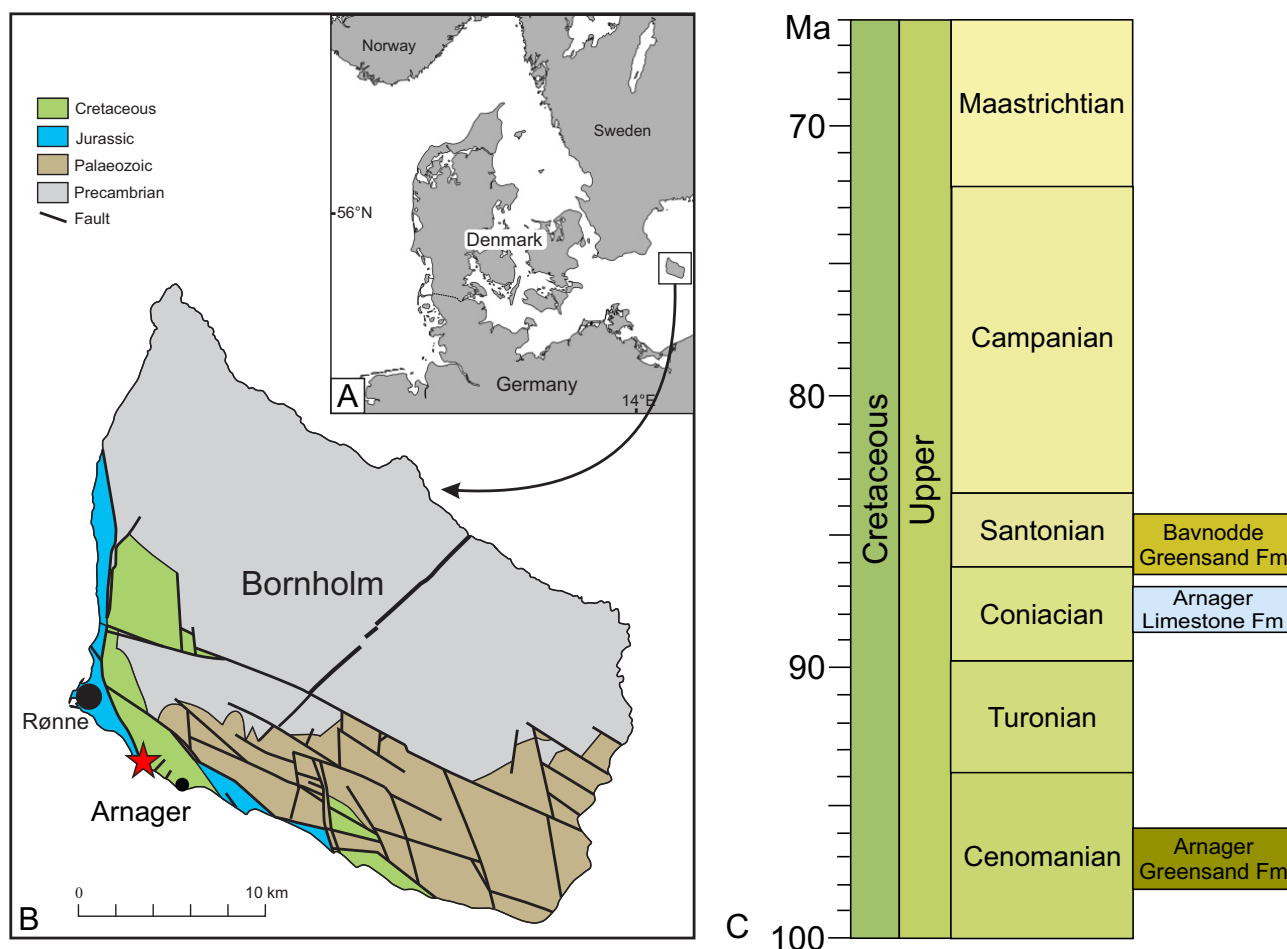


Fig. 1. A. Position of the island of Bornholm in the Baltic Sea south of Sweden. B. Simplified geological Map of Bornholm, showing the extent of the Cretaceous formations along the south coast of Bornholm. Modified after Graversen (2009). The Bavnodde Greensand Formation is exposed in the coastal cliffs between Rønne and Arnager. C. Upper Cretaceous stratigraphy of Bornholm.

author MFN, the finder of the belemnite, the location is in the stretch of the cliff termed F in Christensen & Schulz (1987, fig. 4). This stretch has yielded belemnites showing that it belongs to the oldest part of the formation close to the boundary with the underlying Arnager Limestone Formation and assigned to the upper Coniacian by Christensen & Schulz (1997) and to the Santonian on the basis of foraminifers (Packer 1991).

The belemnite

The brachiopod boring is situated on a belemnite which cannot be satisfactorily determined neither to genus or species as it is a small, juvenile specimen. The belemnite is 4 cm long and 5 mm wide (Fig. 3A). Splitting has been avoided in order not to risk destroying the *Podichnus* boring and the statistics used in species characterizations by Christensen & Schulz (1997) thus cannot be obtained. It tapers slightly towards the posterior end. The specimen is tentatively referred to *Goniocamax lundgreni lundgreni* (Stolley) which is common in the Coniacian – lower lower Santonian.

The brachiopod boring

Ichnogenus *Podichnus* Bromley & Surlyk, 1973

Type species *Podichnus centrifugalis* Bromley & Surlyk, 1973

The type species is found on the dorsal valve of the brachiopod *Carneithyris carnea* (Sowerby) found in the chalk of the Campanian *Belemnittella mucronata* zone, Mousehold, Norwich, England. It was interpreted as formed by the thick, unbranched pedicle like those of the Recent brachiopods *Hemithyris psittacea* and *Macandrevia cranium* (Bromley & Surlyk 1973, p. 364).

The brachiopod boring described here is not easy to see with the naked eye but all details can be studied with a hand lens, or better with a binocular microscope. The colour contrast between the white borehole pits and the brown colour of the belemnite gives, however, a clear picture of the boring (Fig. 3B). We have accordingly chosen not to clean the pits in order to keep their visibility. The brachiopod boring conforms well to the holotype of *Podichnus centrifugalis* Bromley & Surlyk, 1973 and is close to similar with other examples shown in Bromley & Surlyk (1973), notably their figure 6B where the *Podichnus* is situated on an upper Campanian belemnite from the chalk at Westlegate, Norwich, England.

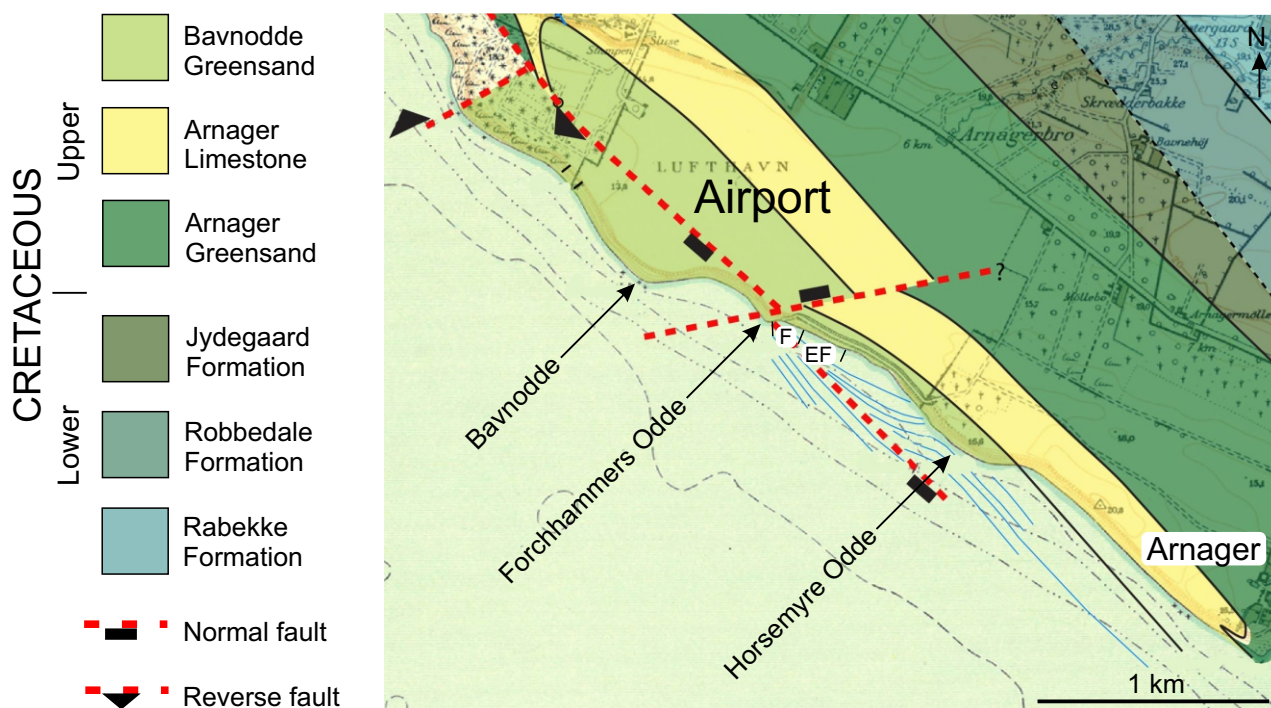


Fig. 2. Preliminary geological map by Arne Thorshøj Nielsen, showing a section of the south coast of Bornholm, covering the area with exposure of the Bavnodde Greensand Formation. The small exposures of the formation are indicated with the letter codes used by Christensen & Schulz (1997) and Brusch (1984). The belemnite with the brachiopod boring *Podichnus centrifugalis* was found in the coastal cliff at section F, just east of Forchhammers Odde.

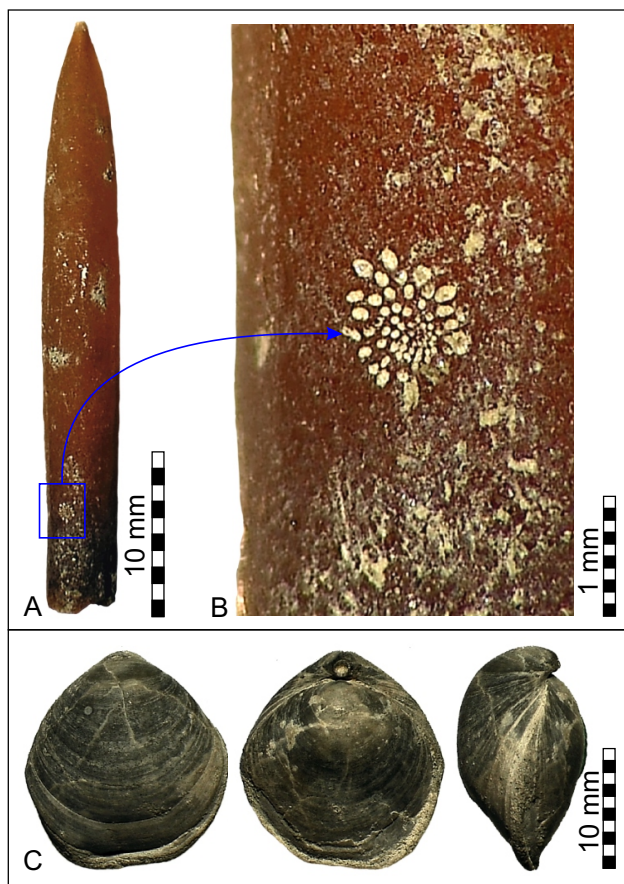


Fig. 3. A. The belemnite (MGUH 35001) with the trace of *Podichnus centrifugalis* Bromley & Surlyk, 1973. The belemnite is tentatively identified as *Goniocamax lundgreni lundgreni* (Stolley). B. detail of A showing the brachiopod boring *Podichnus centrifugalis* Bromley & Surlyk, 1973. Note the circular outline of the group of pits, which increase in diameter away from the centre of the circle. The individual pits are circular close to the centre and gradually become elongate ellipsoidal towards the margins of the circle. The pits were made by individual threads or filaments of the pedicle, the diameter of which was somewhat smaller than 1 mm. C. The figured brachiopod '*Terebratula ciplensis*' is interpreted as the most likely culprit (MGUH 35002). It was found at the same locality as the belemnite with *Podichnus centrifugalis* shown in A and B.

The present specimen (Fig. 3B) referred to *Podichnus centrifugalis* from the Bavnodde Greensand is placed about 6 mm from the posterior end of the belemnite guard. It comprises about 58 small, shallow pits arranged in circle with a diameter of 1.1 mm. A few of the smallest pits are somewhat difficult to distinguish from non-biological marks on the surface of the belemnite. The size of the pits increases from 0.05 to 0.2 mm towards the margins of the circle, in a manner corresponding well to the name '*centrifugalis*'. The largest pits are elongate oval with a length axes pointing radially away from the centre of the circle. The smallest pits at the centre are circular to subcircular in outline.

Originator of the *Podichnus* boring

The originator of the described specimen of *Podichnus centrifugalis* cannot easily be interpreted. However, a number of brachiopods have been found in the Bavnodde Greensand but modern descriptions are lacking and both genus and species designations are outdated. They were described under the following names by Ravn (1921): *Lingula cretacea* Lundgren, *Rhynchonella* cf. *ala* Marklin, *Rhynchonella cordiformis* Posselt, *Terebratula ciplensis* von Hanstein and *Terebratulina striata* Wahlenberg. Brüschi (1984) referred *T. ciplensis* of Ravn (1921) to the genus *Concinnithyris* on the basis of external morphology.

The lingulid brachiopod can be excluded as an originator of the *Podichnus* due to its burrowing mode-of-life. *Rhynchonella* cf. *ala* is difficult to evaluate because Ravn (1921) only had one poorly preserved non-illustrated specimen at his disposal. '*Rhynchonella cordiformis*' is in external view very similar to *Homaletarhynchia limbata* (von Schlotheim) well known from the Maastrichtian chalk of northern Europe (Steinich 1965; Surlyk 2025). Like in this species the pedicle opening of '*R. cordiformis*' is very small and Brüschi (1984) describes the species as having a very thin shell with a strongly reduced foramen which in some shells is closed by secondary shell material. The species is accordingly interpreted as secondarily free-living possibly with a thin threadlike pedicle which could function as a sort of anchor. Only the juvenile specimens seem to have had a thin, threadlike functional pedicle. '*T. ciplensis*' has a suberect beak with a large permesothryrid foramen with a convex symphytium. It probably possessed a stout, functional pedicle although there is not necessarily a direct correlation between the diameter of the foramen and the thickness of the pedicle (Richardson 1997). *Terebratulina striata* occurs in a great variety of facies under a number of different species names such as *striatula* and *chrysalis*. It most likely possessed a rootlike pedicle as its recent relatives (Surlyk 1972). It would probably leave a much more irregular *Podichnus* trace than the one described here. It is rare in the formation and Brüschi (1984) does not indicate it as part of the main fauna, whereas '*Ter-*

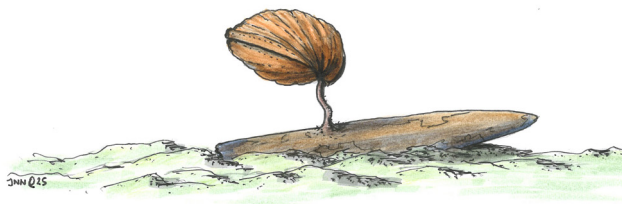


Fig. 4. Reconstruction of the belemnite with the brachiopod boring *Podichnus* and the most likely culprit '*Terebratula ciplensis*' on the seafloor during deposition of the Bavnodde Greensand Formation. Drawing by Jakob Noe-Nygaard.

terebratula ciplyensis' is recorded with 66 specimens. A fine specimen of '*Terebratula ciplyensis*' was recently found at the same locality as the *Podichnus*-bearing belemnite described in the present study. It is thus interpreted as the most likely culprit of the boring (Fig. 3C, 4).

Summary

A fine specimen of the brachiopod boring *Podichnus centrifugalis* Bromley & Surlyk, 1973 is described. It was found on a belemnite from the Santonian Bavnodde Greensand Formation at Sengedynen in the low coastal cliff on the south coast of the island of Bornholm in the Baltic Sea. The belemnite is tentatively referred to *Goniocamax lundgreni lundgreni* (Stolley) from the lowest part of the Bavnodde Greensand. The originator of the trace cannot be determined directly, but the section has yielded five brachiopod species which all have to be considered as representing the potential originator of the trace. The small size of the belemnite substrate and of the trace itself is suggestive of a small originator, either a small species or a juvenile. Among the brachiopods described from the Bavnodde Greensand only one species, '*Terebratula ciplyensis*' (von Hanstein) seems to be a likely originator of the trace.

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Arne Thorshøj Nielsen is thanked for discussion of the age of the Bavnodde Greensand Formation and for placing his revised but unpublished geological map of the south coast of Bornholm at our disposal. We acknowledge Bodil W. Lauridsen for useful comments to the manuscript and Jakob Noe-Nygaard for drawing of the reconstruction in Figure 4.

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Pentaditrupe nickcavei sp. nov. and ‘revived’ *Pentaditrupe interjuncta* (Jessen & Ødum, 1923) (Polychaeta, Serpulidae) from the Paleocene of Denmark, with some remarks on the middle Paleocene mesofauna

TOMÁŠ KOČÍ, JESPER MILÀN, STEN LENNART JAKOBSEN, KAI INGEMANN SCHNETLER, MANFRED JÄGER, LENKA VÁCHOVÁ & MARTINA KOČOVÁ VESELSKÁ



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The serpulid tubeworm genus *Pentaditrupe* is characterized by its gently curved tube with pentagonal cross-section, formed by five longitudinal edges or keels. Unlike most serpulid genera and unlike Jurassic species of *Pentaditrupe*, Cretaceous and Paleocene species of *Pentaditrupe* are never found attached to solid substrates, but instead inhabited soft-bottom environments of fine-grained seafloors that later lithified into chalk, limestone, or marlstone. A new species, *Pentaditrupe nickcavei* sp. nov., is described from the lower part of the Kerteminde Marl Formation (Selandian, middle Paleocene) of the Gundstrup gravel pit, Fyn, Denmark. This species represents the first record of the genus *Pentaditrupe* from the Selandian, thus extending the stratigraphic range of this genus and its temporal overlap with its presumed descendant *Ditrupe* by several hundred thousand years. Previously, the youngest known *Pentaditrupe* tubes were dated to the late Danian (early Paleocene). Moreover, comparative studies on the microstructure of an early Danian tube from Holtug quarry, Sjælland, Denmark, resulted in “revival” of the species *Pentaditrupe interjuncta* (Jessen & Ødum, 1923), originally introduced for early Danian tubes from Voxlev, Jylland, Denmark, but since decades considered a junior synonym of Late Cretaceous *Pentaditrupe subtorquata* (Münster in Goldfuss, 1831). While in the outer aspect the tubes of Cretaceous *P. subtorquata* and Danian *P. interjuncta* are indistinguishable, there are small but distinct differences in microstructure. The early Selandian *P. nickcavei* differs from both of these geologically older species by its larger maximal tube diameter, sharper longitudinal edges or keels, and by details in microstructure.

We also document new occurrences of the serpulid *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023 in the Gundstrup gravel pit. *Neovermilia* and *Pentaditrupe* were characteristic faunal elements already in the Late Cretaceous and Danian limestones. Their presence in the Kerteminde Marl Formation somewhat mitigates the otherwise significant faunal turnover observed between the Danian and the Selandian. Finally, we report the first occurrence of the slit worm-snail *Tenagodus* from the Kerteminde Marl and discuss its paleoecological interactions with associated mesofauna.

Key words. Serpulids, Paleocene, Selandian, Kerteminde Marl, Gundstrup gravel pit

Tomáš Kočí [protula@seznam.cz] Ivančická 581, Prague 9 – Letňany, 19900, Czech Republic, and Paleontological Department of Natural History Museum, National Museum at Prague, Cirkusová 1740, 193 00 Prague 9 Horní Počernice, Czech Republic, and Institute for Palaeobiology and Evolution, Novi trg 59, 1241 Kamnik, Slovenia. Jesper Milàn [jesperm@oesm.dk], KALK/Museums of East Zealand, Østervej 2, 4640 Faxe, Denmark. Sten L. Jakobsen [slj@oesm.dk], KALK/Museums of East Zealand, Østervej 2, 4640 Faxe, Denmark. Kai Ingemann Schnetler [ingemann@schnetler.dk], Fuglebakken 14, Stevnstrup, 8870 Langå, Denmark. Manfred Jäger [langstein.jaeger@web.de], Lindenstrasse 53, 72348 Rosenfeld, Germany. Lenka Váchová [lenka.vachova@nm.cz], Paleontological Department of Natural History Museum, National Museum at Prague, Cirkusová 1740, 193 00 Prague 9 Horní Počernice, Czech Republic. Martina Kočová Veselská [veselskamartina@gmail.com], Institute for Palaeobiology and Evolution, Novi trg 59, 1241 Kamnik, Slovenia, and [kocovam@gli.cas.cz] Institute of Geology, the Czech Academy of Sciences, v.v.i., Rozvojová 269, 165 00 Prague 6, Czech Republic.

<http://zoobank.org/urn:lsid:zoobank.org:pub:78596342-37C1-432A-A947-F4410F8749FD>

The annelid family Serpulidae Rafinesque, 1815 is a highly specialised group of marine segmented worms (class Polychaeta, subclass Sedentaria; see Kupriyanova *et al.* 2023) adapted to inhabiting self-secreted calcareous tubes (hence the common name ‘calcareous tubeworms’). In most species, these tubes are attached to various hard substrates. Serpulids occur in all seas, across all depths, and within habitats of normal marine salinity. Only a few species are adapted to hypo- or hypersaline waters, and just one species is known to inhabit freshwater in karst caves. The calcareous tubes have significant fossilization potential (Jäger 1983, 2005; Sklenář *et al.* 2013; Kočí *et al.* 2017).

The oldest known fossil serpulids date back to the Permian (Sanfilippo *et al.*, 2017, 2018, Ramsdale 2021; Słowiński *et al.* 2024). Serpulids diversified extensively during the Mesozoic and Cenozoic (Ippolito *et al.* 2014) and are currently represented by several hundred species inhabiting modern marine environments (*e.g.*, ten Hove & Kupriyanova 2009; Kupriyanova *et al.* 2020; Rouse *et al.* 2022, and references therein). Kočí *et al.* (2023) reported the first occurrence of serpulids in the Selandian Kerteminde Marl, *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, as a species not reworked from the Danian sediments.

This study aims to: (1) document additional specimens of *N. gundstrupensis*, (2) describe *Pentaditrupa nickcavei* sp. nov., a second known serpulid species from the Kerteminde Marl, including a detailed analysis of its microstructure, (3) describe *P. interjuncta* from the Danian Limestone, (4) report the first occurrence of the gastropod *Tenagodus* from the Kerteminde Marl and (5) interpret the palaeoecology of the associated mesofaunal assemblage.

Geological and geographical setting

After the K–Pg boundary event, sedimentation in the Danish Basin during the early Paleocene was initially dominated by carbonates. Part of the Middle Danian Limestones are excellently exposed in the huge working quarry at Faxe, and the Early Danian Limestone in the long natural cliff of Stevns Klint, including several working and abandoned quarries in the cliff or a few kilometres further inland. In one of these abandoned quarries situated directly at the cliff east of the village of Holtug, the tube of *Pentaditrupa interjuncta* was found.

However, by the end of the Danian, carbonate sedimentation had ceased due to a major regression approximately 61.6 million years ago (Vandenbergh *et al.* 2012; Cohen *et al.* 2013, updated 2022). This regression resulted in an erosional unconformity below the overlying Selandian deposits (*e.g.*, Thomsen & Heilmann-Clausen 1985; Clemmensen & Thom-

sen 2005). The subsequent Selandian transgression established a new depositional regime dominated by siliciclastic sediments, including the Lellinge Greensand in eastern Denmark and its lateral equivalent, the Kerteminde Marl Formation, in deeper depositional settings towards Fyn (Clemmensen & Thomsen 2005). The Selandian Kerteminde Marl Formation is interpreted to have been deposited in an outer shelf environment within the deep neritic zone, at depths of about 100–150 m. This setting was characterized by high sedimentation rates due to significant input of reworked chalk, well-oxygenated bottom waters with low current activity, and low planktonic productivity (Clemmensen & Thomsen 2005; Heilmann-Clausen 2010). The Formation reaches a maximum thickness of up to 150 metres, thinning over the Ringkøbing–Fyn High and thickening northward towards the Sorgenfrei–Tornquist Zone (Sorgenfrei & Buch 1964; Clausen & Huuse 1999, 2002; Clemmensen & Thomsen 2005). The Selandian depocenter of the Kerteminde Marl Formation is interpreted to have been located in the western part of Sjælland (Clemmensen & Thomsen 2005). The Kerteminde Marl Formation is overlain by the Selandian–Thanetian Æbelø Formation, which consists predominantly of clay and represents progressively deeper depositional conditions (Clemmensen & Thomsen 2005).

In recent years, the Kerteminde Marl Formation has been recognized for its rich and diverse fauna, especially in glacially derived blocks at the Gundstrup gravel pit. Schnetler & Nielsen (2018) described a diverse mollusk fauna comprising 133 species. This mollusk assemblage was later expanded by Schnetler & Nielsen (2021), who added one more gastropod species. In the present paper, we describe the first occurrence of the gastropod *Tenagodus* Guettard, 1770, from the Kerteminde Marl. The brachiopod *Terebratulina chrysalis* (von Schlotheim, 1813) was reported by Schröder & Surlyk (2024). King (1994) documented ostracods, sponges, and echinoderm fragments from the Kerteminde Marl, all specimens are housed in the collections of the Natural History Museum of Denmark. Vertebrate remains, including abundant skeletal elements of teleost fishes (King 1994; Schwarzhans *et al.* 2021), turtles (Myrvold *et al.* 2018), and several undescribed shark teeth, are also deposited in the collection of the Natural History Museum of Denmark. Trace fossils are represented by *Lepidenteron mortensenii* (Schwarzhans *et al.*, 2021) and *Kopetichnus rasmussenae* (Vallon & Rindsberg, 2022).

Material and methods

The studied material includes four rock samples containing six serpulid tubes of *Pentaditrupa nickcavei* sp. nov. from the Gundstrup gravel pit; one tube of

Pentaditrupe interjuncta (Jessen & Ødum, 1923) from the early Danian of Holtug quarry, and seven tubes of *Pentaditrupe subtorquata* (Münster in Goldfuss, 1831) from the Campanian of Misburg and Höver in northern Germany, four new specimens of the serpulid *Neovermilia gundstrupensis* Kočí, Milán & Jäger, 2023 from the Gundstrup gravel pit, and two blocks with associated mesofauna. All figured specimens are kept in the collection of the Natural History Museum of Denmark (MGUH & NHMD) and Øst-sjællands Museer (OESM).

The microstructure of the tube wall of *Pentaditrupe subtorquata* was previously studied by Vinn (2005), who analyzed the surfaces of longitudinal sections using the following procedure: „The examined tu-

bes were ground in longitudinal direction, polished, and etched with 1% acetic acid for 1 min prior to SEM examination. Thereafter, the same tubes were re-polished and treated with a 1 : 1 mixture of 25% glutaraldehyde and 1% acetic acid, to which alcian blue was added (GA-solution), for 5–45 min before SEM study.” Ippolitov & Rzhavsky (2008), in their paper on Recent spirorbin serpulids, noted: „The microstructure of tube wall was studied on the surfaces of longitudinal cracks without etching.” For the present study, we applied etching to a naturally broken tube wall at the anterior part of the tube using 1% acetic acid for 3 minutes, followed by drying and examination under SEM in a low vacuum. This method has the advantage of being non-destructive

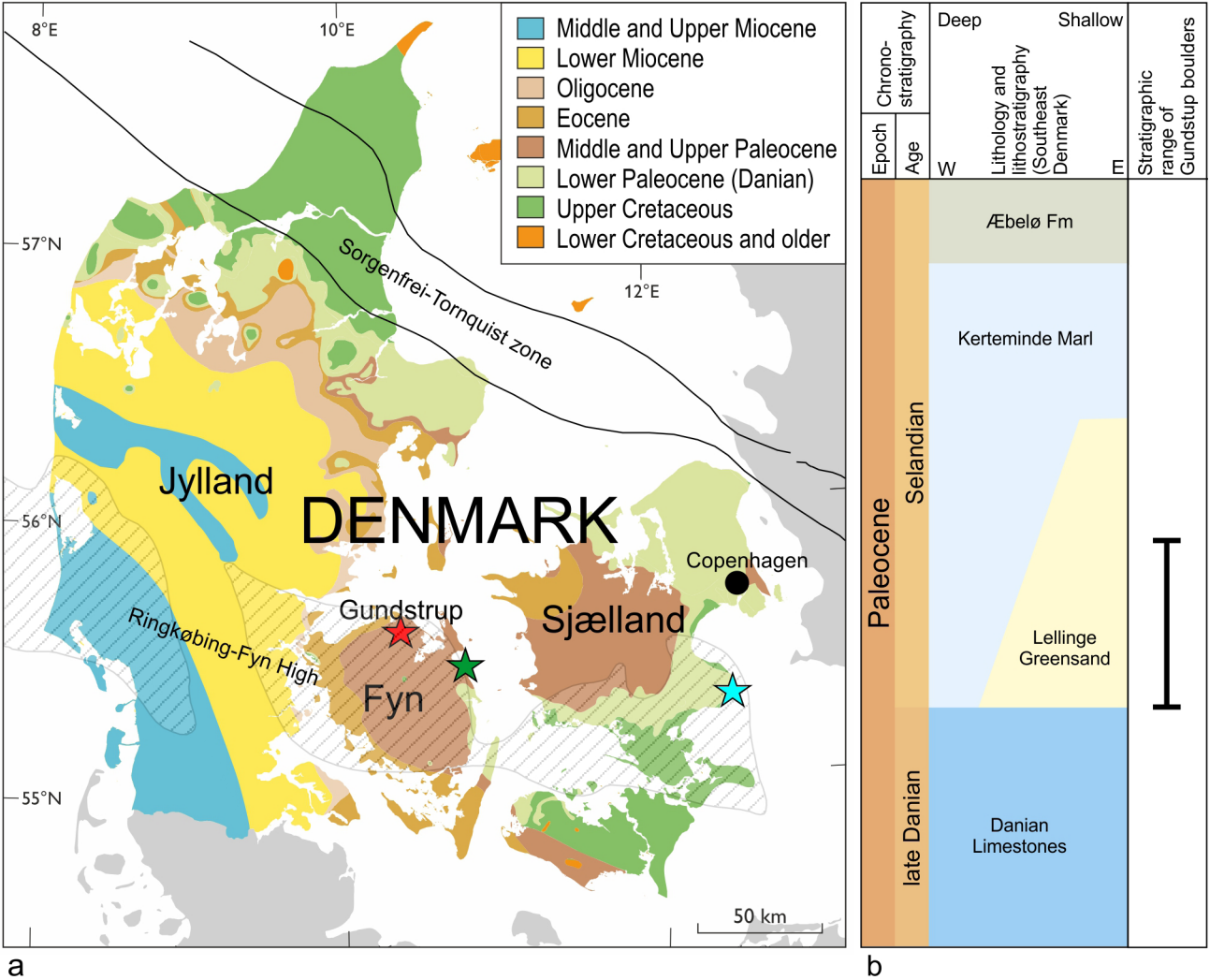


Fig. 1. a. Map of the pre-Quaternary subsurface in Denmark. The Gundstrup gravel pit is located on the isle of Fyn (55.56° N; 10.35° E), indicated by a red asterisk. Even though the boulders of Kerteminde Marl found here had been transported by Pleistocene glaciers, they have been found within the subsurface area consisting of Selandian (middle Paleocene) sediments. The nearest other outcrop of the Kerteminde Marl is at its type locality Lundsgårds Klint, situated south of the town of Kerteminde, indicated by a green asterisk. The Holtug quarry is indicated by a blue asterisk. Modified after Håkansson & Pedersen (1992) and Schwarzhans *et al.* (2021). b. Schematic section showing upper Danian and Selandian stratigraphy of southeast Denmark. Modified after Clemmensen & Thomsen (2005).

to the studied specimens. SEM imaging was performed using a Hitachi S-3700 N at the Palaeontological Department of the National Museum in Prague.

This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/urn:lsid:zoobank.org:pub:11B8BD11-DE59-46F9-8EAC-B31557461BE7>

Systematic palaeontology

Class Polychaeta Grube, 1850

Subclass Sedentaria Lamarck, 1818

Infraclass Canalipalpata Rouse and Fau-chald, 1997

Order Sabellida Levinsen, 1883

Family Serpulidae Rafinesque, 1815

Subfamily Serpulinae Rafinesque, 1815

Tribe Ficopomatini Pillai, 1960

Genus *Pentaditrupa* Regenhardt, 1961

Type species: *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) (type by original designation).

Description. While Early Jurassic representatives consist of a short posterior tube portion attached to a solid substrate and a long free tube portion, Late Cretaceous and Paleocene tubes are free, lacking any rest of an attached tube portion; they are adapted for lying freely on soft seafloor; for discussion of similarly shaped serpulid tubes, see Seilacher *et al.* (2008).

Tube small, medium-sized, or moderately large, slowly increasing in diameter, usually gently and regularly curved like an elephant's tusk, a horn, or a single whorl of a wide open spiral, less often straight or irregularly curved. The free tubes are characterized by five longitudinal ornaments equally spaced all around the circumference, causing the tube's pentagonal or pentalobate cross-section. Usually, these longitudinal ornaments are rounded edges or rounded low keels, but less often, mainly in small juvenile tube parts, they may be sharp keels, but never developed as high combs. In a few Late Cretaceous populations, longitudinal ornamentation is reduced, and the cross-section is almost circular. Transverse ornamentation is usually lacking, except for delicate, not elevated, chevron-shaped incremental lines, which protrude between the keels and retreat at the keels. No peristomes. The surface is smooth and usually a bit shiny; Vinn & Kupriyanova (2011) mentioned *Pentaditrupa* among the taxa possessing a dense out-

er protective tube layer, presumably an adaptation against drilling predation by gastropods and against dissolution in deeper water.

Microstructure. Concerning the method of tube construction, the tube wall consists of two main layers: (1) The thick, usually bright brown or bright yellow outer layer is the parable layer. It is built and prolonged at the aperture at the anterior end of the worm. In longitudinal section, it consists of parable-shaped = chevron-shaped increments, whose outer thighs form a thick sublayer causing a slightly reduced tube diameter at the aperture, whereas their inner thighs form a much thinner sublayer. (2) The thin inner layer is the cylinder layer. It is added to the interior surface of the tube and consists of very thin-walled cylinder-shaped increments that stick inside each other. Often the cylinder layer is pale white, transversely striated, leafy, and slightly scaling-off. (3) Additionally, in well-preserved tubes, a very thin innermost organic sheet may be present.

In contrast, in SEM images of longitudinal and transverse sections, at least of Late Cretaceous and Paleocene *Pentaditrupa* tubes, the visually most conspicuous boundary between outer and inner tube layer is located at a different level in a slightly more exterior position: inside the parable layer, with the conspicuous, strongly curved, chevron-shaped connection between outer and inner thighs of the increments of the parable layer belonging to the inner tube layer. In the present study, we follow this definition of layers and sublayers seen in SEM images, from exterior surface to interior consisting of (1) a rather thick outer layer, which represents the outer thighs of the chevron-shaped increments of the parable layer, and (2) a rather thin inner layer, which comprises (2a) the conspicuous, strongly curved connection between the outer and inner thighs of the parable layer, (2b) the inner thighs, (2c) the cylinder layer, and, if the tube is well preserved, (2d) a thin organic sheet.

In SEM images of longitudinal sections, sublayer (2a) is usually most conspicuous. It consists of long, needle-shaped spherulitic prismatic crystals. Generally, the crystals are oriented approximately (not exactly) perpendicular to the boundaries between the increments, and due to the strong curvature of these boundaries, the orientation of the crystals in the outer layer differs by up to c. 80 degrees from their orientation in the inner layer. In longitudinal sections, both elements – the curved boundaries and the needle-shaped spherulitic prismatic crystals – together form a characteristic pattern resembling water fountains. The crystals are longer and arranged more strictly parallel to each other in the inner layer than in the outer layer, where they are arranged roughly parallel but slightly irregularly.

In longitudinal sections, microstructure shows small but conspicuous differences in the water fountain pattern of sublayer (2a) between species from the Late Cretaceous, Danian, and Selandian ages. These differences concern (1) the relative visual predominance of boundaries between chevron-shaped increments versus visual predominance of the needle-shaped crystals, (2) the length of the crystals, and (3) maybe the grade of curvature – narrow or wide – of the water fountain pattern and of the boundaries between chevron-shaped increments.

All studied Late Cretaceous and Paleocene tubes of the genus *Pentaditrupe* have a spherulitic prismatic (SPHP) microstructure sensu Vinn (2005, Vinn *et al.* 2008c) in the inner layer and outer layer of the tube wall.

Stratigraphical range. *P. nickcavei* sp. nov. prolongs the geological record of the genus *Pentaditrupe* from Hettangian to Selandian. Hitherto, *Pentaditrupe* was known only to reach up to the Danian (Jäger 2005).

Discussion. Apart from its more or less rounded pentagonal cross-section, the tube of *Pentaditrupe* closely resembles the circular tube of its close relative and chronological successor, *Ditrupe* Berkeley, 1835. If neglecting several *Ditrupe*-like but possibly not closely related serpulid species from the Late Jurassic and Early Cretaceous of the Arctic realm, the earliest secured representative of the genus *Ditrupe* is *D. schlotheimi* Rosenkrantz, 1920 from the middle Danian (C) and late Danian (D). In consequence, the timespan of secured stratigraphic co-occurrence (although not at the same localities) of the genera *Pentaditrupe* and *Ditrupe*, which hitherto was believed to last only from Middle to Late Danian, is now prolonged up to the Selandian. As *D. schlotheimi* is very common in some facies in Denmark, the Netherlands, and Belgium, *Pentaditrupe* even survived the first bloom of the genus *Ditrupe*.

Nevertheless, the geological record of the genus *Pentaditrupe* still shows a surprisingly wide gap ranging from late Early Jurassic (Toarcian) to late Early Cretaceous (middle Albian) (Jäger 2005; Kočí *et al.* 2024). Apart from the fact that only the Early Jurassic tubes often possess a short attached posterior tube portion, whereas Late Cretaceous and Paleocene tubes entirely lack such an attached portion, the geologically old and young tubes are morphologically so similar to each other that it seems appropriate to unite them in the same genus. However, we cannot be sure: Homeomorphies between not closely related serpulid taxa are very common, as demonstrated in comparable cases of morphologically very similar ‘pairs’ of tubes, one pair characterized by quadrangular cross-section (fossil *Nogrobs* de Montfort, 1808 versus recent *Spirodiscus* Fauvel, 1909, for discussion

see Kupriyanova and Ippolitov 2015), the other pair or trinity characterized by hexagonal cross-section (fossil *Tectorotularia* Regenhardt, 1961 versus fossil *Pyrgopolon* (*Hamulus*) Morton, 1834 (for discussion see Jäger in Rantuch *et al.* 2024) versus recent *Serpula crenata* Ehlers, 1908).

***Pentaditrupe nickcavei* sp. nov.**

Figs 2–8

Etymology. In honor of the Australian musician, writer, actor, artist, and performer Nick Cave for his life-long dedication to music, literature, and lyrics.

Holotype. The tube shown in Fig. 2a, MGUH 35025.

First paratype. The tube shown in Fig. 2b, MGUH 35026.

Second paratype. The tube shown in Fig. 3a, 3a1, 3a2, MGUH 35207.

Type locality. Gundstrup gravel pit, Fyn, Denmark.

Type stratum. Selandian, lower part of Kerteminde Marl Formation.

Material. Four rock samples with 6 tubes altogether, including the holotype and two paratypes.

Diagnosis. An unattached, medium- to moderately large-sized, usually gently and regularly curved species of the genus *Pentaditrupe*. The five sides are slightly concave and meet each other laterally by forming five sharp longitudinal edges or low and narrow but sharp keels, which are not rounded even in the largest tube parts. In SEM images of longitudinal sections, the boundaries between the chevron-shaped increments predominate in visibility over the needle-shaped spherulitic prismatic crystals (Fig. 7a2, 7a3).

Description. Tube diameter gradually increasing up to c. 5.2 mm. The longest preserved tube length is 41.9 mm as shown in Fig. 5a, though the tubes were undoubtedly longer originally. Cross-section pentagonal with sharp or only very slightly rounded edges. Transverse ornamentation consists of densely spaced, chevron-shaped (V-shaped) delicate striae on a generally glossy surface. No peristomes. The tube wall is relatively thick, 0.6 mm in a paratype. Lumen circular, 1.2–1.3 mm in diameter in a paratype. In SEM images, the needle-shaped spherulitic prismatic crystals are relatively short in the inner layer.

Discussion. The tubes of *P. nickcavei* differ from those of *P. interjuncta* and *P. subtorquata* by their sharper

longitudinal edges or low keels and by reaching a wider maximum tube diameter. Small differences in microstructure are discussed below in the General discussion chapter.

***Pentaditrupa interjuncta* (Jessen & Ødum, 1923)**
Figs 9–11

1923 *Ditrupa interjuncta* n. sp. – Jessen & Ødum, pp. 28–29, Text-Fig. 11, Pl. 2, Fig. 8a–d.

1926 *Ditrupa interjuncta* – Ødum, p. 167.

1931 *Ditrupula subtorquata* Münster. – Nielsen, p. 96.

1961 *Ditrupa* (*Pentaditrupa*) *interjuncta* (Ødum). – Regenhardt, p. 75.

? 1970 *Pentaditrupa* aff. *interjuncta* (Ødum) – Rosenkrantz, p. 426.

pars 1983 *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) – Jäger, p. 56, non Pl. 7, Figs 1–8.

pars 2005 *Pentaditrupa subtorquata* (Münster in Goldfuss, 1831) – Jäger, p. 167, non Pl. 8, Figs 1–2.

Holotype. The tube figured in Jessen & Ødum (1923, Pl. 2, Fig. 8a), Natural History Museum of Denmark, MGUH 34985. In this museum, also the other tubes of *Ditrupa interjuncta* figured in Jessen & Ødum are kept; their numbers are: Pl. 2, Fig. 8b: MGUH 34986; Pl. 2, Fig. 8c: MGUH 34987; Pl. 2, Fig. 8d: MGUH 34988; Text-Fig. 11: MGUH 34996.

Type locality. Voxlev quarry, Jylland, Denmark.

Type stratum. lower Danian, Bryozoan Limestone.

Material. A single damaged tube (OESM 13330).

Diagnosis. An unattached, medium-sized, usually gently and regularly curved species of the genus *Pentaditrupa*. *P. interjuncta* is characterized by its five blunt, but only slightly rounded and conspicuous longitudinal edges or low keels, with slightly concave or plane areas in between. In SEM images of longitudinal sections, the needle-shaped crystals predominate in visibility over the boundaries between the chevron-shaped increments. The crystals are relatively tall in the outer layer.

Description. Tube diameter gradually increasing up to c. 3 mm according to Jessen & Ødum's original description, but reaching only 2.3 mm in the tube from Holtug. Longest preserved tube length is 26 mm according to Jessen & Ødum, who already stated that originally that undoubtedly the tubes had been considerably longer, and c. 21 mm in the incomplete tube from Holtug (Fig. 9 shows only a part of its former length, after the tube had been cut for preparing transverse sections). Cross-section pentagonal with



Fig. 2. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, Holotype, MGUH 35025, b, First Paratype, MGUH 35026.



Fig. 3. *Pentaditrupe nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, a1, a2. Second Paratype, MGUH 35027.

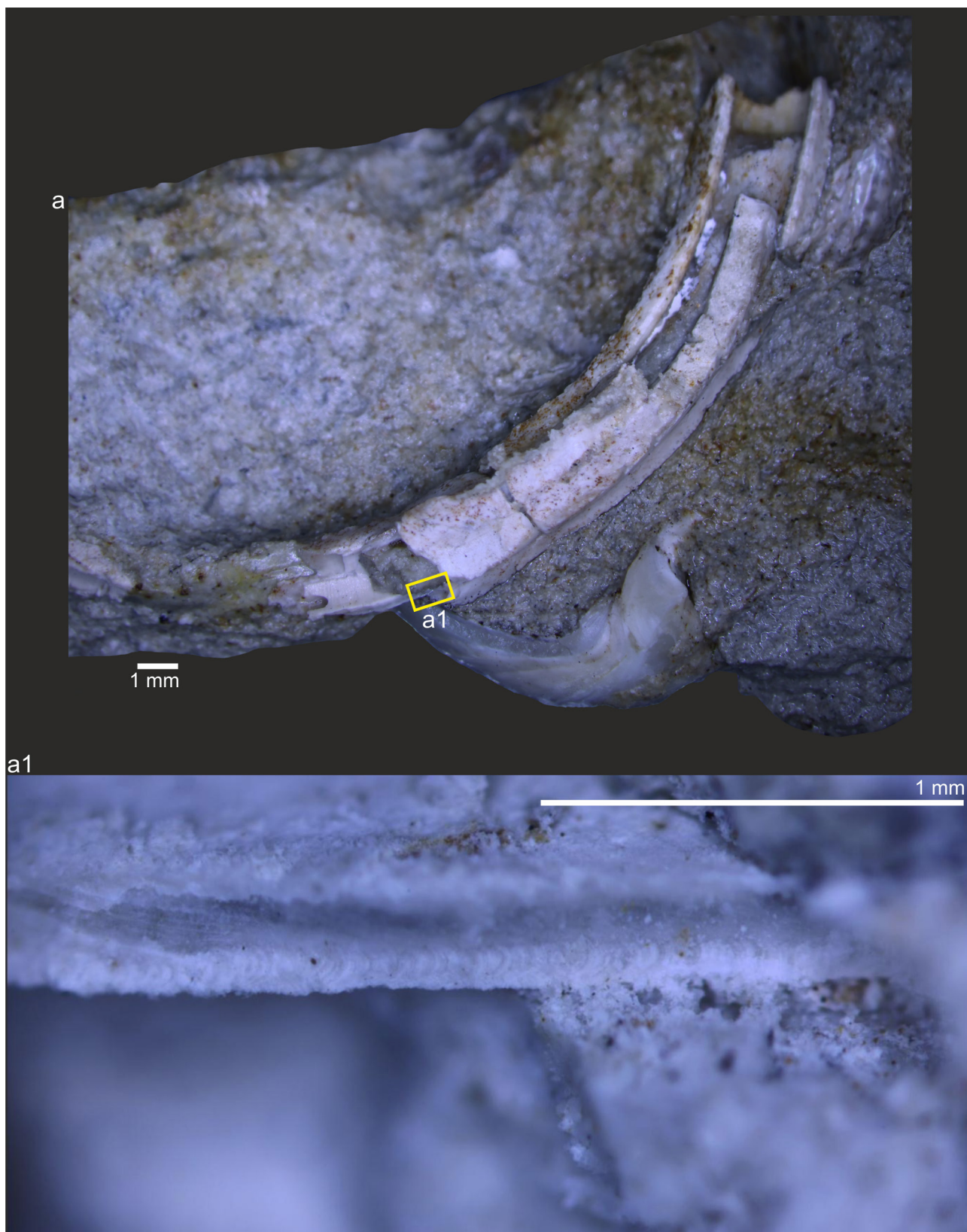


Fig. 4. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a. Damaged tube in sediment, which also includes a valve of the oyster *Pycnodonte* (*Phygraea*) *vesiculare* (Lamarck, 1806). The rectangle shows the region figured in a1. a1. Detail in high magnification showing chevron-shaped increments at the transition from outer to inner parable layer. (Specimen was lost during preparation).

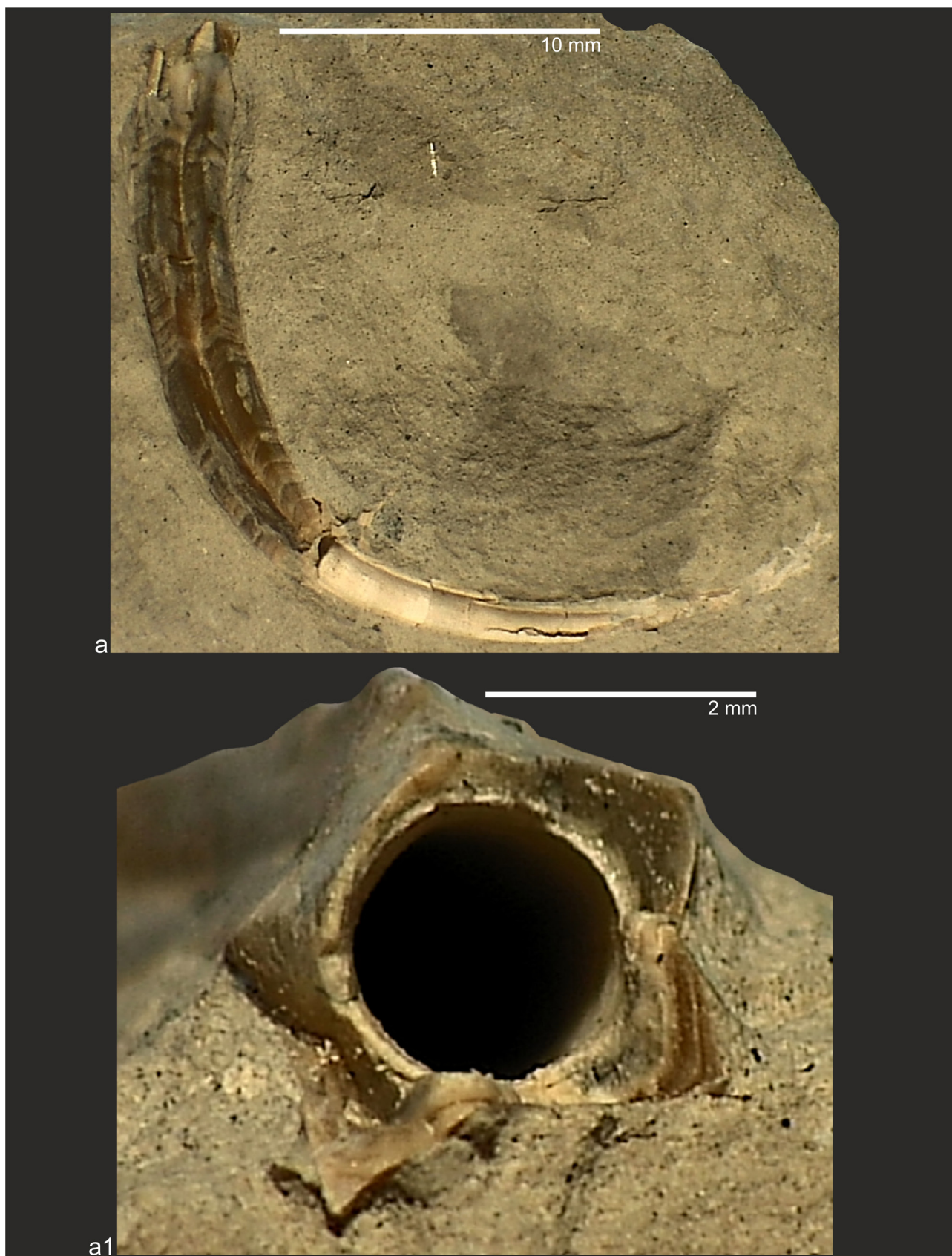


Fig. 5. *Pentaditrupa nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a. Tube in substrate. a1. Pentagonal anterior cross-section, MGUH 35028.

rounded edges or pentalobate. On the interior surface of the tube wall, a thin organic sheet (sensu Vinn 2013a) is preserved (ios in Fig. 11b1).

Discussion. The tubes of *P. interjuncta* as well as those of *P. subtorquata* differ from the tubes of *P. nickcavei* by their more rounded longitudinal edges and by reaching only a smaller maximum tube diameter than in *P. nickcavei*. In external tube morphology and in tube diameter, *P. interjuncta* and *P. subtorquata* are usually indistinguishable. Small differences in microstructure are discussed in the General discussi-

on chapter below.

Rosenkrantz (1970, p. 426) listed *P. aff. interjuncta* from the Upper Danian locality Agatdal, Greenland.

General discussion of the three studied species and their microstructure

Exterior tube morphology. The more common twisting of the longitudinal edges around the longitudinal axis in *P. interjuncta* stated by Jessen & Ødum (1923) is simply a consequence of more common twisting of

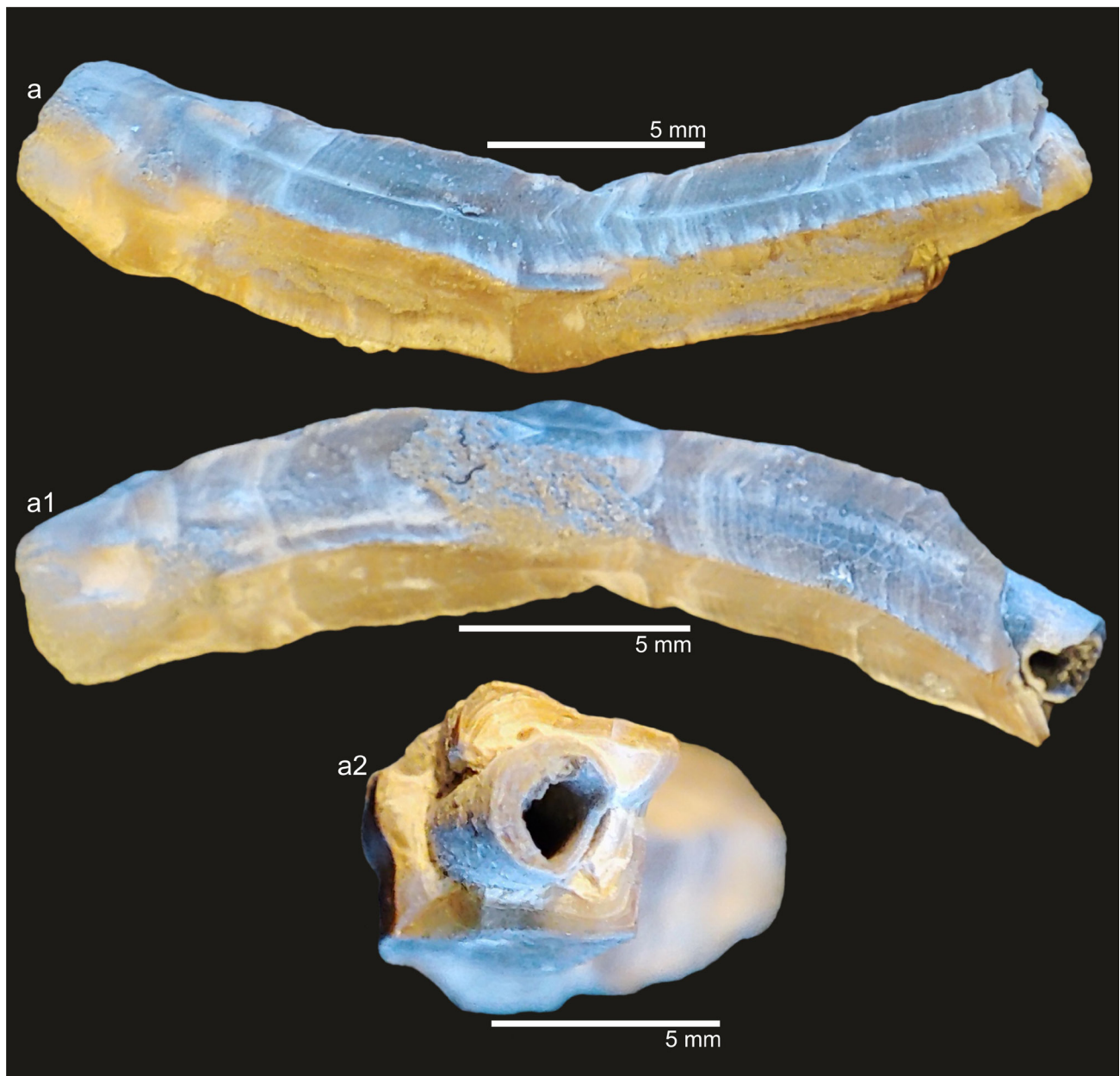


Fig. 6. *Pentaditrupe nickcavei* sp. nov., early Selandian, Gundstrup gravel pit. a, a1. Longitudinal views of the tube with longitudinal and transverse ornamentation. a2. Posterior cross-section, on the left side of the photograph, partly longitudinally broken approximately along the boundary between the outer and inner tube wall layer, MGUH 35029.

the animal around its longitudinal axis during ontogeny, perhaps caused by more often changing the position and orientation of the tube including its animal by agitated water or by action of vagil marine animals. Moreover, a relatively wide morphologic variety concerning rounded longitudinal edges versus sharp keels, and convex versus plane versus concave sides between the edges respectively keels, is seen in most *Pentaditrupe* species.

Only an extremely rounded variety of Late Cretaceous *P. subtorquata* has no morphological equivalent in the two Paleocene *Pentaditrupe* species. Such a variety from the Campanian was named '*Protula pruinosa*' by Regenhardt (1961). Its longitudinal edges are inconspicuous and very much rounded, and the sides between the edges may be convex instead of concave or plain, so that the tube's cross-section becomes almost perfectly circular, resembling the genus *Ditrupe*. From around the lower/upper Cam-

panian boundary to the upper Maastrichtian, such circular tubes co-occur with tubes of the usual *Pentaditrupe* shape in north Germany (Jäger 1983). Apart from the edges and cross-section, the circular tubes perfectly match the morphology and structure of *P. subtorquata*.

Tube microstructure. In the 21st century, SEM images showing tiny crystals and other structural details visible in high magnification in transverse, longitudinal, and surface-parallel horizontal sections became widely used and studied. Following several earlier studies (e.g., Sanfilippo 1996, 1998; Sanfilippo & Mòllica 2000), researchers, predominately Olev Vinn and co-authors, studied a high number of recent and fossil serpulid species and other 'tubeworms' and classified these details (Vinn 2005, 2007, 2008, 2011, 2013a, b, 2020, 2021; Vinn & Kupriyanova 2011; Vinn & Mutvei 2009; Vinn *et al.* 2008a, b, c). They found

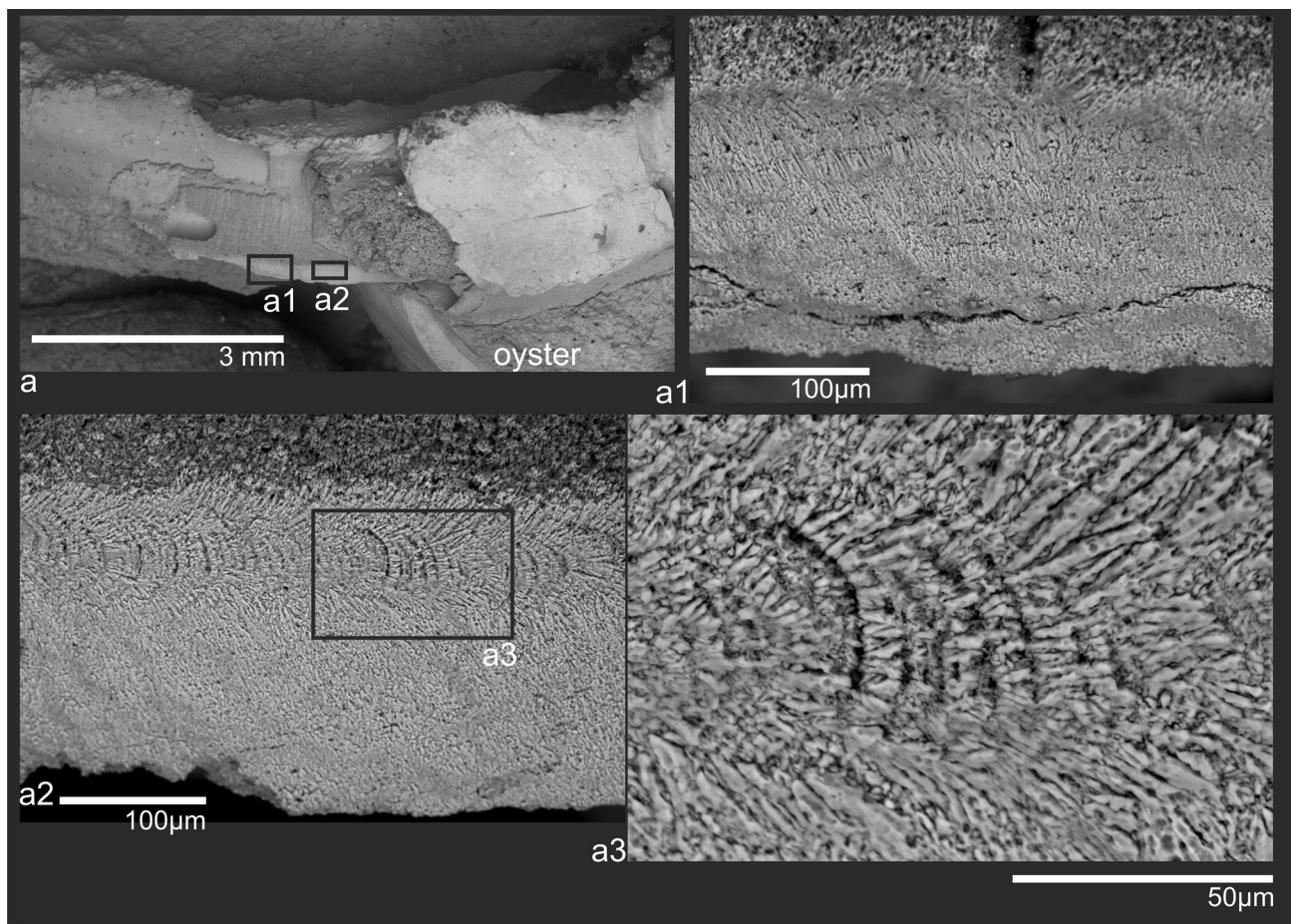


Fig. 7. Microstructure of *Pentaditrupe nickcavei* sp. nov., early Selandian, Gundstrup gravel pit, same specimen as in Fig. 4. Longitudinal section. a. Overview of broken tube wall, SEM image. a1. Outer tube layer consisting of several sublayers, which are the increments of the outer parable layer, constructed of short spherulitic prismatic crystals oriented perpendicular to the tube's longitudinal axis. a2. Inner tube layer showing growth lamellae with spherulitic prismatic crystals. a3. Detail of inner tube layer, distinctly showing the curved boundary lines between increments with short spherulitic prismatic crystals, which are arranged in a pattern resembling water fountains. The microstructure of inner and outer tube layers matches the spherulitic prismatic structure (SPHP) type sensu Vinn *et al.* (2008c).

that serpulid tubes consist of only a single layer in many species, but two, three, or even four layers in other species, and that according to the shape of the tiny crystals of which these layers consist and the orientation of these crystals as visible in transverse, longitudinal, and horizontal sections of the tube, the microstructures can be classified in at least 13 distin-

guishable types.

Such SEM studies constituted a conspicuous step forward in studying tube microstructure by showing hitherto unknown details. It is generally acknowledged that studies, descriptions and comparisons of microstructure are a strong and valuable tool – combined with studies on recent worm animals, their

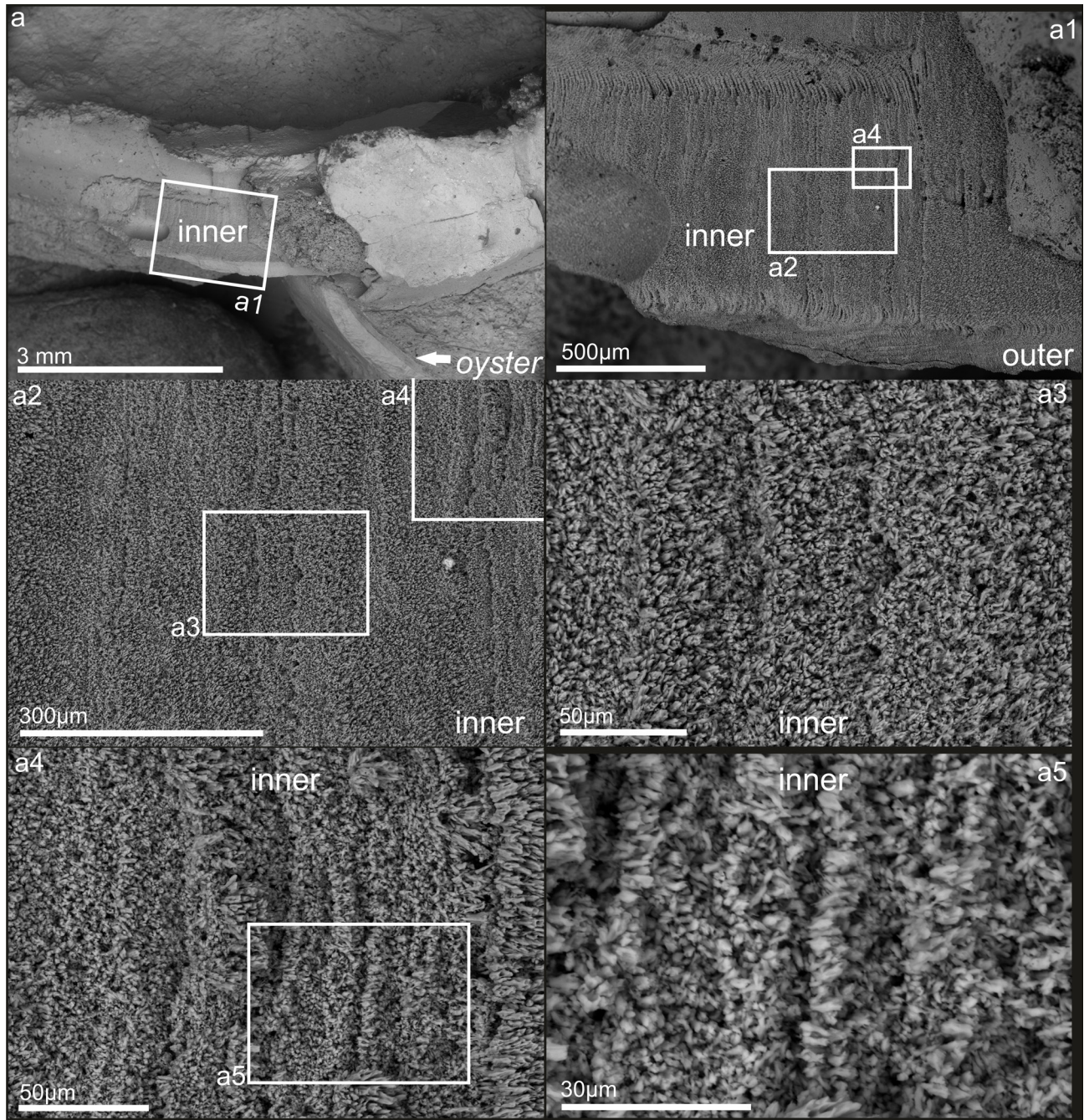


Fig. 8. Microstructure of *Pentaditrupe nickcavei* sp. nov., early Selandian, Gundstrup gravel pit, same specimen as in Fig 4. Longitudinal section. a. Overview of the interior surface of the inner tube layer. a1. Detail of a showing transverse growth lamellae consisting of short prismatic crystals. a2–a5. These growth lamellae are oriented perpendicular to the tube's longitudinal axis, whereas their short crystals are oriented parallel to the tube's longitudinal axis. The microstructure matches the spherulitic prismatic structure (SPHP) type sensu Vinn *et al.* (2008c).

opercula, exterior tube morphologies and genetics – in order to distinguish serpulid tubes from superficially similar tubes of other worm-shaped organisms, and, within family Serpulidae, to distinguish between subfamilies, tribes, genera, subgenera and, in some cases, species, and to investigate their phylogenetic relationships (e.g., Kupriyanova *et al.* 2023).

While microstructure of many different species has been described, figured and discussed, not much is known yet about intraspecific or (palaeo-)geographic variability of microstructure, because usually only few SEM images of only a single tube or very few tubes of each species are provided, and, due to the usually high magnification of SEM images, they



Fig. 9. *Pentaditrupa interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry, OESM 13330. a. Overview. a1. Lateral view. a2. Posterior transverse section. a3. Anterior transverse section.

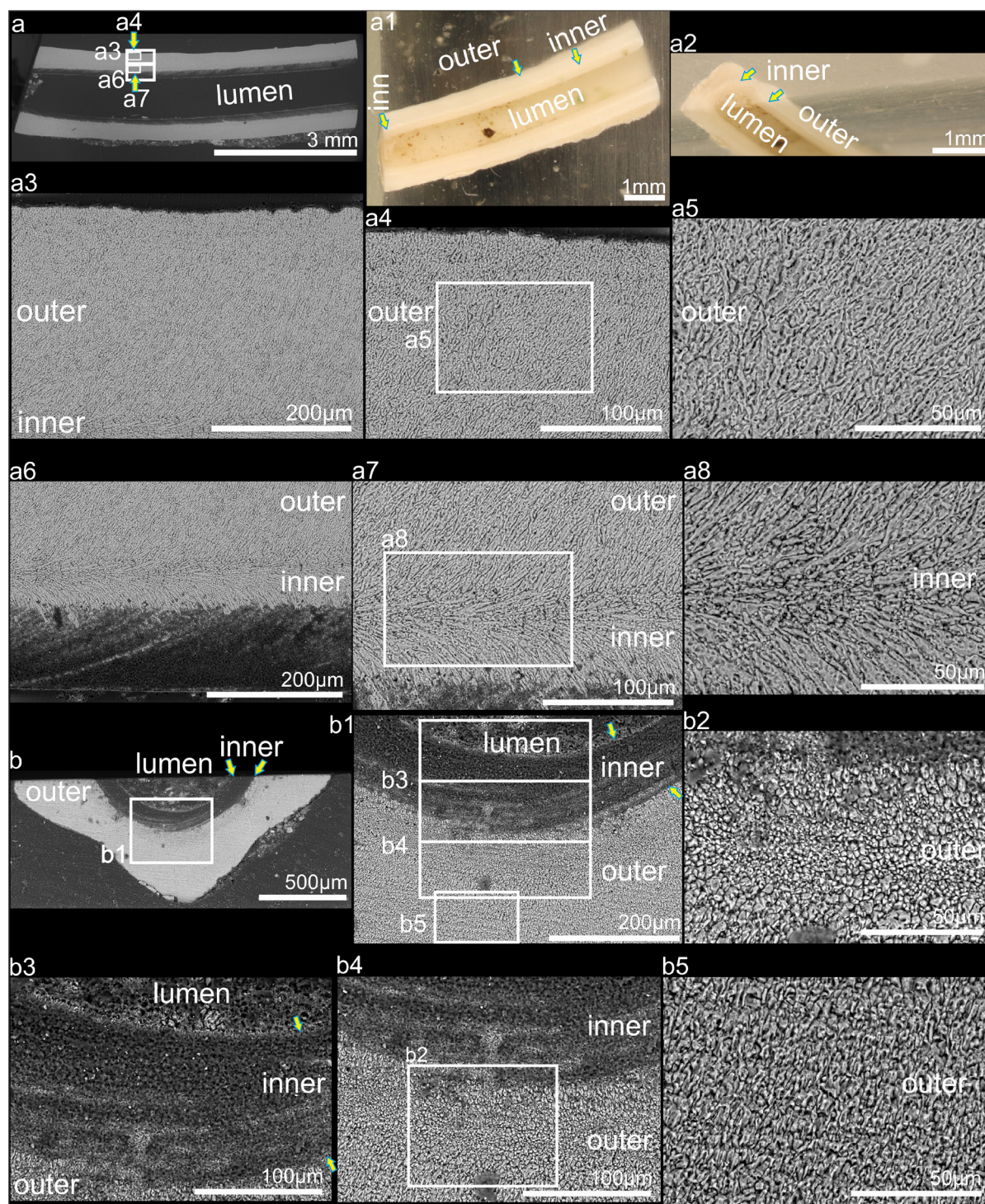


Fig. 10. Microstructure of *Pentaditrupe interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry. a–a8. OESM 13330. Longitudinal section. a–a2. Overviews showing the tube wall, rectangles indicate positions of detailed views in the following subfigures. a3–a7. Details of the outer tube layer in different magnifications showing approximately parallel oriented tall spherulitic prismatic crystals, which are oriented perpendicular to the inner growth lamellae. a6–a8. Details of the inner tube layer at different magnifications. a7–a8. Details of the boundary region between outer and inner tube layers, which is marked by spherulitic crystals arranged in a conspicuous pattern resembling water fountains; these crystals are oriented perpendicular to the less conspicuous chevron-shaped increments at the transition between outer and inner parallel layers. b–b5. Transverse section, rectangles indicate positions of detailed views in the following subfigures. b1–b2, b4–b5. Details of the outer tube layer in different magnifications. b1, b3–b4. Details of the inner tube layer at different magnifications. – The microstructure matches the spherulitic prismatic (SPHP) type sensu Vinn *et al.* (2008c).

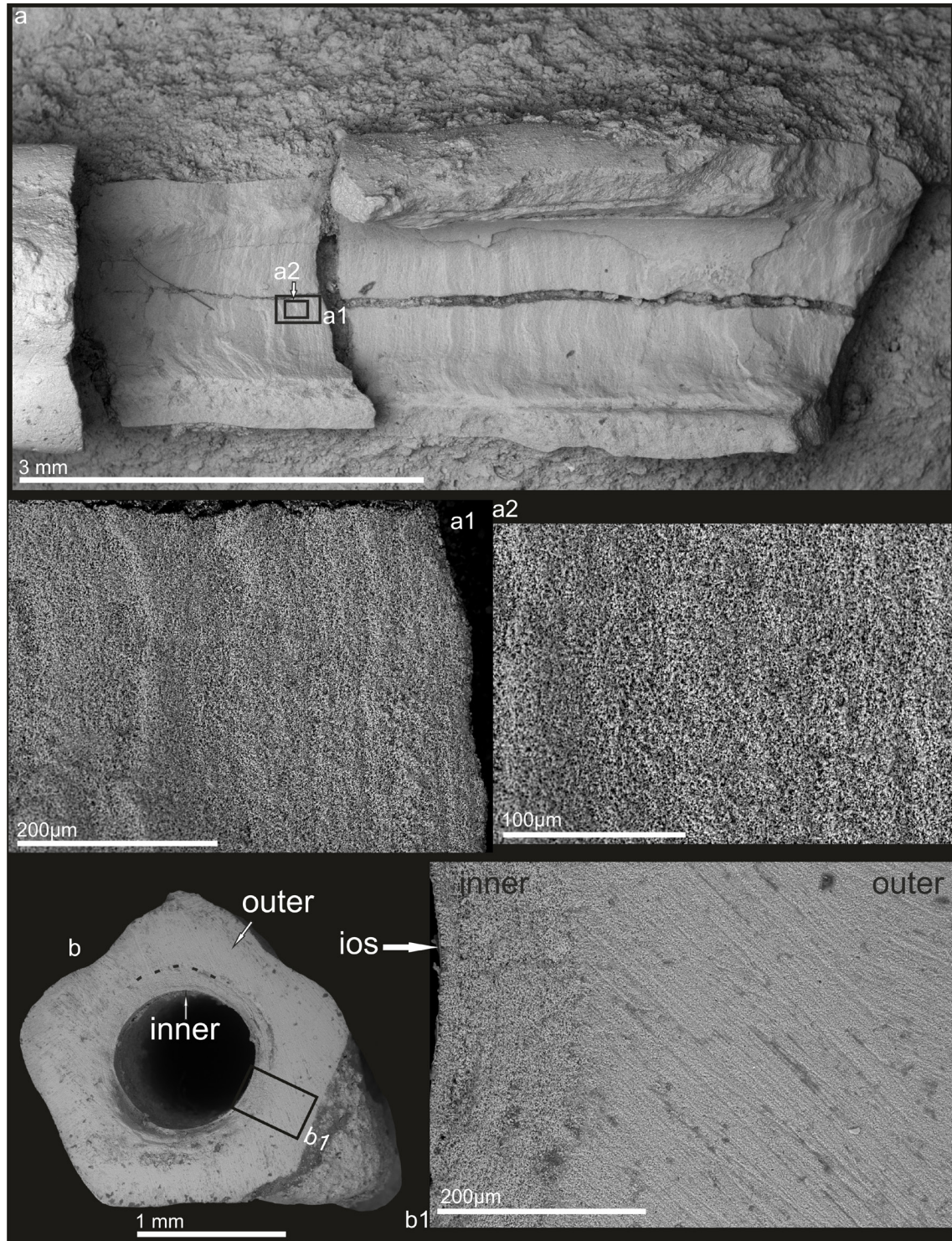


Fig. 11. Microstructure of *Pentaditrupe interjuncta* (Jessen & Ødum, 1923), early Danian, Holtug quarry, OESM 13330. a, a1, a2. Longitudinal section. a. Overview showing the tube wall of the anterior tube portion. Rectangles show positions of detailed views in the following subfigures. a1, a2. The interior surface of the tube showing the base of the inner layer, consisting of transverse incremental lamellae constructed of short prismatic crystals oriented parallel to the tube's longitudinal axis. b. Transverse section, photograph taken before treating the tube with 1% acetic acid for c. 3 minutes, showing the thick outer and thin inner tube wall layers; dashed line indicates boundary between them. b1. Detailed view of inner and outer layers, ios - inner organic sheet is exceptionally preserved. This organic sheet is an adaptation to strengthen the mechanical properties of the tubes in clade A (sensu Aliani et al 1995, Vinn 2011, 2013, 2021). The oblique striation in the outer layer is an artifact caused by cutting or polishing. The microstructure matches the spherulitic prismatic (SPHP) type sensu Vinn *et al.* (2008c).



Fig. 12. *Pentaditrupe subtorquata* (Münster in Goldfuss, 1831), Campanian, quarries east of Hannover. a, b, c, d. Early Campanian, Holcim quarry, Höver, OESM 13331. e, f, g. Late Campanian, Teutonia Nord quarry, Misburg, OESM 13332. a, b, c, d, e, f, g. Lateral views. a1, c1, e1. Frontal views to apertures. b1, d1, f1, g1. Transverse sections.

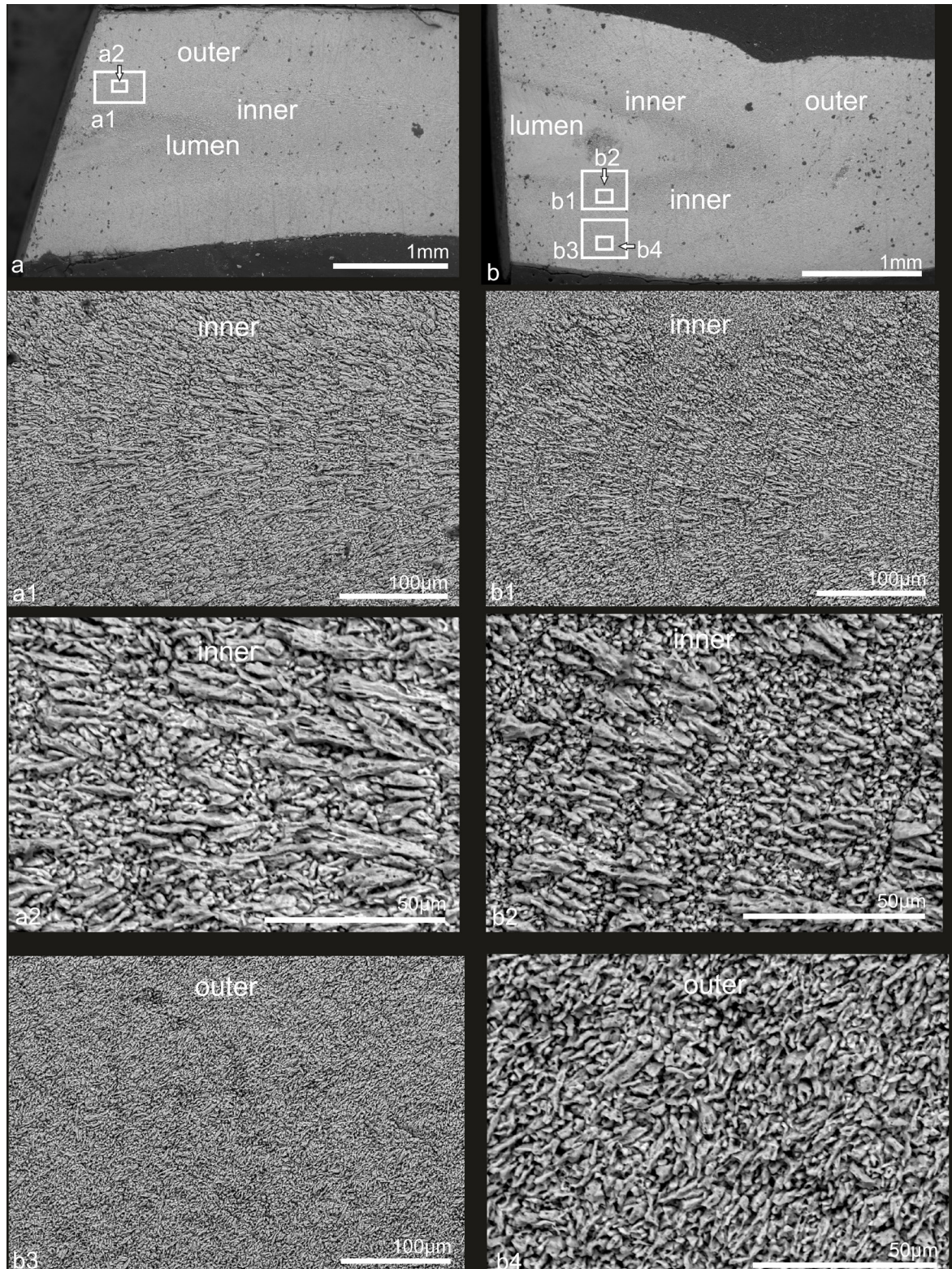


Fig. 13. Microstructure in longitudinal sections of *Pentaditrupe subtorquata*, Campanian, quarries east of Hannover, northwest Germany. a, b. Same specimen as Fig. 12b, d, early Campanian, Holcim quarry, Höver. a, b. Overviews of longitudinal sections, showing positions of details. a1, a2, b1, b2. Inner layer, consisting of regularly oriented spherulitic crystals (a2, b2) of spherulitic prismatic (SPHP) microstructure (sensu Vinn *et al.* 2008); these crystals are arranged in chevron-shaped = parable-shaped increments oriented perpendicular to the longitudinal axis of the tube. b3, b4. Outer layer with crystals of semiregular spherulitic prismatic (SPHP) microstructure.

document only a tiny portion of the entire tube. Concerning the exterior aspect of serpulid tubes, it is well-known that high morphological variability within species, together with many homeomorphisms between different taxa, impedes taxonomic-systematic research of fossil and empty recent tubes. As microstructure has a strong influence on exterior aspect, it may well be assumed that microstructure may display some intraspecific variation, too. Therefore, at least in the present state of knowledge, we should be careful not to over-estimate small differences between SEM images showing generally similar microstructure.

Moreover, tiny structures are more prone to faster crystal growth and other crystallographical and mineralogical changes by re-crystallisation than larger structures. Such changes may occur already during lifetime, or during taphocoenosis or diagenesis, or much later by subfossil or recent weathering. Hitherto, only a few studies focused on re-crystallisation in serpulid tubes in more detail; perhaps the most recent and most comprehensive study is provided by Grenier *et al.* (2024). Moreover, SEM images of perfectly plane and polished artificial sections may look different from those of rough and uneven ‘planes’ of natural breakage. And, of course, not perfectly longitudinal, horizontal, or transverse sections may distort the height/width ratio in the images.

Hitherto, tubes of *Pentaditrupe subtorquata* from the Campanian of Höver near Hannover, north Germany, studied by Vinn (2005: 262–263, Pl. 1, figs 3, 4, 8) seem to be the only specimens of the genus *Pentaditrupe* whose microstructure was studied and published by SEM images. In the outer tube layer, Vinn (2005: figs 3, 4) detected a semiregular spherulitic prismatic structure, abbreviated SPHP in Vinn & Kupriyanova (2011: 138–139, Tab.1), and a transverse section of the inner layer (Vinn 2005: fig. 8) shows a possibly secondary homogeneous structure composed of calcareous granules, named fine-grained homogeneous structure, abbreviated FH, in Vinn & Kupriyanova (2011: 138–139, Tab. 1).

We compared Vinn’s results with SEM images of polished sections of *Pentaditrupe subtorquata* tubes with tubes of *P. nickcavei* from the early Selandian of Gundstrup gravel pit (Figs 7–8), *P. interjuncta* from the early Danian of Holtug quarry (Figs 10–11), and some more tubes of *P. subtorquata* from the same region as studied by Vinn: from the early Campanian of Höver quarry and the late Campanian of Teutonia Nord quarry at Misburg, both located east of Hannover in north Germany (Figs 13–14).

Our SEM images of the inner tube layer are quite consistent across all tubes, supporting the classification of these tubes under a single genus, *Pentaditrupe*. However, slight differences between the three species should be discussed in detail.

The outer tube layer of *Pentaditrupe nickcavei* is composed of several growth sublayers – the increments of the outer parable layer (Fig. 7a1). These increments run somewhat obliquely to the tube’s longitudinal axis and consist of needle-shaped spherulitic prismatic crystals (Fig. 7a2, 7a3), which are oriented approximately, but not strictly, perpendicular to the boundaries between increments. In all three studied *Pentaditrupe* species, the crystals in the outer layer are somewhat shorter and arranged slightly less strictly parallel to each other than similar crystals in the inner layer. Our study confirms the spherulitic prismatic (SPHP) type of microstructure *sensu* Vinn *et al.* (2008c), which belongs to the oriented prismatic structures, where the long axis of the crystals has a uniform orientation and is continuous through successive growth increments (Vinn 2020). Our study shows that the outer tube layer is more or less the same in all examined tubes from the three different localities of three different geological ages.

As stated above, the transverse section in Vinn (2005, fig. 8) shows a fine-grained homogeneous structure (FH). A similar structure is also seen in *P. interjuncta* from the early Danian of Holtug quarry in the transverse section (Fig. 10b3), but in the longitudinal section of the same tube, these only seemingly fine-grained granular crystals turn out in reality to be long sphaerulitic crystals, which are arranged in the shape of beautiful „water fountains“ (Fig. 10a7, 10a8). Vinn (2005) did not provide a longitudinal section of the inner tube layer of *P. subtorquata* from the Campanian. Nevertheless, other *P. subtorquata* tubes from the Campanian of the same quarry area east of Hannover show the same pattern of „water fountains“ (Fig. 13a1, 13b1) as in the tubes of *P. nickcavei* and *P. interjuncta*. In the *P. interjuncta* tube from Holtug (Fig. 10a7, 10a8), the crystals are more clearly visible than the boundaries between increments; therefore, the spherulitic prismatic crystals emphasize the water fountain pattern more distinctly than in *P. nickcavei* (Fig. 7a2, 7a3) and in *P. subtorquata* (Fig. 13a1, 13b1).

We have no transverse section of the inner layer of *P. nickcavei* from the early Selandian of Gundstrup gravel pit, but in the longitudinal section (Fig. 7a2, 7a3) the beautiful ‘water fountains’ most conspicuously show the narrow curvature of the chevron-shaped paraboles (increments), whose anteriorly directed vertices (which are visible already in the lower third of the low magnification SEM image Fig. 8a1 and even in the middle of the ordinary light photograph Fig. 4a1) mark the transition between the thick outer and the thin inner parable layer. Moreover, they show that the long crystals are oriented more or less (not exactly) perpendicular to the boundary lines between the paraboles.

The growth increments with spherulitic prisma-

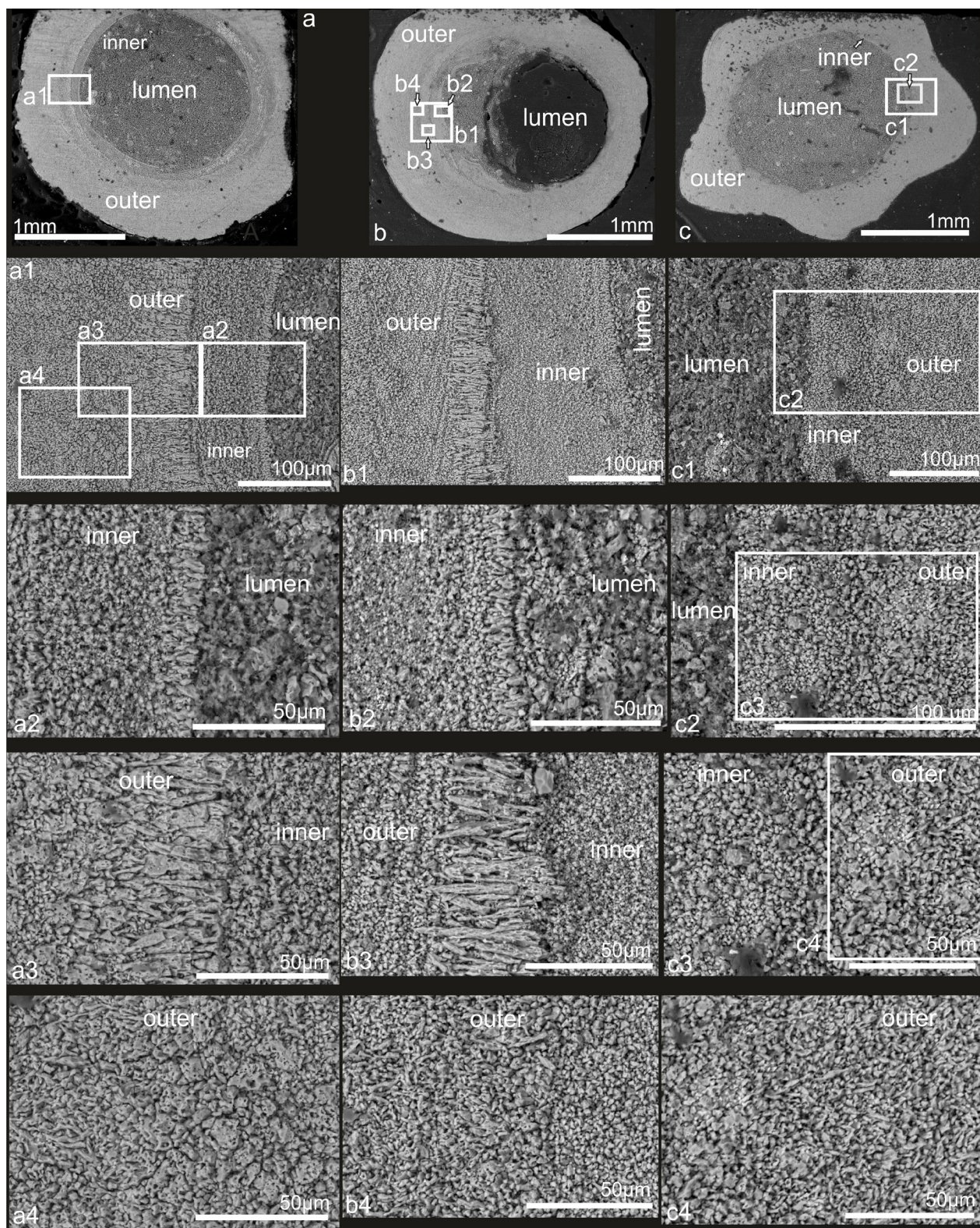


Fig. 14. Microstructure in transverse sections of *Pentaditrupe subtorquata*, Campanian, quarries east of Hannover, northwest Germany. a. Same specimen as Fig. 12b, early Campanian, Holcim quarry, Höver. b, c. Same specimen as Fig. 12e, late Campanian, Teutonia Nord quarry, Misburg. a, b, c. Overviews of transverse sections, showing positions of details. There are three layers named the outer layer, the inner layer, and the very thin innermost organic layer. a1 – a3, b1 – b3, c1 – c3. Details showing boundaries between the lumen, inner and outer layers. a3, b3. Tall prismatic crystals developed between the outer and inner layer. a4, b4, c4. Outer layer with semiregular spherulitic prismatic microstructure.

tic (SPHP) microstructure continue in the inner parable layer. Other SEM images (Fig. 8a2–8a5) of the longitudinally broken *P. nickcavei* tube show a horizontal view of the undamaged or only slightly abraded innermost part of the inner tube layer in the interior surface of the tube wall. It consists of crystals, which in this horizontal view appear to be very short, and incremental lines, which are sometimes visible as transverse striae already under a binocular microscope or even to the naked eye. This thin innermost layer can be interpreted either as a cylinder layer or as an organic sheet. Additionally, the early Danian tube from Holtug features an exceptionally preserved innermost organic sheet, as described by Vinn (2013a); see the arrow labeled ‘ios’ in Fig. 11b1. This organic sheet is an adaptation to strengthen the mechanical properties of the tubes in clade A (sensu Aliani *et al.* 1995; Vinn 2011, 2013, 2021).

In summary, the tube wall of *Pentaditrupe nickcavei* has two layers, the inner and the outer, both are spherulitic layers, classified as SPHP microstructure. The general construction of microstructure, as described above in the chapter on genus *Pentaditrupe*, is the same in the three species of the present study, and justifies assigning these three species to a single genus. In detail, however, there are small but distinct differences in microstructure between the three species, with regard to three features, all detectable in SEM images showing longitudinal sections of the outer sublayer of the inner tube layer – the level (2a), showing the water fountain pattern, and adjacent sublayers:

- (1) The boundaries between the chevron-shaped increments predominate in visibility over the needle-shaped crystals in *P. nickcavei*, whereas in *P. interjuncta* the crystals predominate, and in *P. subtorquata*, boundaries as well as crystals are moderately visible.
- (2) Although in all three *Pentaditrupe* species the crystals in the outer layer are shorter than the crystals in the inner layer, there are small differences in crystal lengths between species. In the inner tube layer, the crystals are relatively short in *P. nickcavei*, but tall in *P. subtorquata*. In the outer tube layer, the crystals are tall in *P. interjuncta*.
- (3) In *P. subtorquata*, the chevron-shaped boundaries between growth increments as well as the water fountain pattern appear to be wider curved than the narrower curves in *P. interjuncta* and *P. nickcavei*. However, this widening may be only an artifact due to optical stretching caused by the non-central cutting plane in *P. subtorquata*.

Genus *Neovermilia* Day, 1961

Type species. *Neovermilia capensis* Day, 1961 (type by original designation).

Neovermilia gundstrupensis Kočí, Milàn & Jäger, 2023

Figs 15, 18h

2023 *Neovermilia gundstrupensis* sp. nov. – Kočí, Milàn & Jäger, pp. 139–146, Figs 3–7.

Additional material. 4 samples, 5 tubes altogether.

Description (short version). Tube moderately large, posterior portion coiled in some tubes. The transverse ornament consists of densely spaced annular striae. Cross-section circular. For more details, see Kočí *et al.* (2023).

Discussion. These new finds are figured (Fig. 15) to demonstrate the variability of tube shape, and to underline their common occurrence in the lower Selandian at Gundstrup pit, and their non-obligate preference of attaching their tube to sponges.

Class Gastropoda Cuvier, 1795

Subclass Caenogastropa L. R. Cox, 1960

Order Caenogastropoda *incertae sedis*

Superfamily Cerithioidea J. Fleming, 1822

Family Siliquariidae Anton, 1838

Genus *Tenagodus* Guettard, 1770

Type species. *Serpula anguina* Linnaeus, 1758 (type by subsequent designation)

Tenagodus sp.

Figs 16, 17, 18c

Material. Several large slab of Kerteminde Marl containing several damaged and poorly preserved fossils. The slabs are registred for their associated fauna under numbers NHMD 1986505 & NHMD 1758095.

Description. Shell medium to large-sized. Protoconch is missing. The early whorls form a regular and tight characteristic spiral, whereas the curvature of the last whorl is wider, so that the anterior portion lost direct contact with the previous whorl and may grow somewhat irregular or even partly straight. Periostracum is not preserved. Surface smooth, lacking any ornamentation. The shell wall is thin.

Discussion. The genus *Tenagodus* is known from the Middle Triassic to the Recent (Wenz 1939; Davies 1971; Squires 1990). The often cited genus *Siliquaria* is a junior objective synonym of *Tenagodus* (see Bieler 1992; Bieler & Petit 2011). The specimens from Kerteminde Marl are similar to *Tenagodus terebellus*

(Lamarck, 1818), which is recorded from the Oligocene of the North Sea Basin, the Adour Basin, northern Italy, and Iran (Harzhauser 2004), but are larger than *Tenagodus* cf. *terebellus* (Lamarck, 1818) mentioned by Harzhauser (2004: 122) from the Late Rupelian to Early Chattian of Abadehin Esfahan-Sirjan Basin in Central Iran.

Palaeoecology

Serpulids

The genus *Pentaditrupe*, characterized by its pentagonal cross-section and its short (in Early Jurassic representatives) or entirely absent (in Late Albian to



Fig. 15. *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, early Selandian, Gundstrup gravel pit. a, b, c. Damaged tubes show the variability of the tube's shape of this species. a, MGUH 35030. b, MGUH 35031. c, MGUH 35032.

Selandian representatives) attached posterior tube portion, belongs to a group of phylogenetically unrelated serpulid taxa adapted to life on soft seafloor, where larger solid substrates suitable for attachment are rare or absent. Other soft-bottom dwelling serpulid species include representatives of the following genera and subgenera: *Ditrupa* Berkeley, 1835, *No-*

grobs de Montfort, 1808, *Pyrgopolon* (*Pyrgopolon*) de Montfort, 1808, *Pyrgopolon* (*Hamulus*) Morton, 1834, *Rotulispira* Chiplonkar and Tapaswi, 1973 (= *Praerotularia* Lommerzheim, 1979), *Tectorotularia* Regenhardt, 1961, *Austrorotularia* Macellari, 1984, *Rotularia* De-france, 1827. Seilacher *et al.* (2008) discussed several representatives of this palaeoecological group in de-



Fig. 16. a, a1. Siliquarid gastropod *Tenagodus* sp., early Selandian, Gundstrup gravel pit, specimens appears as associated fauna on NHMD 1986505.

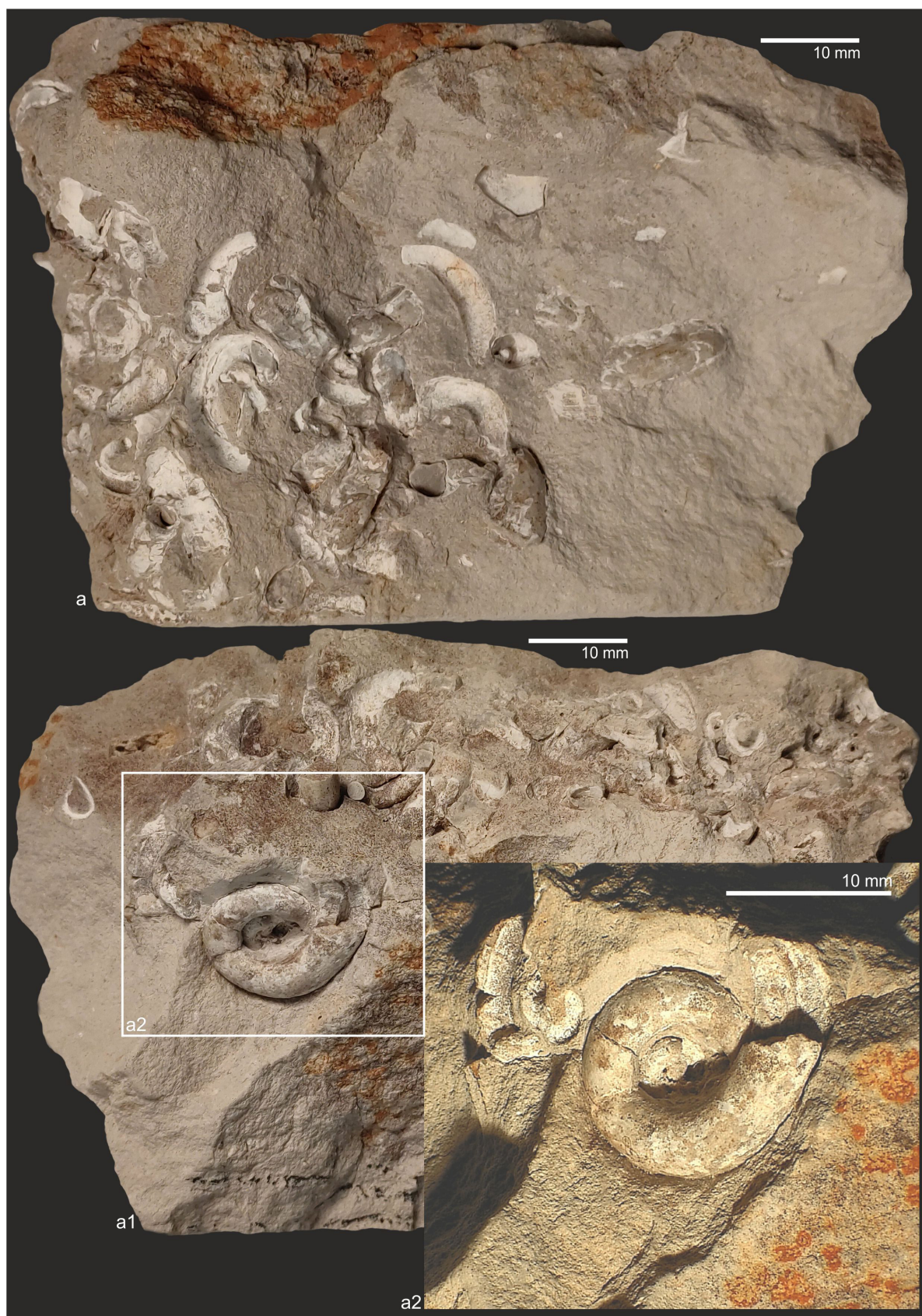


Fig. 17. a, a1, a2. Siliquariid gastropod *Tenagodus*, early Selandian, Gundstrup gravel pit, specimens appears as associated fauna on NHMD 1758095.



Fig. 18. The associated mesofauna and flora, early Selandian, Gundstrup gravel pit. a. *Pentaditrupe nickcavei* sp. nov., b. Brachiopod *Terebratulina chrysalis* (von Schlotheim, 1813). c. The siliquarid gastropod *Tenagodus* sp. d, d1. Gastropod *Aporrhais* sp., fragment of bird-foot-shaped aperture. e. Fragment of undetermined gastropod. f. Bivalve *Lima* sp. g. Gymnosperm cone. h. Serpulid *Neovermilia gundstrupensis* Kočí, Milán & Jäger, 2023. Specimens appear as associated fauna on NHMD 1758095.

tail.

Unlike the soft-bottom dwellers *Pentaditrupe nickcavei* sp. nov. and *P. subtorquata*, *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, typically has its coiled posterior tube portion attached to a large sponge *Ventriculites* (see Kočí *et al.* 2023, p. 141, Fig. 4A, A1, and p. 142, Fig. 5A) or, less commonly, to another hard substrate. This attachment suggests a dependence on such hard substrates, at least during the early stages of its life.

Vinn (2024) measured and discussed the distance between adjacent incremental lines in several serpulid tubes. In the inner layer of the Selandian tubes of *Pentaditrupe nickcavei* from the Kerteminde Marl, we observed up to six incremental lines per 50 µm, with larger tubes showing a tendency toward fewer incremental lines within the same distance. This suggests a greater distance between adjacent incremental lines in larger tubes. Our observations agree with those of Vinn (2024), who reported 5–20 growth lines per 50 µm in Cenozoic serpulids.

Di Geronimo *et al.* (2000) suggested that larger serpulid tube sizes are a response to a lower sea temperature. The relationship between the effect of temperature during tube growth, tube size, and the associated number of incremental lines cannot, however, be confirmed in the Danish serpulids. The tubes of *Pentaditrupe* and *Neovermilia* from the Kerteminde Marl are medium in size: The tube diameter of *Pentaditrupe nickcavei* reaches up to 5.2 mm; this is somewhat larger than in Late Cretaceous *P. subtorquata*. *Neovermilia gundstrupensis* reaches up to 5 mm; this is smaller than the maximum size of 10 mm (Jäger, 1983) of Late Cretaceous *Neovermilia ampullacea*. The Kerteminde Marl was deposited at a depth of 100–150 m (King 1994, 2015; Clemmensen & Thomsen 2005), where seafloor temperatures were relatively low despite a subtropical climate, with palaeotemperature estimates of 11.7–14.7°C (Buchardt 1977). Small- and large-sized serpulid tubes have not yet been found there. Absence of small tubes can easily be explained by sampling bias. Collectors often focus on specimens visible to the naked eye at outcrops, selecting only the best-preserved ones. The scarcity of large tubes may be explained by the scarcity of large substrates. For species whose tubes are attached to some hard substrate, *e.g.*, *Neovermilia*, the size of the substrate plays an important role. The correlation between the size of substrates and the size of epibionts has already been documented (*e.g.*, Kočová Veselská *et al.* 2021). A nice example of this phenomenon can be observed in the middle Danian bryozoan and corallian chalk of the Faxe quarry. These limestones were deposited in cold waters, but serpulids remained predominantly small in size. This size limitation is certainly not related to water temperature but rather to the small diameter of octocoral and scler-

ractinian coral branches, along with the limited size of cryptic cavities within the dense coral thickets, to which many tubes are attached. These cavities were also already occupied by competing invertebrates, further limiting the growth of the serpulid tubes.

The size of serpulid tubes may also be influenced by nutrient richness and availability (Clemmensen & Thomsen 2005). The abundant supply of calcium carbonate from reworked chalk, indicated by the high sedimentation rate, may have contributed to the medium sizes of serpulid tubes in the Kerteminde Marl. Despite this, the bottom water was well-oxygenated, current activity was low, plankton production was minimal, and benthic food availability was reduced (Clemmensen & Thomsen 2005). Similarly, the larger sizes of serpulids observed in the Maastrichtian chalk deposits of Denmark (Kočí, Milàn, personal observations) can be linked to a greater supply of calcium carbonate. However, a thorough paleoecological comparison of serpulids from the Kerteminde Marl and the Maastrichtian chalk, as well as more accurate interpretations, will require further intensive sampling of the Kerteminde Marl. While serpulids from the Gundstrup gravel pit (Kerteminde Marl) have only recently been the focus of more intensive collection, those from Maastrichtian chalk and Danian limestones have been studied since the early 19th century (*e.g.*, von Hagenow 1840 for Maastrichtian serpulids from the Isle of Rügen, Germany). This suggests that collecting bias may once again be a contributing factor.

Mollusks and brachiopods

The oyster *Pycnodonte vesiculare* initially required a hard substrate for attachment during its early ontogeny, but soon became free-lying, stabilized by the increasing weight of its massive shell. The brachiopod *Terebratulina chrysalis* (Fig. 18b, arrow) was adapted to a soft substrate environment, similar to the Cretaceous species *Terebratulina striata* (Wahlenberg, 1821), which anchored itself to skeletal sand on the seafloor using a rootlet pedicle (*e.g.*, Schröder *et al.* 2018: fig. 10; Schröder & Surlyk 2024).

The gastropod *Tenagodus* exhibits a worm-like shell shape and slit band, features thought to be adaptations for living among seaweeds and sponges.

Due to palaeocurrents, mollusks are often found in small to large accumulations. Notable examples include two slabs: one containing approximately 30 specimens of *Kangilioptera gundstrupensis* Schnetler & Nielsen, 2018, and another with about 20 specimens of *Quadrinerous wienekei* Schnetler & Nielsen, 2018. Several specimens of the bivalve *Pteria thomseni* Schnetler & Nielsen, 2018 and the gastropods *Metacerrithium hauniense* (Koenen, 1885) and *Cerithiopsis andreae* Schnetler & Nielsen, 2018 have also been found

in slabs. Occasionally, concentrations of diverse species have been observed.

Bivalves are predominantly represented by infaunal species, including members of Nuculanidae, *Pholadomya* (*Bucardiomya*) *margaritacea* (Sowerby, 1821), and Cuspidariidae. Sessile bivalves, either byssate or cementing, are less common and include pectinids and *Limaria geinitzi* (von Hagenow, 1842). Boring bivalves are represented by Teredinidae, ?*Lithophaga* Röding, 1798, and ?*Netastoma* Carpenter, 1864. The dentalids were endobenthic.

The gastropod fauna includes only a few herbivorous species. All specimens of the gastropod *Scurria rieae* Schnetler & Nielsen, 2018 have been found in association with fossilized wood, probably sunken driftwood, indicating transport. Most gastropod species were carnivorous.

The presence of pelagic cephalopods suggests open marine conditions, with a soft seabed at an estimated depth of 100–150 metres in a nutrient-rich environment.

General palaeoecology

Clemmensen & Thomsen (2005, Fig. 11) described the palaeoenvironment in the Storebælt area as fully marine, with moderately good oceanic connections, a water depth of 100–150 m, and a very high sedimentation rate due to a significant input of reworked chalk. The bottom waters were well-ventilated, with low current activity. The planktonic production was low, resulting in a reduced benthic food supply. A rich and diverse non-mollusks fauna was also documented, including foraminifera, sponges, anthozoans, annelids (serpulids), decapod crustaceans, cirripedes (excluding barnacles), bryozoans, brachiopods, asteroids, ophiuroids, crinoids, echinids, cheilons, ganoids (skeletal parts, otoliths and scales in burrows), sharks (teeth) and birds (breastbone). This fauna supports the palaeoecological interpretation provided.

Schnetler and Nielsen (2018) confirmed that the mollusk fauna inhabited this environment at an estimated palaeodepth of 100–150 metres, and presumed a subtropical climate. The palaeoenvironment is linked to the transgression of the Selandian Sea, which included the erosion of underlying Danian sediments. Initially, a near-shore environment characterized the early Selandian, followed by a gradual increase in water depth, leading to the deposition of fine-grained Kerteminde Marl and, subsequently, the clay of the Æbelø Formation.

Conclusions

The serpulid tubeworm *Pentaditrupe nickcavei* sp. nov. from the Selandian (middle Paleocene) Kerteminde Marl at the Gundstrup gravel pit on Fyn, Denmark, represents the geologically youngest known species of the genus *Pentaditrupe* Regenhardt, 1961.

The species name *Pentaditrupe interjuncta* (Jessen & Ødum, 1923), after being considered a junior synonym of *P. subtorquata* for several decades, is ‘revived’ for Danian representatives of the genus *Pentaditrupe* from Denmark. In exterior view, the tubes of both species are usually indistinguishable, but there are small but distinct differences in microstructure.

Pentaditrupe nickcavei sp. nov. differs from the closely related Late Cretaceous to Danian *P. subtorquata* (Münster in Goldfuss, 1831) by reaching a larger tube diameter, possessing sharper longitudinal edges or low keels, and specific microstructural features.

The palaeoecology of the serpulids *Pentaditrupe nickcavei* sp. nov., *Neovermilia gundstrupensis* Kočí, Milàn & Jäger, 2023, and associated fauna is discussed.

Additionally, the siliquarid gastropod *Tenagodus* is reported for the first time from the Kerteminde Marl.

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Sedimentary facies and cyclostratigraphy of a potential CO₂ storage reservoir: The Early Triassic Bunter Sandstone Formation in the Rødby area, southern Denmark

LARS B. CLEMMENSEN, MALTE MAU & KEN WESNÆS



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The Early Triassic (Olenekian) Bunter Sandstone Formation represents a major prospective reservoir for CO₂ storage in southern Denmark especially in the four-way dip structure in the Rødby area (Lolland, southern Denmark), and is expected to play an important role for reaching climate targets. The Bunter Sandstone Formation in southern Denmark formed along the northern margin of the North German Basin and is composed of terrestrial sediments and subdivided into the Volpriehausen, Detfurth and Solling members. Each member has a basal sandstone unit overlain by a mudstone unit. The sandstone units form potential reservoirs in the formation. Their thickness and composition, however, vary somewhat along the basin margin from west to east in southern Denmark. In this paper focus is on the 256 m thick Bunter Sandstone Formation in the Rødby-1 well on Lolland. Visual analysis of the gamma ray records from wireline logging of the sedimentary succession in the Rødby-1 well indicates the presence of a composite cyclicity both in sandstone and mudstone units. Spectral analysis finds identical, significant cycles both in mudstone-rich and sandstone-rich units; in mudstone-rich units cycles have the following thicknesses: 62, 16, 7.5, 5.8, 4.4, 3.6, 3.0, 2.6, and 2.3 m. Assuming that these sedimentary cycles record astronomical climate control on sedimentation and the 62 m cycle records the 405,000 years eccentricity cycle, then the remaining cycles represent the following periods: 104,500; 49,000; 38,000; 28,500; 23,500; 19,500; 17,000; and 15,000 years. Thus both a 100,000 years eccentricity as well as precession cyclicity with periods between 15,000 and 23,500 years can be identified. More surprising also a likely obliquity signal seems to be present as given by cycles with periods of 28,500, 38,000 and 49,000 years. In Rødby-1, the sandstone units vary in thickness between 23 and 29 m. The new cyclostratigraphy indicates that deposition of the sandstone units took place during the arid parts of a 405,000 years eccentricity cycle, when the central playa lake had its minimum extension. Mudstones units formed during the humid parts of these climate cycles when the central playa lake expanded in size. Internal lithological variation and thereby reservoir properties (sandstone-mudstone ratio) in the sandstone units are related to 100,000 years eccentricity variation in climate as well as to obliquity and precession variation. There is very limited core evidence on facies characteristics in the Rødby-1 well, but comparison with core data from the Tønder area in southern Jutland suggests that the sandstone unit in the Volpriehausen Member is composed of alternating aeolian and ephemeral river deposits with facies change mainly related to climate variation. A similar sedimentary facies pattern is probably also characterizing the sandstone unit of the Detfurth Member. In the Solling Member only fluvial facies are present, and it is suggested that the lithological variation primarily reflects climatic induced variation in fluvial style and transport capacity. Mudstones units that separate the sandstone units are interpreted to have formed on sabkhas and in large playa lakes.

Keywords: Bunter Sandstone Formation, Rødby area, reservoir sandstones, cyclostratigraphy, palaeolandscapes

Lars B. Clemmensen (larsc@ign.ku.dk), Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen, Denmark; Malte Mau (malte-mau@hotmail.com), Rambøll, Olof Palmes Allé 22, 8200 Aarhus N, Denmark. Ken Wesnæs, CarbonCuts, Lyngbyvej 2, Vibenshuset, 2100 København Ø, Denmark.

The Bunter Sandstone Formation, of Early Triassic (Olenekian) age, is widely distributed in the subsurface across a large part of southern Denmark as documented by core data and borehole logs from several deep wells in southern Denmark (e.g. Bertelsen 1980; Michelsen & Clausen 2002; Olivarius *et al.* 2015; Olivarius *et al.* 2017; Abramovitz *et al.* 2024; Fig. 1). Wells cover a wide region from the Tønder area in the west to the Rødby area in the east (Fig. 1), but sediment cores of good quality and from thick stratigraphical intervals are only present in three wells in the Tønder area (Clemmensen 1985; Olsen 1987).

The Bunter Sandstone Formation in southern Denmark is typically between 200 and 300 m thick and composed of the Volpriehausen, Detfurth and Solling members (Michelsen & Clausen 2002; Olivarius *et al.* 2015). Each member has a basal sandstone unit overlain by a mudstone unit. The sandstone units are composed of alternating fluvial and aeolian facies or only fluvial facies, while the mudstone units are composed of fine-grained sabkha and playa-lake sediments (Clemmensen 1985); sediments were deposited at low palaeolatitudes at the northern mar-

gin of the North German Basin and south of the Ringkøbing-Fyn High (e.g. Clemmensen 1985, 1991; Olivarius *et al.* 2015, 2017).

In wells in southern Denmark the formation is found at depths between 1100 and 2100 meters and is estimated to have experienced a maximum burial depth of 1600-2300 meters prior to Neogene uplift (Japsen *et al.* 2007). Many levels in the sandstones units are characterized by high porosity and permeability (Olivarius *et al.* 2015). This, in combination with the appropriate burial depth has led to many investigations of the formation as potential geothermal reservoir (e.g. Hjuler *et al.* 2016, 2019; Hjuler & Kristensen 2017).

Most recently the formation has also been examined as a potential subsurface reservoir for CO₂ storage in the Rødby structure on Lolland (Hjelm *et al.* 2020). The stratigraphy of the Bunter Sandstone Formations is here known from two deep wells, Rødby-1 and Rødby-2 (Hjelm *et al.* 2020). However, sediment cores are only present from four short intervals in the Rødby-1 well (Fig. 2), and interpretations of lithology is therefore primarily based on petrophysical logs



Fig. 1. Simplified geological map with location of wells described in the paper. The outline of the Ringkøbing-Fyn High modified from Olivarius & Nielsen (2016) and Olivarius *et al.* (2017).

and in particular gamma ray readings (Olivarius *et al.* 2015; Abramovitz *et al.* 2024; this study).

In this study we examine the gamma ray logs from the Rødby-1 well on Lolland. An initial recognition of a composite cyclicity (lithological variation in mudstone-sandstone ratio) by visual inspection of gamma ray readings is tested by spectral analysis, and it will be discussed if these cycles can be related to orbital climatic control of precipitation. Orbital forcing of the Bunter Sandstone deposition was first suggested by Clemmensen (1991) and Clemmensen *et al.* (1994) from studies of outcrops on Helgoland. Geluk & Röhling (1997) also used orbital climatic control to explain a composite cyclicity in the Bunter Sandstone Formation (Middle Buntsandstein) in the Dutch North Sea and adjacent areas. Sedimentary cycles documented in core and petrophysical log data in the southern part of the North German Basin (Hessen, Germany) have in a similar way been ascribed to climatic control (Hugh-Diegel 2021).

The purpose of this paper is therefore to examine the cyclostratigraphy of the Bunter Sandstone Formation in the Rødby area by spectral analysis of gamma ray readings and relate the deduced sedimentary cycles to orbital climate change, and to describe the lithological composition of the sandstone units and interpret the variation in facies and related reservoir properties by climate theory and by comparison with core data from the Tønder area and outcrop data from Helgoland. Finally tentative maps will be constructed showing the distribution of Early Triassic landscape elements in the Rødby and nearby areas of Lolland and Falster during both arid and more humid climate intervals.

Geological setting

In the Early Triassic southern Denmark, including the Rødby area, was situated at the northern margin of the North German Basin (e.g. Michelsen & Clausen 2002; Olivarius *et al.* 2015). The intracontinental North German Basin was a region under subsidence in the Early Triassic. Towards the north the basin was bounded by the Ringkøbing-Fyn High (e.g. Michelsen & Clausen 2002; Olivarius *et al.* 2015; Fig. 1). The High is penetrated by several grabens and can be divided into the Grindsted, Glamsbjerg, and Møn Highs (Fig. 1). The grabens connected the Bunter Sandstone Formation in the North German Basin with the Skagerrak Formation in the Norwegian-Danish Basin (e.g. Olivarius & Nielsen 2016).

The Bunter Sandstone Formation in southern Denmark is known from a number of deep wells including Rødby-1, Rødby-2, Sølsted-1, Ørsløv-1, Kegnæs-1, and from five closely situated wells in the Tønder area (Fig. 1). Sediment cores of good quality

and thick stratigraphical intervals are only known from three of the Tønder wells; studies of these cores have given detailed information of sedimentary facies and depositional environments (Clemmensen 1985; Olsen 1987) and have been used to reconstruct the palaeogeography along the complete margin of the basin south of the Ringkøbing-Fyn High (e.g. Clemmensen 1985, 1991, Olivarius *et al.* 2015, 2017).

The Bunter Sandstone Formation in southern Denmark is composed of terrestrial sediments (red beds) with typical thicknesses between 200 and 300 meters. Nearest to the Ringkøbing-Fyn High fluvial and aeolian sand was deposited, while farther south more

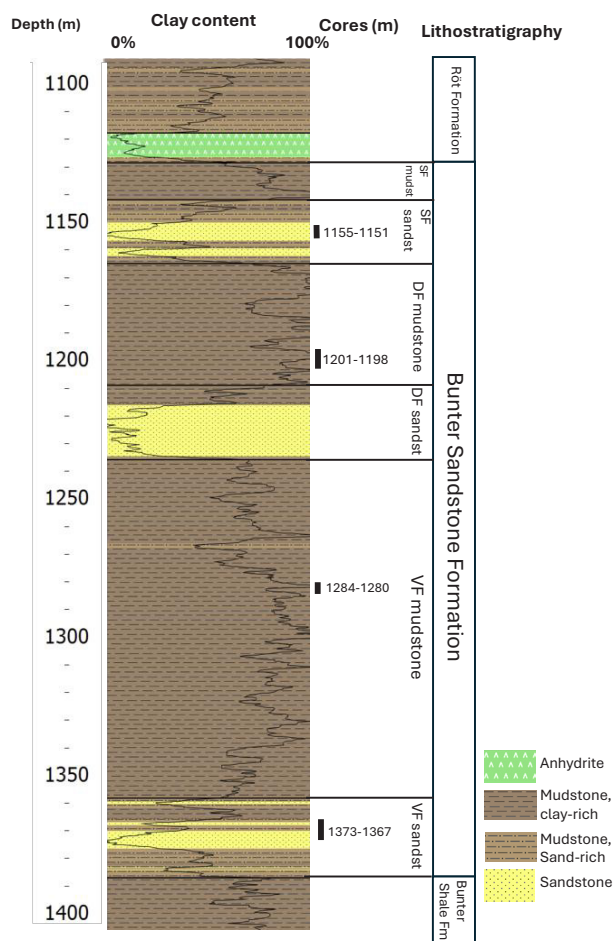


Fig. 2. General petrophysical log of the Lower Triassic (Olenekian) Bunter Sandstone Formation in the Rødby-1 well (Interpretation A). The formation is composed of the Volpriehausen Member (VF), the Detfurth Member (DF), and the Solling Member (SF). Each member is composed of basal sandstone unit overlain by a mudstone unit. Clay content is given by a 'normalised' gamma ray log where all gamma ray measurements are recalculated to have values between 0 (clean sandstones) and 100 (claystones). Sandstones are here defined as lithologies with less than 25% clay. The curve for clay content is given as an unbroken record, but in reality there is a significant time gap at the boundary between the Detfurth and Solling member.

fine-grained sediments were deposited (primarily mud rocks and heterolithic sediments) on sabkha plains and in shallow lakes (Clemmensen 1985, 1991; Olivarius *et al.* 2015). The source of the sediment for most of the fluvial deposits were exposed terrains at the Ringkøbing-Fyn High, while sediments transported from the south formed the main constituent of the aeolian sand deposits (Olivarius *et al.* 2017).

The boundary between the sand-rich fluvial and aeolian deposits towards the north and the fine-grained sabkha and lacustrine deposits towards the south changed much over time (Clemmensen 1991). During arid climatic periods, the fluvial and aeolian deposits formed a relative wide belt, while the mud-rich sabkha and lacustrine sediments covered the majority of the basin during humid climatic intervals. Clemmensen (1991) suggested that climate

variations were related to orbitally controlled variation in precipitation and recognized cycles of 20,000, 100,000 and 400,000 years duration in the Bunter Sandstone (Middle Buntsandstein) Formation at Helgoland (Fig. 3). However, so far climate controlled cyclicity has not been documented from well data of the Bunter Sandstone Formation in Denmark.

Stratigraphy

The Bunter Sandstone Formation in the Rødby area is known from two deep wells; the Rødby-1 well (drilled in 1952) and the Rødby-2 well (drilled in 1953); both wells are situated near the top of the Rødby structure (Hjelm *et al.* 2020). The lithology in the wells is given by petrophysical logs including gamma ray records,



Fig. 3. Part of the Bunter Sandstone Formation (Middle Buntsandstein) exposed on the western side of Helgoland. The uppermost part of the mudstone unit of the Volpriehausen Member (VF) and the lowermost part of the sandstone unit in the Detfurth Member (DF) are seen. The exposed part of the mudstone unit in the Volpriehausen is composed of red, heterolithic lake sediments with a significant but variably sand content (cf. Clemmensen 1991; Binot & Röhling 1988). The boundary to the Detfurth Member is given by the first appearance of a white, and loosely cemented aeolian sand deposit. Five such, 10-50 cm thick, aeolian sand deposits are present and intercalated with thin red, lake and sabkha mudstones and heterolithic deposits; these sediments form a lower sand-rich interval in the member. There is a gradual contact upwards to red, clay-rich playa-lake mudstones of the so-called Zwischenmittel deposits (ZM) of the Detfurth Member that are overlain by a second sand-rich interval (cf. Binot & Röhling 1988). The thickness of the succession between the base of the first sand-rich interval to the base of the second sand-rich interval is approximately 12 m. This sedimentary cycle most likely representing a 100,000 years eccentricity period (cf. Clemmensen 1991; Clemmensen *et al.* 1994).

and by short intervals with sediment cores (Olivarius *et al.* 2015; this study). The gamma ray log was measured during drilling of the well and is considered to be of good quality. The Bunter Sandstone Formation is 256 m thick in Rødby-1 and 242 thick in Rødby-2; the formation overlies the Bunter Shale Formation and is overlain by the Röt Formation (Michelsen & Clausen 2002). The Bunter Shale Formation is 317 m thick and almost exclusively composed of red mudstones; the Röt Formation is 153 to 160 m thick and composed of mudstones with anhydrite horizons in the basal part (Michelsen & Clausen 2002; Abramovitz *et al.* 2024).

The Bunter Sandstone Formation in southern Denmark can be subdivided into three members, the Volpriehausen Member, the Detfurth Member, and the Solling Member; each member has a sandstone unit at the base overlain by a mudstone unit (Michelsen & Clausen 2002). Similar stratigraphical units are named formations in North Germany and the Dutch offshore (Bachmann *et al.* 2009; Geluk & Röhlings 1997). We have used two different approaches here to differentiate between units primarily composed of sandstones and those primarily composed of mudstones. In both approaches threshold values between sandstones and mudstones are based on gamma ray records; in interpretation A sandstones are defined

as lithologies with a clay content below 25% (Fig. 2); while in interpretation B sandstones are defined as lithologies with gamma ray API values below 75 (Fig. 4). In Rødby-1, these sandstone units have according to interpretation A thicknesses from bottom to top of 29, 27 and 23 m, while associated mudstones units have thicknesses of 122, 44, and 13 m (Table 1). In interpretation B, the following thicknesses for sandstone units from bottom to top are: 28, 19, 22 m and for the mudstone units: 124, 52, and 11 m (Table 1). In Rødby-2 (interpretation A) sandstone units are 28, 21 and 12 m thick, while mudstone units are 120, 42 and 18 m thick (Table 2). Thus, there is good agreement between measured thicknesses in the two wells although sandstones units are slightly thicker in Rødby-1. In a nearby well on Lolland, Sølsted-1, the three members in the formation are also present. Here sandstone units are 23, 36, 23 m thick, while mudstone units are 129, 76, and 7 m thick (Table 2). The stratigraphy of alternating sandstone and mudstone units can be traced southwards to Fehmarn Z-1 well on the island of Fehmarn in northern Germany. Here the sandstone unit of the Volpriehausen Member is 26 m thick, the sandstone unit of the Detfurth Member 24 m thick, and the sandstone unit of the Solling Member 9 m thick (Table 2). The Bunter Sandstone Formation is also known from other deep

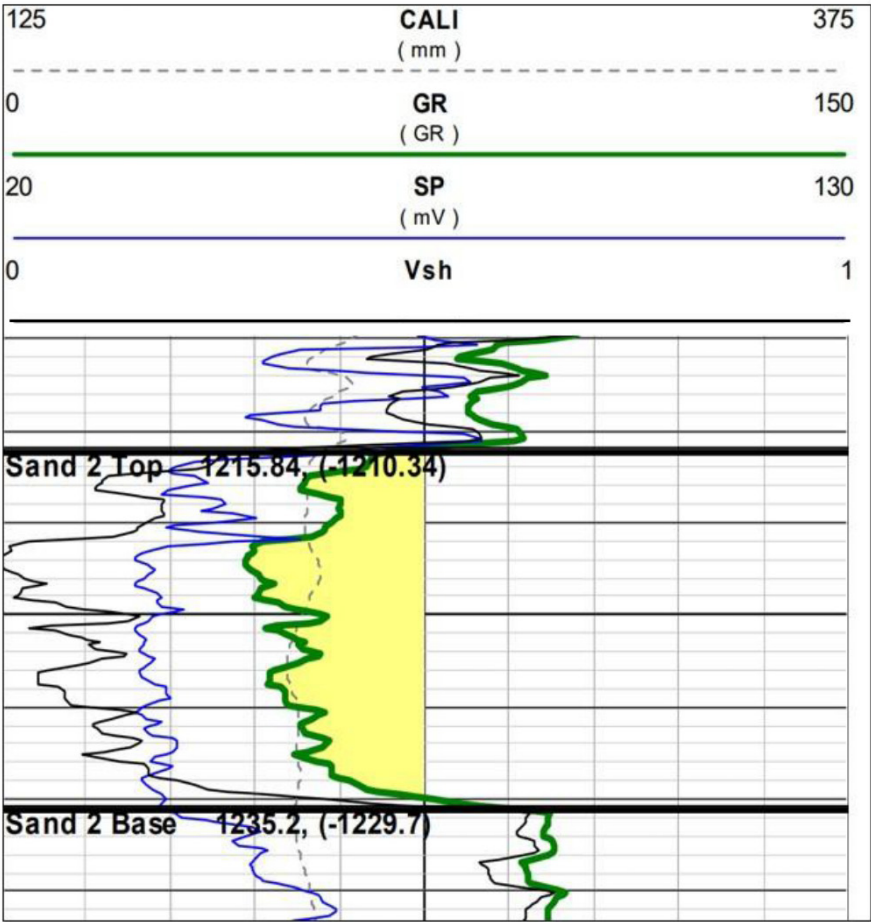


Fig. 4. Petrophysical log showing boundaries of the sandstone unit (Sand 2) in the Detfurth Member (interpretation B). Sandstones are defined by API (gamma ray, GR) values lower than API 75. The sandstone unit has a base in 1235.2 m and a top in 1215.84 m. Also shown are a caliper log (CALI), a spontaneous potential log (SP), and a log showing estimated clay content (Vsh). The sandstone unit is composed of relative clean sandstones with no intervening mudstone layers. Minor variations in clay content of the sandstones are probably related to precession and obliquity forcing of climate.

Table 1. Thickness of members and units, Bunter Sandstone, Rødby-1 well

Stratigraphy, Rødby-1	Interpretation A, m	Interpretation B, m
SF mudstone unit	13.3 (1128.7-1142)	11.4 (1131.1-1142.5)
SF sandstone unit	23 (1142-1165)	21.8 (1142.5-1164.3)
DF mudstone unit	44 (1165-1209)	51.5 (1164.3-1215.8)
DF sandstone unit	27 (1209-1236)	19.4 (1215.8-1235.2)
VF mudstone unit	122.3 (1236-1358.3)	123.6 (1235.2-1358.8)
VF sandstone unit	28.7 (1358.3-1387)	28.3 (1358.8-1387.1)

Interpretation A is based on calculated clay content based on gamma ray readings (sandstones defined as lithologies with a clay content less than 25 %); interpretation B is based on API gamma ray readings (sandstones defined as lithologies with API values less than 75). VF=Volpriehausen Member, DF= Detfurth Member, SF=Solling Member.

wells in southern Denmark including the Ørslev-1, Sølsted-1, Kegnæs-1 and Tønder-4 wells (Table 2). Also in these wells the Volpriehausen, Detfurth and Solling members are recognised. In the Ørslev-1 well on Falster, only two members are present, most likely in our opinion the Detfurth and Solling members (Table 2).

Climate theory

Based on a study of van Hinsbergen *et al.* (2019) it is concluded that the study area at Rødby was situated at about 17° N in an Early Triassic tropical, arid belt where precipitation was seasonal and controlled by summer monsoons (e.g. McKie 2014). Monsoonal intensity in such a climate belt can be demonstrated to be controlled by astronomical forcing of climate including the 20,000-years precession cycle, and the 100,000- and 405,000-years eccentricity cycles (e.g. Ruddiman 2008). Many Triassic sedimentary systems formed at low latitudes possess sedimentary cycles that can be related to precession and eccentricity climate forcing (e.g. Kemp & Coe 2007; Volmer *et al.* 2008; Kent *et al.* 2017; Mau *et al.* 2022). Modern precession cycles have periods of 24,000, 22,000, 19,000, 18,900, and 16,500 years and Early Triassic periods of 20,700, 19,700, 17,100, 17,000, and 15,000 years (Gradstein *et al.* 2012). Obliquity (the tilt of the Earth's rotational axis) with modern cycles of 54,000, 41,000, 39,000, 29,000 and 28,000 years and Early Triassic periods of 42,700, 34,200, 33,300, 26,100, and 25,400 years (Gradstein *et al.* 2012), should on the other hand, have little influence on climate at these latitudes (e.g. Ruddiman 2008). Yet some records have indicated this signal in sedimentary systems formed

at low latitudes (e.g. Li *et al.* 2016). Coupled ocean-atmosphere global climate model without dynamical ice sheets have shown that obliquity-induced changes in tropical climate can occur due to obliquity-induced changes in the cross-equatorial insolation gradient (Borsman *et al.* 2015).

The long eccentricity cycle of 405,000 years is especially important for establishing the exact periods of individual cycles in stratigraphic records (Laskar *et al.* 2004). Unlike other orbital cycles, the period of the long eccentricity cycle is almost unchanged for hundreds of millions of years. The long eccentricity cycle is created by the gravitational interaction with Jupiter and Venus. Due to the large mass and orbital stability of Jupiter, the period of the long eccentricity cycle is very stable. Theoretical calculations of the long eccentricity cycle show that the number of cycles from today to 250 Ma deviates by a maximum of one cycle from the expected number of cycles (Laskar *et al.* 2004), which has also been verified empirically (Kent *et al.* 2018). Therefore, the frequency interpreted as long eccentricity cycle in a stratigraphic record can be attributed to a period of 405,000 years with high confidence. The period of the remaining orbitally forced sedimentary cycles can be calculated based on the period of the long eccentricity cycle.

Methods

Age constraints and accumulation rate

The age of the Bunter Sandstone Formation (Middle Buntsandstein) is given by various sources including conchostracan biostratigraphy and magnetostratigraphy supplemented by cyclostratigraphy related to

Table 2. Thickness of members and units, Bunter Sandstone Formation, selected wells along the northern margin of the North German Basin

Stratigraphy	Rødby-1, m	Rødby-2, m	Sølsted-1, m	Ørslev-1, m	Fehmarn Z-1, m	Kegnæs-1, m	Tønder-4, m
SF mudstone	13	18	7	8	56	25	43
SF sandstone	23	12	23	20	9	38	33
DF mudstone	44	42	76	73	59	37	25
DF sandstone	27	21	36	16	24	19	10
VF mudstone	122	120	129		183	84	66
VF sandstone	29	28	23		26	29	34

Values given are based on Interpretation A of petrophysical logs. VF=Volpriehausen Member, DF= Detfurth Member, SF=Solling Member.

astronomical forcing of climate (e.g. Geluk & Röhling 1997; Bachmann *et al.* 2009).

Sedimentary facies

Detection of lithology, primarily sandstones and mudstones, is based on gamma ray readings. Sandstones are defined as sediments with a calculated clay content less than 25%; while remaining lithologies are crudely classified as mudstones (Interpretation A; Fig. 2). Alternatively, sandstones are given by gamma ray readings lower than 75 API and mudstones by gamma ray reading higher than 75 API (Interpretation B; Fig. 4). These threshold values are commonly used in the industry to distinguish between reservoir sandstones and non-reservoir mudstones. These classifications of lithologies are used to define the boundaries of the three members in the formation as well as their sand-rich and mud-rich subunits. Supplementary information of sedimentary facies is given by investigation of sedimentary cores from four short intervals in the Rødby-1 well, and by comparison with well-described sedimentary facies from long core intervals in three Tønder wells (Clemmensen 1985; Olsen 1987, and by comparison with outcrops on Helgoland (Clemmensen 1991). Detection of reservoir properties in the Rødby-1 well is based on a limited number of thin sections and on porosity and permeability measurements from conventional core analysis (Olivarius *et al.* 2015).

Cyclostratigraphy and signal processing

The gamma ray record and derived clay content (Fig. 2) are given as unbroken curves and we decided in a first attempt to use the measured gamma ray curve to detect sedimentary cycles by spectral analysis in the complete formation.

The gamma ray record shows a clear composite cyclicity both developed in the sand-rich and mud-rich intervals. In the spectral analysis of sedimentary cycles, it has been decided to carry out the analysis separately on mud-rich and sand-rich intervals. This is because the abrupt and marked changes in gamma ray readings from sand-rich to mud-rich intervals significantly impact the detection of cyclicity by multitaper analysis. Thus, the gamma ray record is here clipped at 105 API and only show higher values to detect cyclicity in mud-rich intervals (Fig. 5) and clipped at 60 API and only show lower values to define cyclicity in sand-rich intervals (Fig. 6).

The Thomson multitaper method (MTM) is used as a robust estimator for detection of cyclicities in the gamma ray record. The power spectral density (PSD) is calculated using the signal processing toolbox in MathWorks MATLAB (the MathWorks Inc. 2024). This represents the proportion of the total power contributed by each frequency component of the climate signal. The time-bandwidth product is set to 2.5 for the mud-rich intervals and to 3.5 for the sand-rich intervals. The number of tapers used to calculate the PSD is $2 \times \text{NW}-1$. The fast Fourier transform is set to the next power of 2 greater than the length of the dataset. To remove unwanted effects, the datasets are

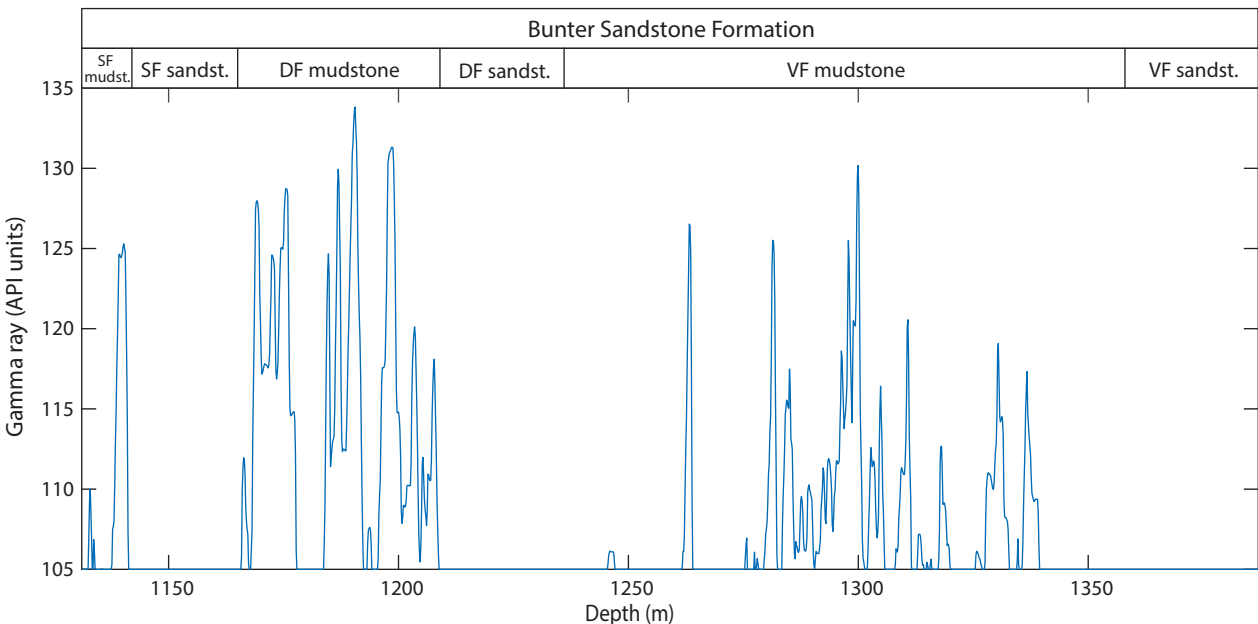


Fig. 5. Gamma ray data for clay-rich intervals (SF=Solling Member, DF= Detfurth Member, VF=Volpriehausen Member). The gamma ray data are clipped at 105 API showing only values equal to or higher than 105 API.

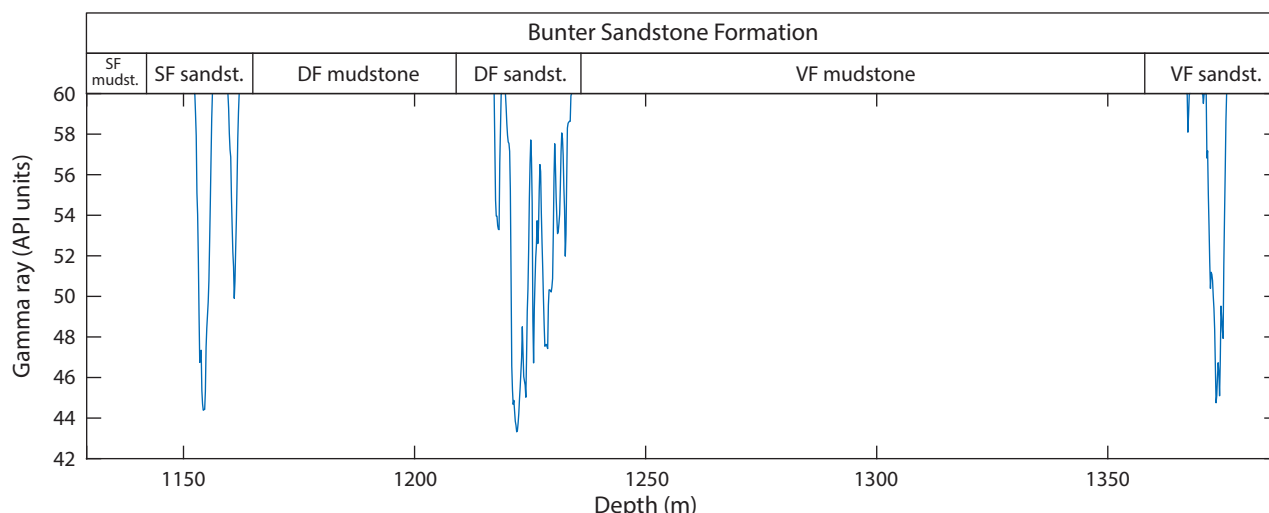


Fig. 6. Gamma ray data for sand-rich intervals (SF=Solling Member, DF= Detfurth Member, VF=Volpriehausen Member). The gamma ray data are clipped at 60 API showing only values equal to or lower than 60 API.

detrended before the MTM analysis by removing the best linear fit to the datasets. MTM confidence levels are estimated with the robust autoregressive noise model AR1 (Li *et al.* 2019). The PSD plots show several significant peaks above a 99.9 % confidence level. Peaks are best defined in the mud-rich intervals but also present in the sand-rich intervals (Figs 7, 8).

Sedimentary cycle variation throughout the complete formation is extracted with bandpass filters showing the stratigraphic position of specific significant cycles (Fig. 9). Bandpass filters were constructed with the bandpass function from the signal processing toolbox in MathWorks MATLAB. By defining specified bands of frequencies, the filters reveal the position,

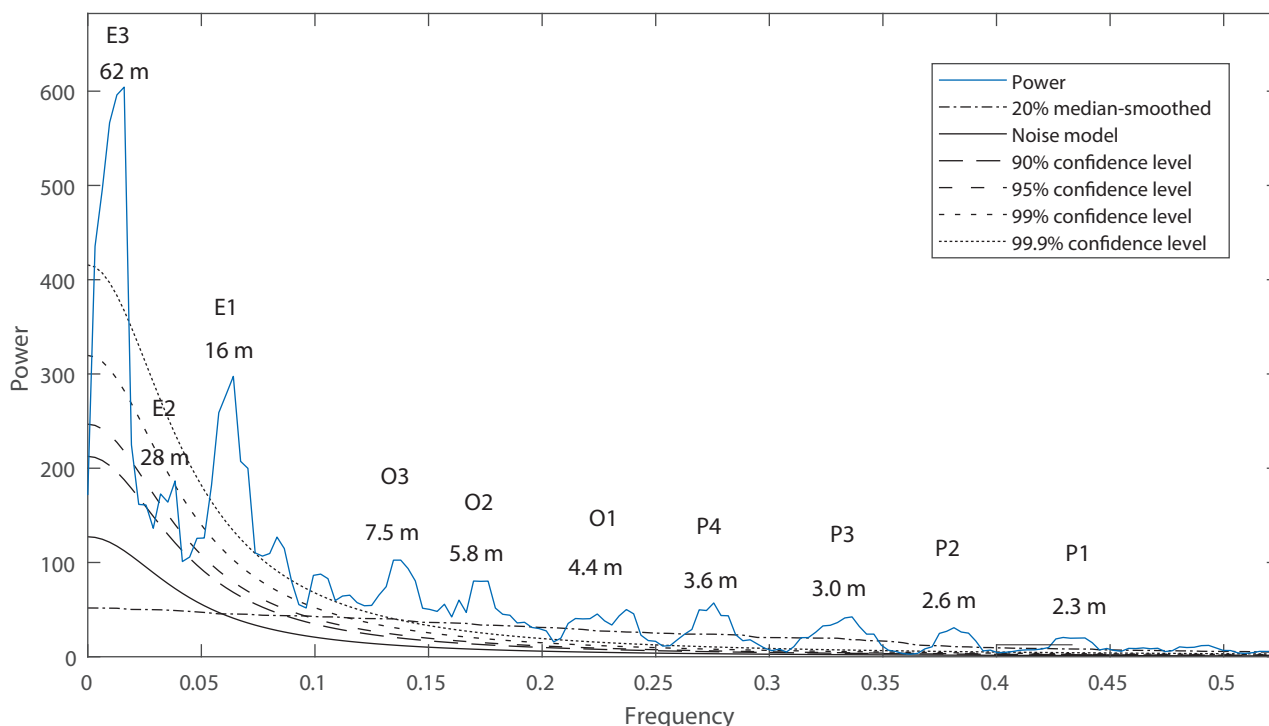


Fig. 7. Power spectral density of gamma ray data for the clay-rich intervals (Fig. 5) using Thomson's multitaper method. Density plot shows multiple significant (>CL 99.9%) and well-defined peaks. The most powerful peaks average around periods 2.3 m (P1), 2.6 m (P2), 3.0 m (P3), 3.6 m (P4), 4.4 m (O1), 5.8 m (O2), 7.5 m (O3), 16 m (E1), 28 m (E2), and 62 m (E3); where peaks marked with P are interpreted as precession cycles, peaks marked with O are interpreted as obliquity cycles and peaks marked with E are interpreted as eccentricity cycles. Interpreting the E3 peak as the 405,000-years eccentricity cycle, the remaining periods correspond to temporal periods of 183,000, 104,500; 49,000; 38,000; 28,500; 23,500; 19,500; 17,000; and 15,000 years (Table 3a).

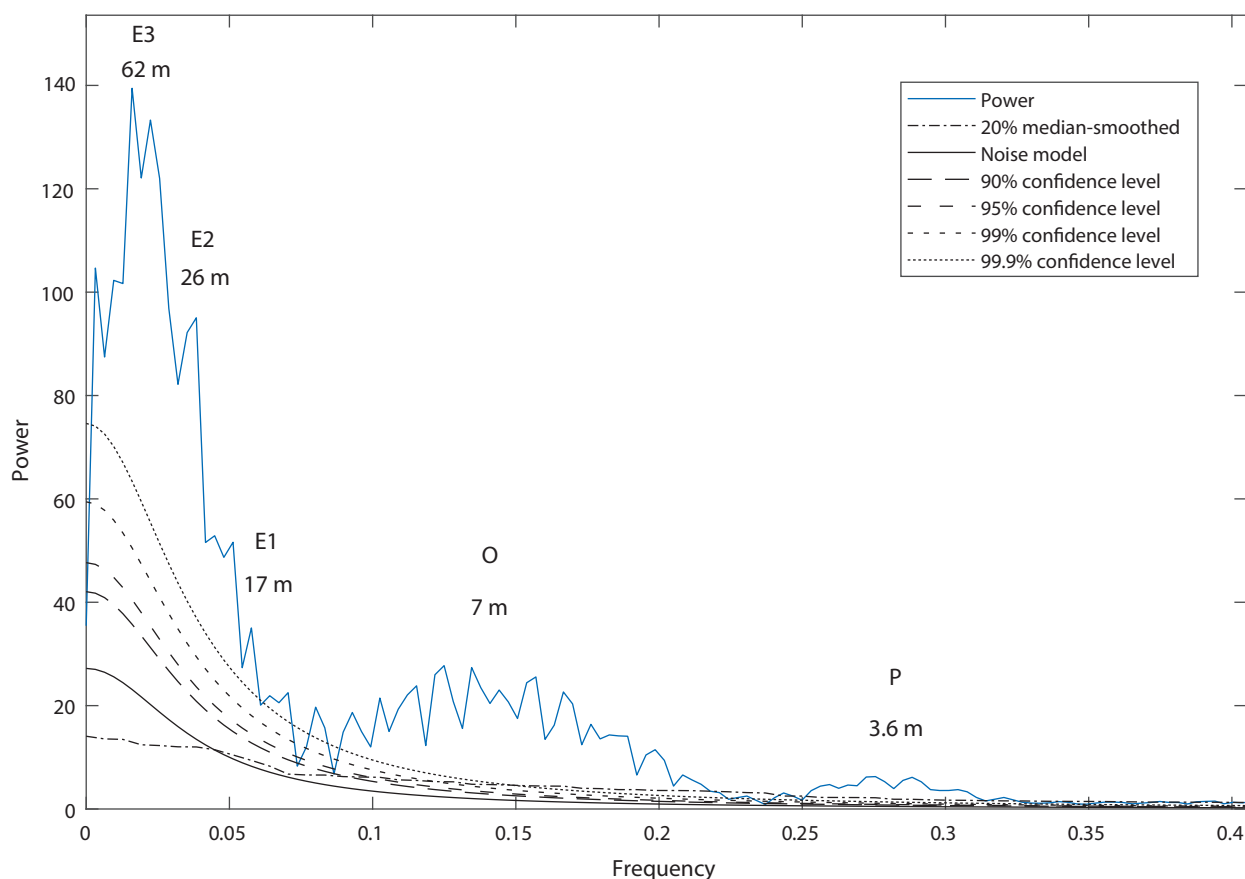


Fig. 8. Power spectral density of gamma ray data for the sand-rich intervals (Fig. 6) using Thomson's multitaper method. Density plot shows multiple significant (>CL 99.9%) but not well-defined peaks. The most powerful peaks average around periods 3.6 m (P), 7.0 m (O), 26 m (E2) and 62 m (E3). The peaks marked with P is interpreted as the precession band. The peak marked with O is interpreted as the Obliquity band. The peaks marked with E1, E2 and E3 are interpreted as the 100,000-, 200,000-, and 405,000-years eccentricity cycles respectively.

amplitude, and phase of the 405,000-years eccentricity cycle, the 100,000-years eccentricity cycle, and the 20,000-years precession cycle. The 405,000-years filter is created with frequency limits 0.014 and 0.018. The 100,000-years filter is created with frequency limits 0.054 and 0.071. The 20,000-years filter is created with frequency limits 0.262 and 0.349.

Finally, the evolution of sedimentary cycles throughout the formation was investigated by evolutionary wavelet analysis (Fig. 10). This is done to add knowledge of evolution of cycle frequencies by depth. Contrary to the evolutionary wavelet analysis, the Thomson multitaper method assumes a uniform geological record, which is rarely a valid assumption for most geological records because they often undergo significant changes in accumulation rate. The evolutionary wavelet spectrum was computed with a morlet wavelet using a MathWorks MATLAB script (Torrence & Compo 1998). The evolutionary wavelet analysis shows the power to a specific period and depth. Red dashed lines have been added to the density plot to show the interpreted development of the

405,000-year cycle (E3), the 200,000-year cycle (E2), the 100,000-year cycle (E1), the obliquity cycles (O), and the precession cycles (P).

Palaeogeography

Early Triassic palaeogeographical reconstruction of parts of southern Denmark has previously been constructed by Clemmensen (1985, 1991), Olsen (1987), and Olivarius *et al.* (2015). Only Clemmensen (1991) concluded that it was necessary to make maps for both arid and humid climatic periods as climate strongly controlled landscape evolution. This approach is followed here and new maps showing the palaeolandscapes during the deposition of the Detfurth Member are given for the Rødby and nearby areas on Lolland and Falster. The maps are primarily based on petrophysical log data in the Søllested-1, Ørslev-1, and Rødby-1 wells.

Table 3a. Sedimentary cycles identified by spectral analysis in mudstone units; Rødby-1 well

Orbital period	Sedimentary cycle thickness, m	Duration, years
E3	62	405,000
E2	28	183,000
E1	16	104,500
O3	7.5	49,000
O2	5.8	38,000
O1	4.4	28,500
P4	3.6	23,500
P3	3.0	19,500
P2	2.6	17,000
P1	2.1	15,000

E=eccentricity cycles, O=obliquity cycles, P=precession cycles.

Table 3b. Sedimentary cycles identified by spectral analysis in sandstone units; Rødby-1 well

Orbital period	Sedimentary cycle thickness, m	Duration, years
E3	62	405,000
E2	26	170,000
E1	17	111,000
O	7	46,000
P	3.6	23,500

E=eccentricity cycles, O=obliquity cycles, P=precession cycles.

stratigraphical subdivision and is of Olenekian age (Bachmann *et al.* 2009). This stage spans a time interval of 4 myr between 247.2 and 251.2 Ma (Bachmann *et al.* 2009). According to Bachmann *et al.* (2009), however, two hiati are present in the formation at many sites (at the base of the Detfurth and Solling members) causing the actual accumulation time to be less than 4 myr. Using magnetostratigraphy and cyclostratigraphy the following age constraints are given for accumulation time in northern Germany: Volpriehausen Member 0.9 myr, Detfurth Member, 0.4 myr, Hardeggen Member 1.2 myr, and Solling Member 0.3 myr (Table 4).

Results

Age constraints and accumulation rate

The Bunter Sandstone Formation (Volpriehausen, Detfurth, Hardeggen and Solling members) belongs to the Middle Buntsandstein of the German Triassic

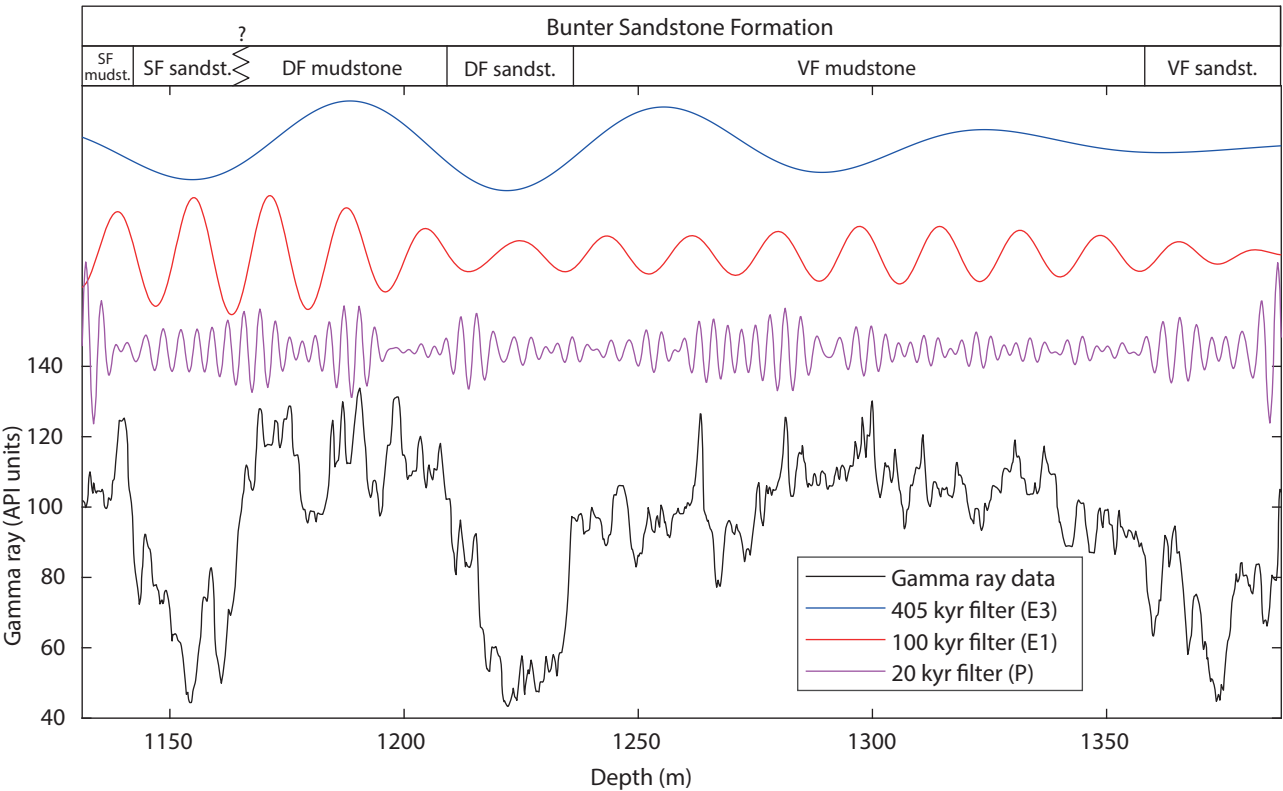


Fig. 9. Gamma ray data (black) with bandpass filters showing 20,000-year cycles (purple), 100,000-year cycles (red), and 405,000-year cycles (blue). The filters show around 80 precession cycles, 15 short eccentricity cycles, and 4 long eccentricity cycles. Peaks of the 405,000-years cycle filter mostly corresponds to clay-rich intervals (humid climate) in the Bunter Sandstone Formation while valleys of the filter correspond to sand-rich intervals (arid climate). There is a significant time gap at the boundary between the Detfurth and Solling members. Thus the continuation of orbital cycles across this boundary is a statistical artefact. Still we believe that the sand-rich interval in the Solling Member corresponds to an arid interval in the long eccentricity curve and the overlying mud-rich interval to a humid interval in this orbital period.

The spectral analyses and suggested interpretation of climate cycles (see later) show that Volpriehausen Member in Rødby is composed of about 9 short eccentricity (100,000 years) cycles recording accumulation over about 0.9 myr, and that the Detfurth Member is composed of about 4 short eccentricity cycle recording accumulation over about 0.4 myr (Fig. 9; Table 4). The Solling Member is composed of slightly more than 2 short eccentricity cycles and thereby recording accumulation over about 0.22 myr (Fig. 9; Table 4). These data give time spans of the members in very good agreement with the age estimates given for the members in North Germany (Table 4).

As only the Volpriehausen, Detfurth and Solling members are present in the Rødby area (and at most other sites in southern Denmark), it can be concluded that the Bunter Sandstone Formation here should records accumulation over 1.6 myr. However since the Hardeggen Member is not present at Rødby a significant time gap must exist at the boundary between the Detfurth and Solling members in the Rødby well (Fig. 9). The Volpriehausen and Detfurth members apparently form a continuous succession with a combined thickness of 218 m (interpretation A); the succession formed over 1.3 myr with an average accumulation rate of 0.17 m/1000 years. The overlying Solling Member with a thickness of 36 m (interpretation A) formed over 0.22 myr with an average accumulation rate of 0.16 m/1000 years.

It should be mentioned, however, that Geluk &

Röhling (1997) reached somewhat different age estimates of the members in the Bunter Sandstone Formation using presumed 100,000 years cycles of this formation in the Dutch North Sea. They found 18 such cycles in the Volpriehausen Member, 4 in the Detfurth Member, and 4 in the Solling Member (Table 4). Thus while the number of identified short eccentric cycles in the Detfurth and Solling members is almost identical to those recognized in North Germany and in this study, the number of 18 cycles in the Volpriehausen Member is surprisingly high. At present we are not able to explain this discrepancy convincingly, but tentatively suggest that the identified sedimentary cycles could be obliquity cycles with an age of about 50.000 years and thereby comparably to obliquity cycles identified in this study with an age of about 49.000 years (see later).

Sedimentary facies

Gamma ray records are used to identify main lithologies as sandstones and mudstones by using thresholds values of 75 API (Fig. 4) and a clay content of 25% (Fig. 2) as stated above. From the distribution of the main lithologies the Bunter Sandstone Formation is divided into the Volpriehausen, Detfurth and Solling members and further subdivided into sandstone and mudstone units (Fig. 2). Depth of boundaries in the Rødby-1 well indicated on the gamma

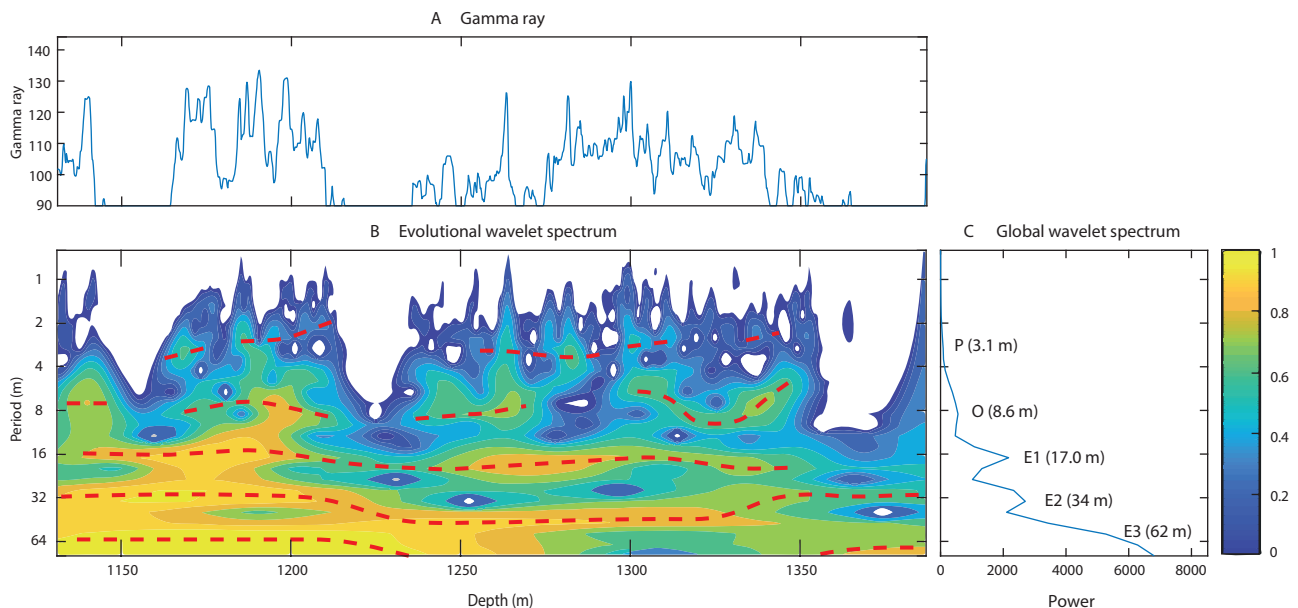


Fig. 10. Evolutionary wavelet analysis (see Torrence & Compo 1998 for analytic methods). (A) Gamma ray data clipped at 90 API. (B) Evolutionary wavelet spectrum of the gamma ray data. The spectrum shows high densities around 17.0 m, 34 m and 62 m interpreted as the 100,000-, 200,000-, and 405,000-years eccentricity cycles respectively. Less prominent densities show two cycles with thicknesses around 3.1 m and 8.6 m interpreted as the precession cycle band and the obliquity cycle band respectively. Red dashed lines show the interpreted frequency evolution of the five identified cycles. (C) Global wavelet spectrum shows the prominent peaks of power around 17 m (E1), 34 m (E2) and 62 m (E3).

ray log is given in Table 1. The lower boundary of sandstone units of all members is given by the first appearance of a sandstone deposit; the upper boundary is defined by the last appearance of a sandstone or muddy sandstone/sandy mudstone deposit.

Gamma ray records using API values indicate that relatively clean sandstone comprise the complete thickness of the 19 m thick sandstone unit in the Detfurth Member (Fig. 4). In the Volpriehausen Member relatively clean sandstones make up 14 m of the 28 m thick sandstone unit, and in the Solling Member sandstones comprise 12 m of the 22 m thick sandstone unit (Interpretation B). An alternative gamma ray log interpretation using clay content indicates that sandstones comprise 7 m of the 29 m thick sandstone unit in the Volpriehausen Member, 17 m of the 27 m thick sandstone unit in the Detfurth Member, and 8 m of the 23 m thick sandstone unit in the Solling Member (Interpretation A). Mud-rich intervals are present in between sand-rich intervals in the Volpriehausen and Solling members defining a cyclic pattern. The thickest relative clean sandstone intervals are about 7 m thick both in the Volpriehausen and Solling members.

The gamma ray records do not reveal details on the characteristics of the sandstone facies in the three members. By comparison with core data from wells in the Tønder area (Clemmensen 1985), it is assumed, however, that the sandstones in the Volpriehausen Member comprise both aeolian and fluvial (ephemeral river) facies; the frequency of aeolian facies in the Tønder wells varies between 35 and 75 %. The only core data from this stratigraphic interval in Rødby (see below) comprises fluvial overbank and sabkha facies; typical fluvial channel and/or aeolian sand facies are not present in the sampled core section in Rødby-1. There are no core data from the sandstone unit in the Detfurth Member. Comparison with facies observations in outcrops on Helgoland (Fig. 3; Clemmensen 1991) and from well cores in Germany (Hug-Diegel 2021), however, suggest that also this unit has aeolian as well as fluvial facies. Core data from the sandstone unit in the Solling Member in Rødby indicate the presence of fluvial facies (see below), and core data from the Tønder wells indicate that all sandstones of this member are fluvial, in many cases as part of terminal fan systems (Clemmensen 1985; Olsen 1987).

Limited core data from Rødby (see below) indicates that the mudstones units are composed of variety of sabkha and playa-lake sediments including claystones, heterolithic sediments and mud-rich sandstones. Core data from mudstone units in the Tønder wells (Clemmensen 1985) as well as outcrop data from Helgoland (1991) also indicate the occurrence of heterolithic sabkha and playa-lake sediments and that these deposits are the primary facies in thick in-

tervals in the mudstone unit of the Volpriehausen Member (Fig. 3). The clay content of the heterolithic sediments and associated facies on Helgoland varies on a decimeter-scale clearly reflected in fluctuating gamma ray signatures (Binot & Röhligh 1988 and own unpublished results). These facies variations impose a cyclic pattern to the sedimentary succession (Clemmensen *et al.* 1994; Geluk & Röhligh 1997).

Available data from conventional core analysis of sand-rich intervals in Rødby-1 (n=6) show a porosity between 22 and 30 % and permeability between 100 and 500 mD (Olivarius *et al.* 2015). These values are relatively high and suggest that sandstone-rich intervals may form good reservoir units. Comparable data from sandstones elsewhere in the basin indicate that fluvial sandstones have a porosity between 1 and 34 % and a permeability between 0 and 6538 mD, and aeolian sandstones have a porosity between 1 and 27 % and a permeability between 1 and 2838 mD, though these values are underestimated since many aeolian sediments are unconsolidated and could not be analysed, so aeolian sandstones are considered to have the best reservoir properties (Olivarius *et al.* 2015). The data show, however, that the aeolian facies have only marginally better reservoir properties than the fluvial facies. One reason for this could be that many fluvial deposits formed by reworking of pre-existing aeolian sand.

Available data from conventional core analysis of mud-rich intervals in Rødby-1 (n=11) show a porosity between 7 and 17% and a permeability between 1 and 8 mD. These values would indicate that the mud-rich deposits form relative tight intervals. The reported values are somewhat lower than those reported from fine-grained desert lake and sabkha sediments elsewhere in the basin; here porosity is between 1 and 26% and permeability between 0 and 369 mD (Olivarius *et al.* 2015).

Cyclostratigraphy

Gamma ray records

The sedimentary facies and their cyclic development are here examined in the Rødby-1 well based on gamma ray readings. Visual inspection of gamma ray records in the Rødby-1 well was carried out within each of the two main lithologies comprising the three sandstone units and the three mudstone units. Sedimentary cycles are present both in sandstone and mudstone units. The identified cycles have thickness between 3 and 16 m both in the sandstone units and mudstone units, and they are best developed in the mudstone unit of the Detfurth Member. There is no apparent shift in visual cyclicity in the Solling Member as compared to cyclicity seen in Volpriehausen and Detfurth Members.

Table 4. Number of short (100,000 years) eccentricity cycles and deduced duration in the members of the Bunter Sandstone Formation in the North German Basin

Stratigraphy	Rødby	North Germany	Dutch North Sea
Solling Member	2.2 (0.22 myr)	3 (0.3 myr)	4 (0.4 myr)
Hardeggen Member	0	12 (1.2 myr)	20 (2.0 myr)
Detfurth Member	4 (0.4 myr)	4 (0.4 myr)	4 (0.4 myr)
Volpriehausen Member	9 (0.9 myr)	9 (0.9 myr)	18 (1.8 myr)

The number of identified short eccentricity cycles in the Volpriehausen, Detfurth and Solling members are almost identical in Rødby and North Germany.

The analysis of the gamma ray record in Rødby-1 indicates that the formation contains significant cyclicities with a composite cyclicity that here initially is related to the long eccentricity (405,000 years), the short (100,000 years) eccentricity and the precession (20,000 years) periods (Fig. 9). To analyze the gamma ray record in more detail it was decided to carry out spectral analysis in sand-rich and mud-rich units separately. Thus, the gamma ray record is clipped at 105 API and only show higher values to detect cyclicity in mud-rich intervals (Fig. 5.) and clipped at 60 API and only show lower values to define cyclicity in sand-rich intervals (Fig. 6). Looking only at the mud-rich layers the following significant (>99.9 % CL) cycles can be seen: 62, 16, 7.5, 5.8, 4.4, 3.6, 3.0, 2.6 and 2.3 m; a less prominent but still significant (>95 % CL) cycle is seen at 28 m (Fig. 7; Table 3a). Looking only at the sand-rich layers the following significant (>99.9 % CL) but less well-defined cycles are seen: 62, 17, 7, and 3.6 m; a less prominent cycles is seen at 26 m (Fig. 8; Table 3b). The long eccentricity cycle of 405,000 years is considered to be of constant duration during Cenozoic ad Mesozoic time (Kent *et al.* 2018). Assuming that the 62 m cycle records the 405,000-years eccentricity cycle (E3), then the remaining cycles defined in the mud-rich intervals represent the following periods: 104,500; 49,000; 38,000; 28,500; 23,500; 19,500; 17,000 and 15,000 years; the less prominent cycle at 28 m has an assumed period of 183,000 years. In sand-rich intervals the significant cycles have the following periods: 405,000; 111,000; 46,000 and 23,500 years; the less prominent cycle at 26 m has a period of 170,000 years. The deduced orbital periods agree well with other Triassic cyclostratigraphical records from terrestrial successions (e.g. Kemp & Coe 2007; Volmer *et al.* 2008; Kent *et al.* 2017; Mau *et al.* 2022) as well as with theoretical values for Early Triassic orbital periods (Gradstein *et al.* 2012). Thus both a 100,000 (E1) years eccentricity as well as a 20,000 years precession cyclicity (P1-P4) can be identified (Figs 7, 8). More surprising also a likely obliquity signal seems to be present as given by cycles with periods of 28,500 (O1), 38,000 (O2) and 49,000 (O3) years (Figs 7, 8). The less prominent 183,000 (170,000) years cycle is here interpreted as a weak eccentricity cycle (E2); alternatively, it can be viewed as a long obliquity cycle (Hilgen *et al.* 2020).

Evolutionary wavelet analysis of the gamma ray record in Rødby-1 indicates multiple cycles of high power throughout the entire Bunter Sandstone Formation (Fig. 10). To avoid unwanted effects from the long-term shifts in lithology, the gamma ray data is cut at 90 API and only higher values are used for the analysis corresponding to the mud-rich intervals. This makes the power spectral density plot more well-defined but also limits the detection of high frequency cycles (obliquity and precession cycles) in the more sand-rich intervals. The three identified eccentricity cycles (E1, E2 and E3) are most significant in the evolutionary wavelet analysis. The analysis shows cycles with periods averaging around 17 m corresponding to the 100,000-years eccentricity cycle, 34 m corresponding to the 200,000-years eccentricity cycle, and 62 m corresponding to the 405,000-years eccentricity cycle. The analysis also shows less significant cycles with periods of around 8.6 m interpreted as obliquity cycles and 3.1 m interpreted as precession cycles. The evolutionary analysis shows some change in accumulation rate. Most significant seems to be an increase in accumulation rate from around 1225 m depth to around 1300 m depth corresponding to the upper part of the Volpriehausen mudstone unit.

The deduced short eccentricity (100,000 years) cycles in Rødby have an average thickness of about 16 m (Table 3a and 3b). Similar cycles have an average thickness of 11-12 m on Helgoland, (Clemmensen 1991; Clemmensen *et al.* 1994), thicknesses between 5 and 25 m in the Dutch North Sea (Geluk & Röhling 1997), and thicknesses between 10 and 30 in northern Germany (Bachmann *et al.* 2007).

Sedimentary core data

The sedimentary facies in the Rødby area are examined in 4 short cores in the Rødby-1 well; these cores are here described and interpreted in light of the new cyclostratigraphical data.

Interval 1367-1373 m (4486-4506'), lower part of Volpriehausen Member, sandstone unit. Based on gamma ray readings the core interval seems to represent a nearly full 7 m thick sedimentary (obliquity) cycle with two sandstone intervals separated by a 2 m thick mud-rich interval. Recovery was only 35% and sampled



cores (150 cm) of sabkha and fluvial overbank deposits seem to comprise the most mud-rich part of the cycle (Figs 2, 11).

Interval 1280-1284 m (4200-4212'), upper part of Volpriehausen Member, mudstone unit. Based on gamma ray readings the core interval seems to represent the initial part of a 6 m thick sedimentary (obliquity) cycle with varying content of mud (clay). Recovery was 60% and sampled cores (230 cm) of sabkha and playa-lake deposits seem to comprise the most mud-rich part of the cycle (Figs 2, 12).

Interval 1198-1201 m (3930-3941'), upper part of Detfurth Member, mudstone unit. Based on gamma ray readings the core interval seems to represent the basal and middle part of a 7 m thick sedimentary (obliquity) cycle with varying content of mud (clay). Recovery was 80% and sampled cores (240 cm) of sandflat and sabkha deposits seem to comprise the most sand-rich part of the sedimentary cycle (Figs 2, 13).

Interval 1151-1155 m (3775-3790'), Lower part of Solling Member, sandstone unit. Based on gamma ray readings the core interval seems to represent the upper half of a sandy 7 m thick sedimentary (obliquity) cycle. Recovery was 40% and sampled cores (155 cm) of fluvial channel sandstones and a fluvial channel base conglomerate seem to comprise a sand-rich part of the sedimentary cycle (Figs 2, 14).

Palaeogeography

Hornung & Aigner (2002) proposed a palaeoclimate-driven sedimentary model to explain sedimentary cycles of fluvial and playa-lake deposits in the Late Triassic of Germany. The playa lake in the basin center was modulated by climate changes; the lake had its largest extent at the end of a humid phase and its smallest extent at the end of an arid phase. Climate variation in the Late Triassic was probably related to orbital control of the intensity of summer monsoons (e.g. Volmer *et al.* 2008). Here we use a similar approach to evaluate the origin of the sedimentary cycles and landscape evolution in the Early Triassic Bunter Sandstone Formation in Rødby by orbitally controlled climate variation. This study suggests that the major 62 m cycles was controlled by the 405,000

Fig. 11. Interval 1367-1373 m (4486-4506'), Volpriehausen Member, sandstone unit.

Cores from 150 cm with mud-rich sabkha and heterolithic fluvial overbank deposits; both facies contain anhydrite nodules. Shown core interval is illustrating the heterolithic, fluvial overbank sediments at the topmost 40 cm of the core. Scale in cm.



years eccentricity cycle (Tables 3a, 3b). We interpret this cyclic lithological change as a record of long-term shifts in the character of the palaeolandscape. The general setting of the palaeolandscape was a central playa lake flanked northwards by sabkha flats, and marginal aeolian and fluvial sedimentary systems; closets to the uplands alluvial fans probably existed (e.g. Olivarius *et al.* 2015). Lake size reached its maximum during the humid phases of this cycle and its minimum during the arid phases; marginal aeolian and fluvial deposits accordingly had their maximum distribution during arid phases and their minimum distribution during humid climatic phases. It should also be mentioned that the suggested climatic fluctuations that drove these variations in palaeolandscape took place over the complete spectrum of orbital climatic change from 20,000 to 405,000 years probably with the strongest and most predictable change in landscape evolution coupled to the eccentricity cycles (Fig. 9). While the fluvial deposits were sourced by material eroded on the Ringkøbing-Fyn High, most aeolian sand was transported to the study area from southerly directions (Olivarius *et al.* 2017).

The new data indicates that one arid phase in the long eccentricity variation of climate is not linked to the formation of prograding sand plains of ephemeral river and aeolian deposits and the middle part of the mudstone unit in the Volpriehausen Member only becomes slightly more sandy during this arid phase indicating that the lake environment was only little modified by this climatic change (Figs 2, 9). At present we are not able to explain this unusual landscape response to climate change.

Clemmensen (1991) concluded that it was necessary to construct two palaeogeographical maps for each member as the landscape changed drastically during climatic shifts from arid to humid and back again. In this paper we follow this approach and discuss the evolution of the palaeolandscape during maximum aridity and humidity respectively during a 405,000 years eccentricity cycle. Landscape evolution during the Volpriehausen and Detfurth members were probably almost identical apart from the fact that the lake phase (mudstone deposition) was of longer duration in the Volpriehausen Member. During the time the sandstone units of the Volpriehausen and Detfurth members were deposited, the aeolian

Fig. 12. Interval 1280–1284 m (4200–4212'), Volpriehausen Member, mudstone unit.

Cores from 230 cm with heterolithic sabkha and clay-rich playa-lake deposits; both facies contain anhydrite nodules. Shown core interval is illustrating the sabkha deposits (sa) overlain by playa-lake deposits (la) in the middle part of the core. Uppermost part of sabkha deposits is deformed and lake sediments are strongly fragmented. Scale in cm.



sand plains were frequently eroded by ephemeral rivers causing a succession of alternating aeolian and fluvial facies. Available data from the Tønder wells indicate that the proportion of aeolian and fluvial facies not only was controlled by short-term orbital climatic change but also by frequent shifts in the position of ephemeral rivers. While the sandstone unit of the Solling Member was deposited, the marginal sand-rich depositional environments were composed of fluvial facies only; these fluvial deposits frequently formed terminal fans at the margin to the central sabkha flats/lake environment (Clemmensen, 1985, Olsen 1987). Only maps for the Detfurth Member are shown here as it was during the long-term arid phase of the long eccentricity period that the best potential reservoir deposits in the Rødby area formed. The map focuses on the Rødby and nearby areas on Lolland and Falster.

Detfurth Member, sandstone unit

The palaeolandscape of the Lolland and Falster area in southern Denmark south of the Møn High during deposition of the sandstone unit of the Detfurth Member is shown in Fig. 15. In this part of the basin uplands were situated at the Møn High and on the Glamsbjerg High. The map shows the distribution of landscapes during maximum aridity of the long eccentricity cycle with low lake levels and a wide distribution of marginal sand flats with aeolian deposits cut by ephemeral rivers (cf. Clemmensen 1985, 1991; Olivarius *et al.* 2015). Sabkha flats and the central playa lake were situated far to the south of the study area. It is tentatively suggested that aeolian sand, driven by resultant sand-transporting winds towards the west-northwest, covered a large part of the study area and even reached the margins of the river plain and alluvial fans flanking the northern uplands. The aeolian sand plain composed of small dunes and sand sheets were cut by river systems. These river systems were primarily active during the rainy summer seasons when monsoons brought precipitation to the area. It is likely that the river systems frequently shifted positions and thereby caused repeated reworking of the aeolian material when they cut through the aeolian sand belt (cf. Krapf *et al.* 2003).

Fig. 13. Interval 1198-1201 m (3930-3941'); Detfurth Member, mudstone unit.

Cores from 240 cm with sandflat and sabkha deposits composed of red (or occasionally greenish grey), very fine-grained, muddy sandstones with a few anhydrite nodules; the structureless, muddy sandstones alternate with thin heterolithic intervals with lamination (hl). Shown core interval is illustrating the sandflat and sabkha deposits at the topmost 50 cm of the core. Scale in cm.



The complete lack of core material in the sandstone unit of Detfurth Member in Rødby-1 (and elsewhere in wells in southern Denmark) makes the map tentative in particular with respect to the presence and distribution of aeolian facies. Outcrops on Helgoland (Fig. 3), however, supports the existence of aeolian facies in this time interval as do core data from Hessen in NW Germany (e.g. Hug-Diebel 2021).

Detfurth Member, mudstone unit

The palaeolandscape of the Lolland and Falster area in southern Denmark, south of the Møn High, during deposition of the mudstone unit of the Detfurth Member is shown in Fig. 16. The map shows the distribution of landscapes during maximum humidity during the long eccentricity cycle with high lake levels and minimum extent of the river plain flanking the Ringkøbing-Fyn High; the aeolian sand plain is no longer existing and marginal alluvial fans are now flanked by a narrow, mud-rich river plain (cf. Clemmensen 1991). The scarcity of core material of mudstone units in Rødby-1 reduces the precision of the map and in particular the knowledge of the size and distribution of the more sand-rich sabkha belt flanking the mud-rich playa lake.

Discussion

The new cyclostratigraphical analysis suggests that the long eccentricity period of 405,000 years was the main control on Bunter Sandstone landscape evolution and that sand was deposited in the study area in up to 200,000 years long periods with an overall dry climate. The strong influence of this long eccentricity period on landscape evolution and thereby the character of the resulting sedimentary facies was also shown by cyclostratigraphical analysis of the Late Triassic lake system (Newark Group) in Northeast USA (Kent *et al.* 2017). Change in climate related to the short eccentricity, obliquity and precession periods, also strongly affected landscape evolution and thereby the character of the Bunter Sandstone sedimentary facies including periods with increased and decreased aeolian sedimentation in the Volpriehusen and Detfurth members.

Aeolian facies are considered to have the best reservoir properties, and according to Olivarius *et al.* (2017) most aeolian sand in the Bunter Sandstone

Fig. 14. Interval 1151-1155 m (3775-3790'), Solling Member, sandstone unit.

Cores from 155 cm with fluvial channel sandstones and a channel bottom conglomerate. Shown core interval is illustrating the channel bottom conglomerate at the topmost 30 cm of the core; conglomerate (cgl) is under- and overlain by channel sandstones (sst). Scale in cm.

Formation of southern Denmark had source areas south of the study area. Clemmensen (1979, 1991) suggested from data on Helgoland that dry winters with winds from northeasterly directions were replaced by wet summers where monsoonal winds from southeasterly directions brought precipitation to the area. Knowing now that the Germanic basin has been rotated 30 degrees clockwise since the Anisian (van Hinsbergen *et al.* 2019) these estimates must be corrected to alternating east-southeasterly and southerly (or less likely northerly) palaeowinds. The east-southeasterly winds are here interpreted as dry winter trade winds deflected by the topography of the Ringkøbing-Fyn High; while the southerly winds are interpreted as summer monsoon winds bringing precipitation to the area. Dominant southerly palaeowinds have been reported from Early Triassic aeolian sandstones in central Poland (Gradzinsky 1979) and may have been the primary sand-transporting palaeowind direction in much of the North German Basin (Mader 1982); precipitation here may have been less intense than farther north in the study area close to the Ringkøbing-Fyn High.

The new interpretation of Early Triassic palaeowinds gives an annual resultant sand drift direction towards the west-northwest in the southern Denmark obliquely towards the trend of the Ringkøbing-Fyn High; it is therefore suggested that aeolian sand initially was transported across the North German Basin by dominant southerly winds before it was trans-

ported towards the west-northwest along the lake margin forming the aeolian sand belt in southern Denmark during dry climatic intervals. It is possible that aeolian sand reached far northwards and even to the margins of the river plains and alluvial fans south of the Møn High during arid climatic intervals of the long eccentric period in Volpriehausen and Detfurth time (Fig. 15). It also possible that aeolian sand did not form an unbroken belt along the margin of the North German Basin south of the Ringkøbing-Fyn High but was concentrated in smaller areas separated by more permanent river systems. During humid climatic intervals in the long eccentricity period marginal depositional plains were of restricted size and probably composed of relatively mud-rich fluvial systems; sabkha flats and playa-lake sediments now covered the complete study area (Fig. 16).

The ancient aeolian sand facies form excellent reservoir deposits, and it is therefore important to determine the amount and stratigraphical distribution of such facies in the sandstone units of the Volpriehausen and Detfurth members in Rødby-1. The present data, however do not allow a recognition of aeolian facies in these members although it is speculated that aeolian facies primarily form in arid intervals during the precession, obliquity, and short eccentricity periods in the arid part of the long eccentricity period. Present data suggest that the mudstone units formed during the humid part of the long eccentricity period constitute tight reservoir intervals. The new

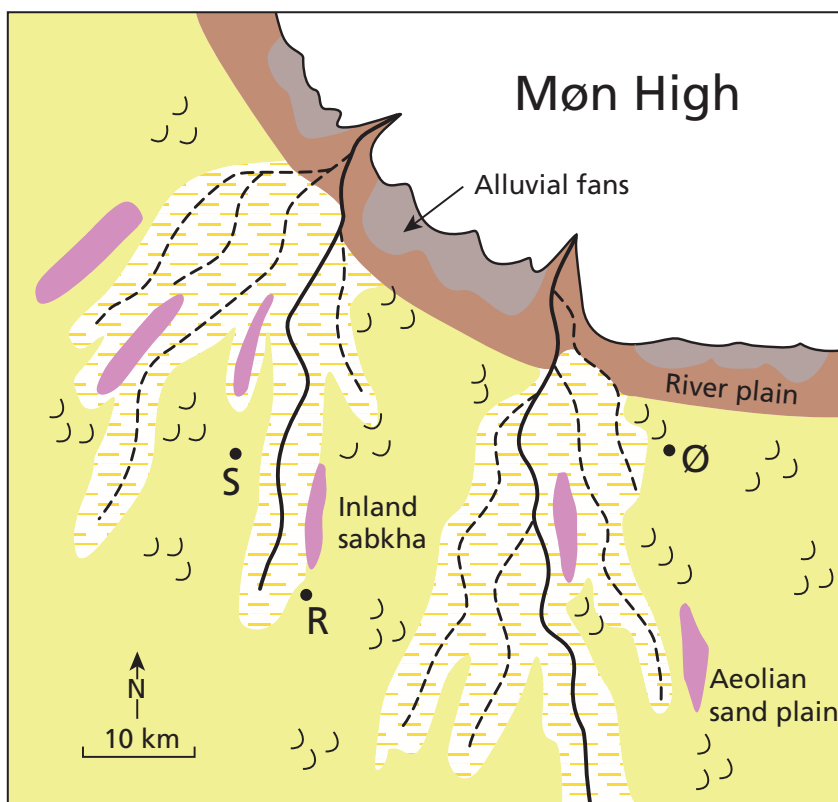


Fig. 15. The map shows a tentative distribution of palaeolandscapes in the study region of Lolland and Falster in southern Denmark south of the Møn High in the time interval forming the sandstone unit of the Detfurth Member. The time interval represents the most arid phase of the long eccentricity period. The approximate positions of the Søllested-1 (S), Ørslev-1 (Ø), and Rødby-1 (R) wells are given. Fluvial sand was derived from the Møn High, while aeolian sand was brought to the study area from southerly sources before it was transported towards the west-northwest and formed relative wide sand plains in the study area.

cyclostratigraphical interpretation, however, also suggests that the upper part of the mudstone unit in the Volpriehausen Member, which formed during decreasing humidity in the long eccentricity period is relatively sandy and might form a less tight sedimentary interval. A new petrophysical log including gamma ray readings is planned and may hopefully create new data useful for supplementary interpretations of sedimentary facies as well as for additional detection of porosity and permeability both in sandstone and mudstone units.

Conclusions

The cyclostratigraphical analysis of the Bunter Sandstone Formation in Rødby-1 indicates that deposition took place during strong influence of orbital climate control. Long-term climatic variation related to the long eccentricity period of 405,000 years not only controlled landscape evolution in the Rødby area, but also the alternating formation of sandstone and mudstone units.

In Rødby-1, the sandstone unit in the Volpriehausen Member is 29 m thick. The new cyclostratigraphy indicates that deposition of the complete sandstone unit took place during the arid part of a 405,000 years cycle. Internal lithological variation and thereby reservoir properties (sandstone-mudstone ratio) in the unit are related to 100,000 years eccentricity precession variation in climate as well as to obliquity variation of 28,500 to 49,000 years and precession variation of 15,000 to 23,000 years. There is very limited core

evidence on lithology in Rødby-1, but by comparison with core data from the Tønder area in southern Jutland, it is suggested that the sand-rich intervals of this unit is composed of alternating aeolian and fluvial deposits with facies change primarily related to climate variation. Mud-rich intervals that separate the sand-rich interval probably comprise inland sabkha and fluvial overbank sediments and formed during the most humid intervals of the precession and obliquity cycles.

The sandstone unit of the Detfurth Member in Rødby-1 is of a rather uniform character with 19 m thick clean sandstones; deposition of the sandstone unit took place during an overall arid climate in the 405,000 years cycle. Minor variations in lithology and reservoir properties (mud content of sandstones) seems primarily related to the precession period probably changing the depositional environment from aeolian to fluvial. However, no core data exist to support this interpretation.

The sandstone unit of the Solling Member has a thickness of 23 m in Rødby-1 and probably represents deposition during an overall arid climate in a 405,000 years cycle. Sand-rich intervals are separated by mud-rich intervals and by comparison with core data from wells at Tønder, it is suggested that the lithological variation observed at Rødby primarily reflects climatic induced variation in fluvial style and transport capacity linked to the full spectrum of orbital cycles. Frequent shifts in river courses caused more unsystematic variation in facies and lithology.

All three sandstone units form reservoirs. But while sandstone intervals in the Volpriehausen and Solling

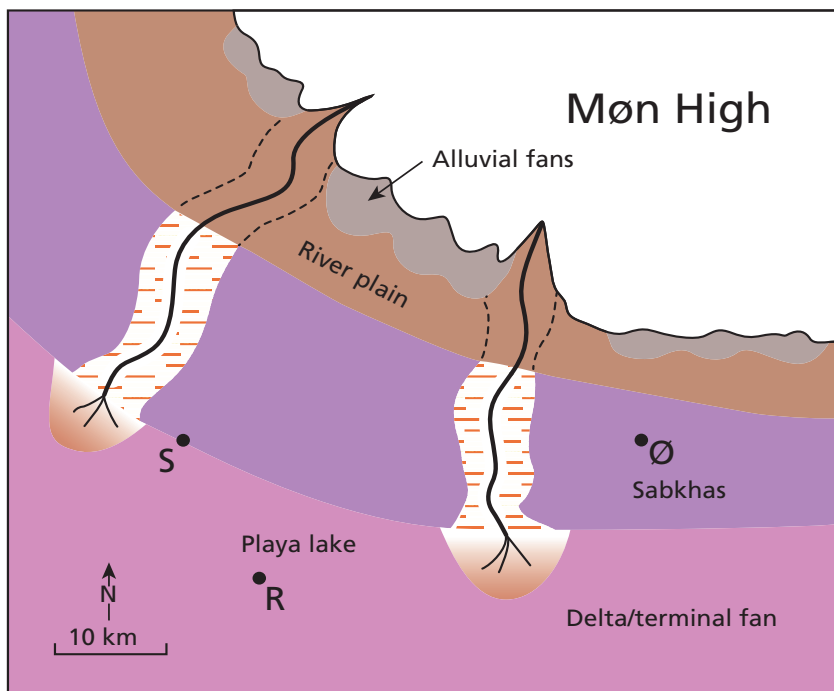


Fig. 16. The map shows a tentative distribution of palaeolandscapes in the study region of Lolland and Falster in southern Denmark south of the Møn High in the time interval forming the mudstone unit of the Detfurth Member. The time interval represents the most humid phase of the long eccentricity period. The approximate positions of the Søllested-1 (S), Ørslev-1 (Ø), and Rødby-1 (R) wells are given.

members are separated by mud-rich intervals reducing the overall quality of these reservoir units, the sandstone unit of the Detfurth Member is of rather uniform lithology and forms an excellent reservoir.

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New plesiosaur fossils from the Pliensbachian (Early Jurassic) of Bornholm, including the first juvenile specimen from Denmark

ZOE C. KINZELLA, LAURA J. COTTON & LENE L. DELSETT



Geological Society of Denmark
<https://2dgm.dk>

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Plesiosaurs were an extremely successful, globally distributed group that thrived from the Late Triassic to the end of the Cretaceous Period. The Early/Middle Jurassic faunal turnover greatly affected plesiosaur evolution, although it remains poorly understood, partly due to the scarcity of plesiosaur fossils from the Pliensbachian age (192.0–184.2 Ma). This paper describes five fossil plesiosaur skeletal elements found in the Pliensbachian aged Hasle Formation on the Danish island of Bornholm. The five specimens are isolated remains, including a tooth, spinal fragments, a rib and a propodial. The tooth can be assigned to Pliosauridae indet. due to its robust form and ornamentation, and the spinal fragments to Plesiosauria indet. The neural spine is detached and could therefore either be from an osteologically immature individual or show signs of pedomorphism. Lastly, but most importantly, an osteologically immature propodial is described. It is the first of its kind found in Denmark.

Keywords: Plesiosaur, marine reptile, juvenile, Pliensbachian, Denmark, Hasle

Zoe C. Kinzella (zokin20@student.sdu.dk), University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark. Laura J. Cotton (laura.cotton@snm.ku.dk), Natural History Museum Denmark, Gothersgade 130, 1123 Copenhagen K, Denmark. Lene L. Delsett (l.l.delsett@nhm.uio.no), Natural History Museum, University of Oslo, Sars' gate 1, 0562 Oslo, Norway.

The plesiosaurs (Plesiosauria) were an extremely successful, globally distributed group of Mesozoic marine tetrapods. They thrived over a period of approximately 130 million years, from the Late Triassic (200 Ma) to the end of the Cretaceous Period (66 Ma; Bardet *et al.* 2014). Plesiosauria was the only clade within the superorder Sauropterygia that survived beyond the Triassic Period (Bardet *et al.* 2014) and by the Early Jurassic plesiosaurs had a worldwide distribution. The relationships between and within major plesiosaur clades remain debated, although consensus is increasing in more recent years (Benson & Druckenmiller 2013; Roberts *et al.* 2020; Sachs *et al.* 2024). In addition to long-necked species with small heads in the clade Plesiosauroidea, Plesiosauria include taxa with short necks and larger heads, a body shape that evolved more than once within the two families Rhomaleosauridae and Pliosauridae (Fischer *et al.* 2020).

The Early/Middle Jurassic faunal turnover (*c.* 175 Ma) affected plesiosaur evolution, including a near extinction of the rhomaleosaurids, paving the way for the plesiosaur clades that came to dominate the oceans from the Middle Jurassic until the end-Cre-

taceous (Fischer *et al.* 2021; Sachs *et al.* 2024). Pliensbachian plesiosaur occurrences preceding the Early/Middle Jurassic faunal turnover are globally sparse and currently only three plesiosaur taxa are formally named: *Westphaliasaurus simonsensis* (Schwermann & Sander, 2011), *Cryonectes neustriacus* (Vincent *et al.*, 2013) and *Arminisaurus schuberti* (Sachs & Kear, 2018). In addition, Perrson (1963) reported three species from France that are incompletely described, and there are also undiagnostic plesiosaur specimens found in the UK (Storrs 1995; Evans 2003; Forrest 2006; Evans 2012), Spain (Bardet *et al.* 2008), Germany (Sachs 2014) and Australia (Kear 2012; Table 1).

Additionally, plesiosaur fossils from the Pliensbachian have been found in the Hasle Formation on the Danish island of Bornholm (Bonde 1993; Milàn & Bonde 2001; Bonde & Christensen 2003; Smith 2008). Smith (2008) represents the only scientific description and taxonomic assessment of plesiosaur material from Denmark. All specimens described in that contribution were found to be insufficiently diagnostic for referral to genus or species level, contrary to previous suggestions (Milàn & Bonde 2001; Smith 2008). The plesiosaur diversity is nonetheless high in

Table 1. Overview of plesiosaur specimens described from Pliensbachian strata

Specimens	Locality/country	Reference
<i>Westphaliasaurus simonsensii</i>	Germany	Schwermann & Sander 2011
Juvenile plesiosaur	Germany	Sachs 2014
Plesiosaur indet.	Lincoln, England	Forrest 2006
Plesiosaur indet. (LEICT G1.2002)	Gloucestershire, England	Evans 2000
Juvenile plesiosaur (BRSMG Cel17972)	Dorset, England	Storrs 1995
Adult plesiosaur (NHMUK R16330)	Lyme-Regis, England	Evans 2012
<i>Microcleidus</i> cf. <i>homalospondylus</i>	France	Perrson 1963
<i>Plesiosaurus</i> cf. <i>dolichodeirus</i>	France	Perrson 1963
<i>Sthenarosaurus dawkinsi</i>	France	Perrson 1963
<i>Cryonectes neustriacus</i> (MAE 2007.1.1)	Normandy, France	Vincent, Bardet & Mattioli 2013
Juvenile plesiosaur (MUHA 0518)	Asturias, Spain	Bardet <i>et al.</i> 2008
Isolated remains of plesiosaurs (MGUH GM-V-2006-8, MGUH DKV-2002-70)		
MGUH DKV-2002-149, MGUH DK-2002-69, MGUH DK417, MGUH DK416		
MGUH 2002-65, MGUH DKV-2002-74 and MGUH 2003-1720)	Bornholm, Denmark	Smith 2008
<i>Arminisaurus schuberti</i>	Germany	Sachs & Kear 2018
Isolated plesiosaur remains (QM F983-QMF5500)	Australia	Kear 2012

the Hasle Formation with at least three (and possibly six) distinct taxa (Smith 2008). Smith (2008) confirmed the presence of the family Rhomaleosauridae in Europe during the Pliensbachian and thus extended the known range of this family into Scandinavia.

Since Smith (2008) five additional plesiosaur specimens have been found in the Hasle Formation of Bornholm and are described in this contribution. Of particular interest is a small and probably juvenile propodial which is the first of its kind found in Denmark, and only the fourth confirmed juvenile plesiosaur specimen from the Pliensbachian of Europe (Table 1). Description of these specimens is significant as it adds to our understanding of the Pliensbachian marine reptile diversity and distribution at higher latitudes.

Geological setting

Bornholm is located in the Baltic Sea, 169 km south-east of Copenhagen and 37 km southeast of the coast of Sweden. It is a faulted block within the Sorgenfrei-Thornquist Zone, which separates the Danish Basin from the Baltic Shield (Milàn & Surlyk 2015). Sedimentary geology consists of Palaeozoic to Mesozoic sandstones, limestones and shales. The Jurassic of Bornholm consists of four formations: Rønne, Hasle, Sorthat and Bagå, which are all part of the Bornholm Group. The fossils described here originate from the Hasle Formation, an 80–140 m thick sequence of strata located on the southwestern part of the island (Fig. 1). It is of the Lower Pliensbachian Age (192–184 Ma) and has been correlated with the *Uptonia jamesoni* to *Prodactylioceras davoei* ammonite zones (Rees 1998; Donovan & Surlyk 2003). The sediments of this formation consist of hummocky and swaley cross-stratified and siltstones and sandstones with sparse layers of coarse-grained sandstone and gravel, indicating

shoreface to offshore depositional environment that was storm influenced (Larsen & Friis 1991; Michelsen *et al.* 2003; Milàn & Surlyk 2015). Near Rønne intercalated clays are also present (Michelsen *et al.* 2003). Numerous fossils have been found in the deposit, including both vertebrate and invertebrate taxa. Ammonoids, belemnites, bivalves, gastropods, and brachiopods all occur within the Hasle Formation

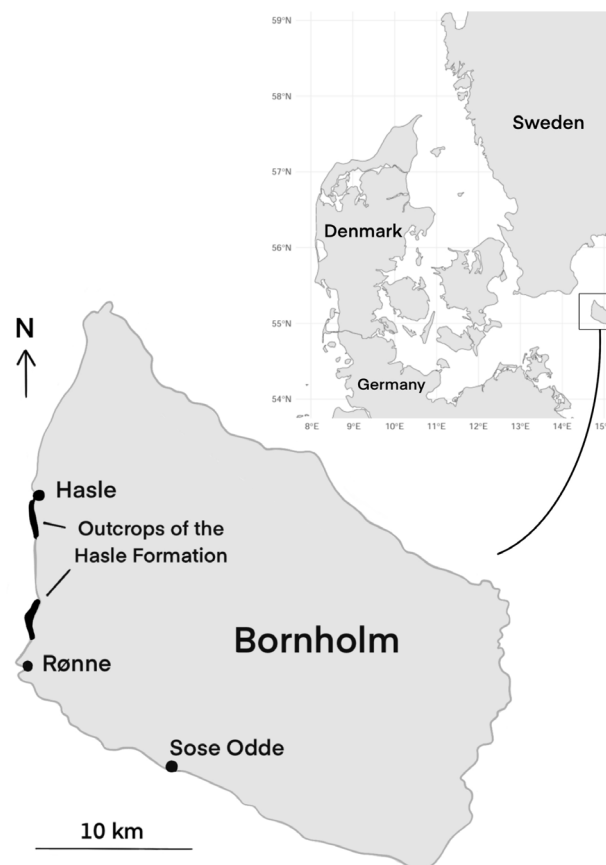


Fig. 1. Map of the Danish island of Bornholm showing the location of the Hasle Formation. Modified from Molin *et al.* (2024).

(Donovan & Surlyk 2003; Vajda & Wigforss-Lange 2009; Milàn & Surlyk 2015) and vertebrate fossil finds are becoming increasingly diverse with dinosaurian remains (Bonde & Christensen 2003; Milàn & Surlyk 2015; Milàn & Mateus 2024), crocodile (Milàn & Mueller 2021), holocephalians (Duffin & Milàn 2017; Duffin & Milàn 2022), a mammal-like cynodont (Molin *et al.* 2024) and a number of plesiosaur bones and teeth (Bonde 1993; Smith 2008). There remains a lack of ichthyosaurs in the formation, which is interesting as this group is commonly found alongside plesiosaurs in other Early Jurassic strata in Europe (Milàn & Bonde 2001).

Methods and materials

The five plesiosaur specimens (Table 2) described here were found in the Hasle Formation between 2009 and 2019 and consists of isolated tooth and skeletal elements, including spinal fragments, a rib and a propodial. They are currently stored within the Danekræ collection of the palaeontological collections at the Natural History Museum Denmark (NHMD) in Copenhagen.

The specimens were photographed using the NHMD photography studio with a Canon EOS RS and EOS Utility Program and measured using an Absolute AOS Digimatic caliper of the model number CD-15AXR.

Comparisons are made with specimens within Rhomaleosauridae, Pliosauridae, Plesiosauridae, and Microcleididae.

Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Pliosauridae Seeley, 1874

Pliosauridae indet.

Referred specimen. NHMD 625447 (Fig. 2a).

Description. NHMD 625447 is a single tooth in sandstone matrix. The tooth is robust and slightly curved. Its base is 12.3 mm wide and this is also the widest part of the tooth. It narrows to 10.7 mm midway and tapers to 7.8 mm at its tip, which is damaged. As preserved, the crown measures 26.4 mm from base to broken apex. The ornamentation of the tooth consists of longitudinal enamel ridges arranged in an even pattern that runs along the tooth, from the base of the crown to the apex. Thirteen tightly spaced ridges are visible in lateral view. The base of the tooth is smooth compared to the rest of the tooth due to poor preservation, and no root is visible. The cross section of the tooth is circular.

Comparison. Previously described plesiosaur teeth from the Hasle Formation were categorised into three different tooth types A, B, and C based on morphology; the latter including 14 of the 16 described teeth (Smith 2008). Tooth type A is typical for Lower Jurassic Plesiosauroidea as it is slender and has a tightly packed pattern of seven longitudinal ridges in lateral view. The crown of type A is 4.0 mm wide compared to 12.3 mm of NHMD 625447, whereas A is 18.0 mm long and NHMD 625447 is 26.4 mm long. This makes NHMD 625447 significantly larger and more robust than the characteristic slender morphology of Plesiosauroidea.

Tooth type B from the Hasle Formation is most similar to the genus *Rhomaleosaurus* (Smith 2008). It is more robust than tooth type A and has a slight recurved form. Smith (2008) estimated it to be approximately 30 mm long in life, which is similar to NHMD 625447. Type B is sparsely ridged, with only five ridges visible in lateral view that do not extend to the apex. This contrasts with NHMD 625447 where all ridges run the entirety of the tooth.

Type C were identified as Pliosauroidae, a clade comprising pliosaurids and rhomaleosaurids, based on the robust construction and broad bases by Smith (2008), and it has been suggested that they belong to the species *Attenborosaurus conybeari* (Milàn & Bonde 2001), due to the closely striated ornamentation. Type C teeth display a distinct ornamentation of ridges along the whole crown with most extending to the tip. The number of ridges ranges from 9 to 11 in lateral view. These teeth are robust and resemble

Table 2. Plesiosaur material from Bornholm described in this paper

Specimen number	Brief description	Found by	Determined by	Locality and date
NHMD 625145 (DK 610)	Incomplete humerus or femur	Mette Hofstedt	Niels Bonde	Hasle Klint, 4 December 2009
NHMD 625357 (DK 803, 1-2)	Neural arch and spine (1), rib from neck or tail (2)	Mette Hofstedt	Niels Bonde, Adam Smith	Hasle Klint, 4 December 2015
NHMD 625435 (DK 881)	Neural spine	Mette Hofstedt	Niels Bonde	Hasle Klint, 2017
NHMD 625447 (DK 913)	Single tooth in matrix	Mette Hofstedt	Niels Bonde	Hasle Klint, 5 May 2017
NHMD 625503 (DK 976)	Base of spinal process of vertebra	Marianna Nattestad	Bent Lindow	Hasle Klint, 11 September 2019

NHMD numbers: collection numbers of the specimens, DK numbers: numbering system specifically for Danekræ specimens

NHMD 625447 more than type A and B as they share approximately the same amount of ridges in lateral view and have a similar shape and curve. However, NHMD 625447 is longer than any of the type C teeth, even if they vary in size (length 5–20 mm).

The teeth of plesiosaurs are long, slender, curved and have a deeply rooted base with a large pulp cavity (Andrews 1910). Pliosaur teeth tend to be more robust. NHMD 625447 is a robust tooth, and thus different from the long and slender teeth of the basal pliosaur *Cryonectes neustriacus* (Vincent *et al.*, 2013). They are also more robust than *Macroplata tenuiceps* (BMNH R5488) from the Hettangian (Ketchum & Smith 2010), but instead resemble *Thaumatodracon wiedenrothi* from the Sinemurian (Smith & Araújo 2017).

Plesiosauroid teeth are often sub-circular in cross section (Andrews 1910), whereas some Late Jurassic pliosauroids, e.g. *Pliosaurus* are triangular (Benson *et al.* 2013; Sander 2023). The cross section of NHMD 625447 is circular, similar to most Jurassic

plesiosauroids, e.g. *Microcleidus tournemirensis* (Bardet *et al.* 1999; Evans *et al.* 2012), *Macroplata tenuiceps* (Ketchum & Smith 2010), *Seeleyosaurus guilelmiimperatoris* (Sachs *et al.* 2025) and *Thaumatodracon* (Smith & Araújo, 2017), whereas *Cryonectes neustriacus* (Vincent *et al.*, 2013) has teeth that are sub-circular in cross section with compressed tips.

NHMD 625447 is ornamented with longitudinal enamel ridges from the base of the crown to the apex, resembling that of *Microcleidus* (Bardet *et al.* 1999; Evans *et al.* 2012). The ornamentation of *Macroplata tenuiceps* extends from the crown to the apex, however only one or two reaches the very tip (Ketchum & Smith 2010). In *Thaumatodracon wiedenrothi* (Smith & Araújo, 2017), the enamel ridges are tightly spaced, and most reach from the base of the crown to the apex, similar to NHMD 625447. They are thus more closely striated than in *Rhomaleosaurus zetlandicus* (Taylor 1992) and more similar to *Atychodracon megacephalus* (Cruickshank 1994). All ridges of *Rhomaleosaurus zetlandicus* do not extend to the tip, however, making these teeth unlike NHMD 625447.

Compared to the size of the teeth in *Cryonectes neustriacus* (Vincent *et al.*, 2013), which are 50 mm in height, NHMD 625447 is significantly smaller. *Microcleidus*, in contrast, had teeth between 31 and 54 mm long (Bardet *et al.* 1999; Evans *et al.* 2012), probably similar to the actual size of NHMD 625447 in life, whereas *Macroplata tenuiceps* was somewhat smaller (Ketchum & Smith 2010). *Thaumatodracon* on average have teeth no larger than 15 mm (Smith & Araújo 2017), whereas *Rhomaleosaurus zetlandicus* (Taylor 1992) and *Atychodracon megacephalus* (Cruickshank 1994) have teeth approximately 25 mm in length, comparable to NHMD 625447.

In summary, NHMD 625447 shares similarities with both pliosaurs, microcleidids and rhomaleosaurians. NHMD 625447 does not resemble the rhomaleosaurid tooth known from the Hasle Formation (MGUH DKV 2002-70), and thus, based on the ornamentation, robustness, shape and size, NHMD 625447 is concluded to be a tooth of an early pliosaurid. Given previous finds on Bornholm, it could be a tooth of *Attenborosaurus*, as the teeth of this species have very closely spaced ridges (Smith 2007), however as this is hard to confirm, the tooth is identified to Pliosauridae indet.

A study on long-term ecological changes in a seaway of the Middle-Late Jurassic focused on the shape and function of marine reptile teeth, dividing the marine reptiles into the pierce, generalist, and cut guilds (Massare 1987; Foffa *et al.* 2018). According to this scheme, NHMD 625447 best coincides with the 'generalist' guild, in which either the 'cut' or 'pierce' sub-guild could fit. 'Pierce' is most likely, given the shape and the circular cross section of the tooth. This sub-guild is characterised by large, conical and variably

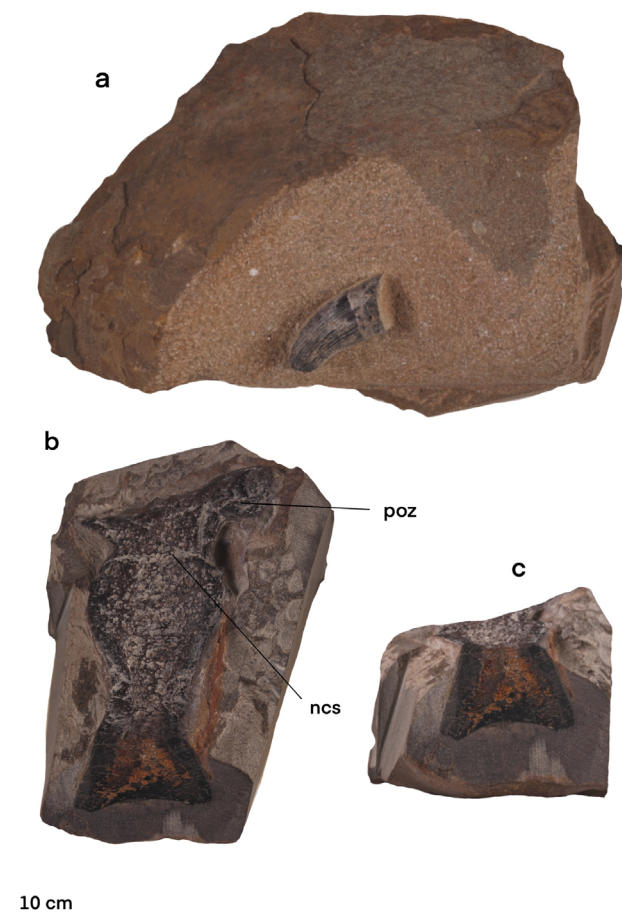


fig. 2. tooth in sandstone matrix (NHMD 625447) in a) dorsal view. Partial vertebra (NHMD 625503) in b) partial anterior view c) distal view. poz: postzygapophysis, ncs: neurocentral-suture.

ornamented teeth and mostly includes large Callovian pliosaurs. This indicates that NHMD 625447 is most likely from an early relative of the large Middle Jurassic thalassophonean pliosaurids.

Plesiosauria indet.

Referred specimen. NHMD 625503 (Fig. 2b-c)

Description. NHMD 625503 is a partial vertebra with its neural spine missing. The fossil is encased in a grey sandstone matrix with a rust-coloured surface, evident by the reddish tones present in the distal end of the fossil. The vertebra is presumably preserved in lateral view, showing the neural arch with zygapophyses. The neurocentral suture is visible (fig. 2, b), showing the fusion of the neural arch to the centrum. The preservation of the fossil makes it difficult to fully predict how much of the bone is preserved and the exact orientation within the matrix. The length of the fossil is 71.2 mm.

The neural arch presumably belongs to a posterior cervical or anterior dorsal vertebra, based on the shape of the spinal process and the post-zygapophysis. The preserved part of the neural arch has an irregular, elongate shape that narrows dorsally. The rounded facet on one side of the fossil is likely the right post-zygapophysis, whereas the left is eroded. Collectively the post-zygapophysis and the preserved neural arch have a width of 49.4 mm. The inner bone microstructure is spongy, especially prevalent in the centrum. The cross section of the centrum has a trapezoid shape, and a thick outer layer is present, surrounding a fine spongy structure of secondary trabeculae arranged longitudinally.

Comparison. The preservation of NHMD 625503 makes it difficult to assign taxonomically. The matrix obscures the features in a way that a direct comparison of other vertebrae is difficult. In addition to Plesiosauria, both Dinosauria and Ichthyosauria have been proposed in the original identification reports. The longitudinal pattern of the spongy tissue and the shape of the neural arch lead us to tentatively assign the specimen to Plesiosauria.

Referred specimen. NHMD 625435 (Fig. 3a-d)

Description. NHMD 625435 consists of a well-preserved neural arch and spine with five accompanying sandstone matrix pieces. The neural arch is loose (i.e. not connected to a centrum) and it is three-dimensionally preserved. Measured from one pedicle to the other, the arch measures 56.9 mm in medio-lateral width. Both pre- and post-zygapophyses

are well preserved, although the specimen exhibits taphonomic surface abrasion. The neural spine is straight and broken anteriorly, measuring 31.1 mm from the apex of the broken part to the neural canal. The neural canal itself is 9.7 mm wide with a length of 11.6 mm. The angle in which the pedicles protrude from the neural canal is wide at 90 degrees, and the shape of the neural canal is almost square. The width between the post-zygapophyses is 32.6 mm. The entirety of the fossil measures 59.6 mm from apex of the broken neural spine to the base of the pedicles. Distally to the robust pedicles is the neurocentral junction and based on the rugged texture of the facets, it appears that the neural arch was not fused to the vertebral centrum. The posterior facets of the pedicles are flat and oval with no rim.

Comparison. This is only the third plesiosaur neural arch recovered from the Hasle Formation, and the first that is not fused to a vertebral centrum. This fea-

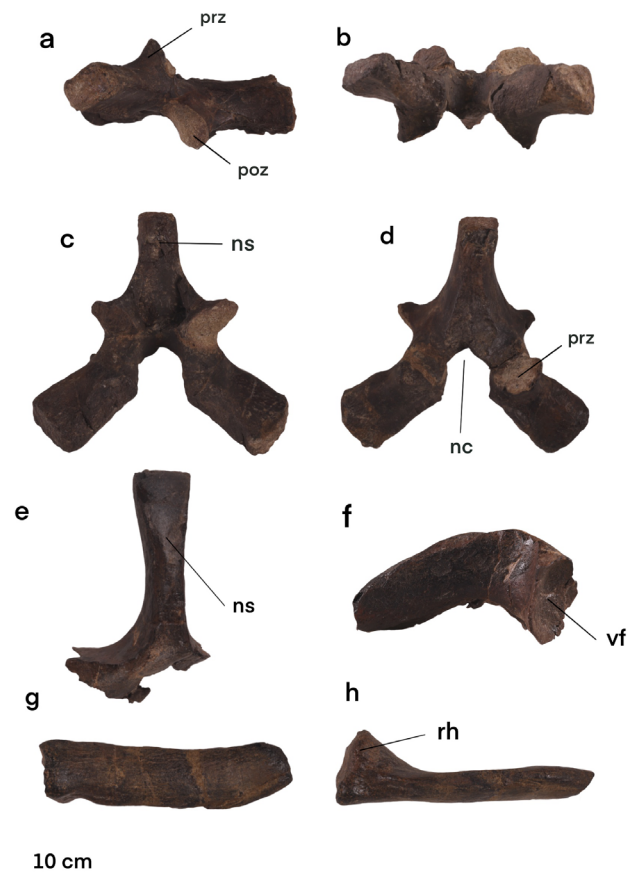


Fig. 3. Neural arch and spine (NHMD 625435) in a) lateral view, b) posterior view, c) posterodorsal view, d), anterodorsal view. Neural spine (NHMD 625357-1) in e) dorsal view, f) lateral view. Complete rib (NHMD 625357-2) in g) lateral view, h) dorsal view. poz: postzygapophyses, prz: prezygapophyses, ns: neural spine, nc: neural canal, vf: vertebral facet, rh: rib head.

ture indicates an osteologically immature individual, and could perhaps belong to a juvenile, however detached arches are also found in presumed adult individuals within Rhomaleosauridae, Pliosauridae, Elasmosauridae, Polycotylidae and Leptocleididae (except *Gronausaurus wegneri*; Araújo & Smith 2023).

As NHMD 625435 does not possess transverse processes, it is not from the dorsal region. The 90-degree angle of the pedicels in NHMD 625435 correlates with either a pectoral vertebra, as in *Stratesaurus taylori* (Benson *et al.*, 2015), *Microcleidus tournemirensis* (Bardet *et al.*, 1999) and *Plesiopharos moelensis* (Puértolas-Pascual *et al.*, 2021), or a sacral vertebra, as in *Colymbosaurus svalbardensis* (Roberts *et al.*, 2017), *Microcleidus tournemirensis* (Bardet *et al.*, 1999), and an indeterminate plesiosaur vertebra (NHMD 188220/MGUH 2003-1720) from the Hasle Formation (Smith 2008).

The pectoral vertebrae of *Stratesaurus taylori* possess neural canals that are circular with pedicles nearly horizontal, compared to the 90-degree angle of NHMD 625435 (Benson *et al.* 2015). The vertebrae of *Microcleidus tournemirensis* have very small circular neural canals (Bardet *et al.* 1999), unlike NHMD 625435, whereas *Plesiopharos moelensis* have pectoral vertebrae with larger, square shaped neural canals and straight, posteriorly oriented neural spines (Puértolas-Pascual *et al.* 2021). The neural arches of *Plesiopharos moelensis* resemble the shape of the neural canal and neural spine of NHMD 625435, although as the neural spine of NHMD 625435 is broken the size and shape are difficult to fully estimate. The sacral vertebrae of *Colymbosaurus svalbardensis* has small pedicles with a nearly triangular neural canal and therefore does not correlate very closely with NHMD 625435 (Roberts *et al.* 2017). The neural arch of the sacral vertebra found in the Hasle Formation of Bornholm described by Smith (2008; NHMD 188220/MGUH 2003-1720) is, unlike NHMD 625435, fused to the centrum body. The neural canal of NHMD 188220 is 10.3 mm long and 9.3 mm wide and thus similar to NHMD 625435 (11.6 mm length, 9.7 mm width), albeit the neural canal of NHMD 625435 is larger. The neural canal of NHMD 188220 has a more pointed shape dorsally, whereas NHMD 625435 is square. The pedicles of NHMD 188220 are wide, measuring 50.8 mm from the outer edges, making it slightly smaller than NHMD 625435 which is 56.9 mm wide.

Many well-preserved plesiosaurian neural arches has been found in the Oxford Clay (Middle Jurassic), e.g. *Muraenosaurus durobrivensis*, *Muraenosaurus platyclis*, *Muraenosaurus leedsi*, *Cryptocleidus oxoniensis*, *Tricleidus seeleyi* and *Picrocleidus beloclis* (Andrews 1910). The anterior cervical vertebra of *M. durobrivensis* has a similar angle of the pedicels, but the neural canal is more oval than NHMD 625435, whereas *Cryptocleidus oxoniensis* has a more rounded neural canal. The thin

lateral neural spine resembles that of NHMD 625435. The prezygapophyses of *Cryptocleidus* and *Tricleidus* are quite pointed and oriented parallel to the neural spine in anterior view, compared to the prezygapophyses of NHMD 625435 being angled horizontally. Prezygapophyses of *M. platyclis* are less parallel to the neural spine than in *Cryptocleidus* but still show a more vertical angling than NHMD 625435. Cervical vertebrae of *Picrocleidus beloclis* have quite small prezygapophyses oriented close to the median of the neural spine. The neural canal is square, much like NHMD 625435 (Andrews 1910).

Due to the arch being detached (i.e. unfused to a centrum), NHMD 625435 could be from a rhomaleosaur (Araújo & Smith 2023), however given that other families also experience paedomorphism (such as Pliosauridae), it is not possible to taxonomically assign NHMD 625435 beyond Plesiosauria indet.

Referred specimen. NHMD 625357-1 (Fig. 3e-f)

Description. NHMD 625357-1 is a disarticulated, three-dimensionally preserved neural arch with a complete spine, accompanied by a sandstone impression. In dorsal view, the neural spine is mediolaterally flattened with a width of 13.6 mm. Distally the spine flattens to a square tipped paddle shape and is strongly oriented posteriorly. The entire length of the neural spine and the remaining arch is 57.3 mm. The arch is 32.1 mm wide. The neural arch has been fused to the vertebra centrum, but is broken off, leaving only parts of the neural arch on both sides, with a piece of the centrum preserved on the right side of the specimen. The left base of the neural arch has been broken off, however, the right side is well preserved with a large facet. This facet is oval with a surrounding rim. The pedicles protrude in a strong convex shape on each side of the dorsal spine. Laterally the pedicles are smooth and flat with some cracks dorsoventrally. Part of the neural canal has been preserved.

Comparison. *Microcleidus tournemirensis* has dorsal spines that flare dorsally when seen in lateral view, which is both apparent in cervical and pectoral vertebrae (Bardet *et al.* 1999). In anterior view, they are very narrow and often yielding to one side, unlike NHMD 625357-1 which is straight. NHMD 625357-1 is flattened, but to a much lesser degree: the dorsal spine flares distally in dorsal view, instead of having a narrow tip, which is more common. The pectoral vertebrae of *Stratesaurus taylori* from the Hettangian of England have distally flared neural spines in a rod-like shape (Benson *et al.* 2015), as in NHMD 625357-1, but *Stratesaurus* does not possess the flat, paddle-like shape at the distal end of the neural spine, character-

istic of NHMD 625357-1. However, they do share a robust, thick neural spine.

Plesiopharos moelensis from the Sinemurian has well preserved vertebra (Puértolas-Pascual *et al.* 2021). These vertebrae have approximately the same width the entirety of the neural spine length. Only the third pectoral vertebra (fig. 2A:4 (Puértolas-Pascual *et al.* 2021) share a similar pattern to NHMD 625357-1 as it, seen from above, flares distally. Dorsal vertebrae from the Hettangian of Ireland have straight neural spines, both in dorsal and lateral view, in contrast to NHMD 625357-1 that is only straight from above, but curves posteriorly when seen in lateral view (Smith 2010).

The neural spines of *Muraenosaurus duribrivensis* are nearly straight in lateral view and therefore much less posteriorly inclined than NHMD 625357-2, whereas *Muraenosaurus leedsi* has a slight posterior curve. The neural spines of the latter are broken though, so the full shape cannot be compared. The posterior caudal vertebrae of *Cryptoclidus oxoniensis* display a prominent posterior incline in a similar fashion to *Picrocleidus beloclis*, however only *Tricleidus seeleyi* share a robust shape like NHMD 625357-1. None of *Tricleidus* vertebrae display the same strong posterior curve though (Andrews 1910).

A Plesiosauria indet. sacral vertebra (NHMD 188220/MGUH 2003-1720; pers. obs. ZK) from the Pliensbachian of Bornholm, has a neural spine that is equally wide from the base to the tip and that appears to be straight (Smith 2008). NHMD 625357-1 in contrast, flares distally and is curved. Neural spines of *Westphaliasaurus simonsensi* from the Pliensbachian displays the same straight shape laterally, as in NHMD 625357-1, although some of them bend strongly to the side in dorsal view (Schwermann & Sander 2011).

Thus, the shape of the neural spine of NHMD 625357-1 is unusual with its strong posterior curve in lateral view, together with the distal flaring that leads to a paddle shape. The neural spine is also more robust than other compared fossils. For now, it is assigned to Plesiosauria indet.

Referred specimen. NHMD 625357-2 (Fig. 3g-h)

Description. NHMD 625357-2 is a complete rib with a length of 61.7 mm. The rib is mediolaterally compressed and reversely spatulate with the rib head curved in a convex fashion dorsoventrally. The rib head has an irregular oval outline surrounded by a slight rim. The margins of the rib are slightly upwards curling, which are most noticeable posteriorly at the tapered, rounded tip. The base of the rib has a width of 19.6 mm that narrows to 14.3 mm at the tip. Subtle longitudinal ridges span across the entirety of

the rib. It has been affected by taphonomy with the posterior side having a longitudinal crack from the tip.

Comparison. Based on its short length, the rib is most likely either a cervical, sacral or caudal rib. It could, however, also be a juvenile. The rib is most likely not a chevron, as these are shown to be proximally expanded and tapering to a narrow point distally, e.g. *Muraenosaurus leedsi* (Andrews 1910).

Cervical ribs of many Lower Jurassic plesiosaurs are often short and hatchet shaped (Andrews 1910), e.g. *Franconiasaurus brevispinus* (Sachs *et al.*, 2024), *Stratesaurus taylori* (Benson *et al.*, 2015) and *Seeleyosaurus guilelmiimperatoris* (Sachs *et al.*, 2025). The form of NHMD 625357-2 is instead spatulate and therefore most likely not a cervical rib.

For sacral ribs a spatulate form is common. Sacral ribs from *Colymbosaurus svalbardensis* shows equally expanded proximal and distal ends (Roberts *et al.* 2017), differing from the spatulate sacral ribs found in *Tatenectes laramiensis* (O'Keefe *et al.* 2011) and *Pantosaurius striatus* (Wilhelm & O'Keefe 2010), which have expanded distal ends. In *Cryptoclidus eurymerus* (Brown, 1981) the proximal end is dorsoventrally thicker than the distal end, similar to *Muraenosaurus durobrivensis* (Andrews 1910). In NHMD 625357-2 the distal end is narrower than the proximal end and the rib itself has a spatulate shape, more similar to *Cryptoclidus*.

The rib may be caudal, based on the nearly flat facet on its distal end, the curved posterior portion, and the circular rib head (Andrews 1910). *Stratesaurus taylori* has caudal ribs that share a similar shape and size as NHMD 625357-2, although the rib head appears larger and more irregular on *Stratesaurus* (Benson *et al.* 2015). Caudal ribs of *Colymbosaurus svalbardensis* have a similar size and shape as NHMD 625357-2, although these ribs display a more curved shape distally, when seen in lateral view (Roberts *et al.* 2017). They do, however, share the same spatulate form as NHMD 625357-2. This is also true for *Muraenosaurus platyclis* and *Muraenosaurus leedsi* (Andrews 1910), as well as *Seeleyosaurus guilelmiimperatoris* (Sachs *et al.* 2025).

Given the size, rib head and overall morphology of NHMD 625357-2, we identify it as a caudal rib, assigned to Plesiosauria indet.

Referred specimen. NHMD 625145 (Fig. 4)

Description. NHMD 625145 consists of an incomplete propodial with a broken off counterpart. Both are partially encased in sandstone matrix with a margin of iron oxidation, limited to one side of the bone. The bone is curved, with the minimum anteroposte-

rior width of 35.6 mm at the proximal end. Distally to this, the bone widens to 40.2 mm mid shaft and flares distally to a maximum width of 47.8 mm. The proximodistal length of the entire element is 117 mm. In dorsoventral view, the anterior margin is slightly convex and curves posteriorly, whereas the posterior margin is more concave, due to the postaxial expansion of the distal end.

Ontogeny. The propodial is juvenile based on its osteologically immature morphology and small size. In dorsal view, the distal end of the limb bone displays a soft, rounded edge, in contrast to the well-defined lines associated with adult plesiosaur limb bones (Araújo & Smith 2023), where the distal end often flares anteroposteriorly. This rounded edge is similar to plesiosaur material found in the Jurassic of Wyoming (Wahl 2006). There are no distinct surfaces for the epipodials or other well-defined anatomical structures, all indicating that this is a juvenile. The specimen does not possess a strong concave postaxial margin as is often characteristic of adult plesiosaurs (Storrs 1997; Bardet *et al.* 1999; O’Keefe 2001).



Fig. 4. Propodial with accompanying sandstone counterpart (NHMD 625145). a) sandstone encased side of propodial, b) sandstone encased counterpart that is broken off, c) propodial, d) broken off counterpart. All shown in dorsal view. e) propodial and its counterpart shown interlocking, left lateral view, f) right lateral view.

The propodial of NHMD 625145 is 117 mm long, which is small compared to adult specimens from the Lower Jurassic, where propodials found in the UK have a measured range from 140 mm (Storrs 1997) to around 350 mm (Smith & Vincent 2009; Ketchum & Smith 2010; Smith 2015), whereas most other finds in Table 3 in general are smaller, ranging from 124 to 290 mm for the mature individuals, except *Meyerasaurus victor* from Germany that has propodials measuring 385 mm (Smith & Vincent 2010).

Taphonomy has affected the bone in which the anterior margin shows obvious signs of poor preservation, where the distal end is partly eroded, showing the fine striations of the outer layer of the bone. A juvenile would probably be more susceptible to being affected by taphonomy because of the less advanced ossification.

Comparison. The comparable juvenile specimens that are preserved with propodials from the same time interval, resemble NHMD 625145 in size given that the length of the propodials are 111 mm (Bardet *et al.* 2008), 101 mm (humerus) and 122 mm (femur; Vincent 2010). A juvenile specimen from the Cretaceous of Australia has propodials that are 122 mm (Kear 2007). It is worth noting however that *Plesiopharos moelensis*, an adult specimen, has a femur length of only 130 mm and a humerus length of 150 mm (Puértolas-Pascual *et al.* 2021). This is still larger than NHMD 625145 but indicates the wide size range of plesiosaur propodials.

A juvenile specimen of *Rhomaleosaurus zetlandicus* described by Smith & Vincent (2009) has propodials with underdeveloped trochanter, which is a juvenile character. These propodials are nearly symmetrical, with the expansion being slightly more postaxial than preaxial (Smith & Vincent 2009). Similar to this, a juvenile plesiosaur from Germany (Vincent 2010) has an almost symmetrical femur with the preaxial border being straight and the postaxial being slightly concave. The propodials of the Cretaceous juvenile specimen from Australia have straight anterior margins with strong concave posterior margins (Kear 2007). The distal flaring of this specimen is more pronounced than the other two specimens mentioned and more similar to the Pliensbachian juvenile specimen from Spain (Bardet *et al.* 2008).

Humeri and femora of plesiosaurs are relatively similar in shape, and it is often hard to differentiate, and this is further complicated by the juvenile stage of NHMD 625145. The humerus of *Atychodracon megacephalus* has a straight shaft and a strongly concave postaxial margin with a distal flare (Smith, 2015) traits which look similar to *Marcoplata tenuiceps* (Ketchum & Smith, 2010) and the isolated humerus that has been found on Bornholm (Smith 2008). Other plesiosaurs like *Plesiopharos moelensis* have

Table 3. Comparison of different propodial lengths of plesiosaurs

Specimen	Length of propodial (mm)	Age	Formation/locality/country	Reference
<i>Macroplata tenuiceps</i> (BMNH R5488)	350	Hettangian	Blue Lias Formation, UK	Smith & Ketchum 2010
<i>Rhomaleosaurus zetlandicus</i> (WM 851.S), possible juvenile	365	Toarcian	Yorkshire, UK	Smith & Vincent 2009
<i>Atychodracon megacephalus</i> (BRSMG Cb 2335)	350	Triassic-Jurassic boundary	Somerset, UK	Smith 2015
<i>Plesiopharos moelensis</i> (ML 2302)	130 (femur)			
	150 (humerus)	Sinemurian	Coimbra Formation, Portugal	Puértolas-Pascual <i>et al.</i> 2021
Unidentified plesiosaur (MGUH DK416)	190	Pliensbachian	Hasle Formation, Denmark	Smith 2008
Juvenile plesiosaur (SMNS 51141)	101 (humerus)			
	122 (femur)	Toarcian	Posidonia Shale, Germany	Vincent 2010
<i>Franconiasaurus brevispinus</i> (BT 011224.00)	220 (humerus)			
	240 (femur)	Toarcian	Jurensismergel Fm, Germany	Sachs <i>et al.</i> 2024
Juvenile plesiosaur (MUHA 0518)	111	Pliensbachian	Asturias, Spain	Bardet <i>et al.</i> 2018
<i>Westphaliasaurus simonsensii</i>	290	Pliensbachian	Germany	Schwermann & Sander 2011
Juvenile plesiosaur (SAM P15980)	122	Aptian	Australia	Kear 2007
<i>Meyerasaurus victor</i> (SMNS 12478)	385	Toarcian	Germany	Smith & Vincent 2010
<i>Plesiosaurus dolichodeirus</i> (BMNH 22656); (OXFUM J.10304); (BMNH 36183) (YPM-PU 3352); (NHMN 8592)	190 (humerus)			
	180 (femur)			
	210 (humerus)			
	200 (femur)			
	210			
	140			
	220 (humerus)			
	190 (femur)	Sinemurian	Lyme Regis, England	Storrs 1997

Unless otherwise stated, the specimens are adult individuals. The list is not all inclusive.

tear-drop shaped humeri with postaxial expansions in the distal region that makes the posterior outline concave with straight anterior expansions. This is a primitive character found in Lower Jurassic plesiosaurs (Puértolas-Pascual *et al.* 2021). In contrast, the femur is almost symmetrical with equal anterior and posterior expansions distally. *Franconiasaurus* shares a similar pattern of having propodials with straight anterior margins that flares distally. It, however, is not as concave as *Plesiopharos*, nor does the humerus and femur differentiate as much in *Franconiasaurus* (Sachs *et al.*, 2024). If NHMD 625145 shares the basal characters found in Lower Jurassic plesiosaurs, it is most likely a humerus, as the bone has a somewhat concave postaxial margin that could, if the individual had reached adult age, have evolved a more pronounced shape with distal flaring, characteristic of Lower Jurassic humeri. Assigning NHMD 625145 to a family is difficult as it is an isolated bone and because of its juvenile traits.

Discussion

First juvenile plesiosaurs from Denmark

The propodial and possibly the detached neural arch discussed in this paper represent the first unequivocally juvenile plesiosaur specimens from Denmark. The very small size of the propodial, together with the lack of well-defined anatomical structures and the rounded shape, means that we can confidently

conclude that that it is from a juvenile individual.

The juvenile propodial (NHMD 625145) is a unique specimen, as it is one of few juvenile specimens known from the Lower Jurassic (Table 1), particularly from the Pliensbachian. While the two presumably juvenile propodials from Germany and the one of *Rhomaleosaurus zetlandicus* share similarities to NHMD 625145, the juvenile humerus found in Spain (Bardet *et al.* 2008) and the one found in Australia (Kear 2007) displays a shape more similar to adults, with a straight anterior shaft and a distal flare that makes the posterior margin somewhat concave. This indicates that there is considerable variation in juvenile propodial shape, and scope for future research into plesiosaur ontogeny and growth.

It is more uncertain whether the neural arch (NHMD 625357-1) represents a juvenile or is a result of paedomorphism – the retention of juvenile traits in adult individuals, which have been found to be widespread in several plesiosaur clades (Araújo & Smith 2023). Araújo & Smith (2023) explain that this is due to the retention of the plesiomorphic condition of Pistosauria. It is especially worth noting that neural arches remain separated throughout ontogeny in every taxon of the rhomaleosaurid clade. Araújo & Smith (2023) argue that one should be careful to assign a fossil to being a juvenile, unless the traits for this is obvious, as many previously considered juveniles simply may be paedomorphic adults. With regard to the propodial, the size and shape together show that it is clearly a juvenile, whereas this is less clear for the neural arch. Should one instead look at

what family is most plausible for the detached neural arch to belong to, it would be the Rhomaleosauridae, given their arches remain detached throughout life, they emerged in the Early Jurassic, and the family have been confirmed on Bornholm (Smith 2008). Pliosauridae would also be plausible as this family existed alongside Rhomaleosauridae during the Pliensbachian. If so, this is the first rhomaleosaurid neural arch from the Hasle Formation.

Conclusion

In this contribution we describe five new plesiosaur specimens from the Pliensbachian (Lower Jurassic) of Bornholm, Denmark. This increases the number of formally described specimens to sixteen, adding to previous work (Smith 2008). It also expands the range of described skeletal elements with neural arches. Plesiosaurs are commonly found only with their centra preserved, because of the fragility of the arches and spines. This hampers a thorough comparison to other taxa, but showcasing new material like in this case are valuable additions to our understanding of plesiosaur anatomy. Most significantly, this contribution increases the ontogenetic diversity of plesiosaurs from the formation by the addition of at least one juvenile specimen.

Even if inconclusive taxonomically, our work supports Smith's (2008) suggestion of the potential presence of rhomaleosaurids in Scandinavia, and in addition, indeterminate plesiosauroids and large pliosaurids. This means that the Pliensbachian seas at Bornholm contained marine ecosystems with both short- and longnecked plesiosaurs, covering most, if not all, ontogenetic stages.

The Pliensbachian was historically considered a poorly sampled interval in plesiosaur evolution, but recent discoveries (Table 1) have significantly improved the record. Nevertheless, disarticulated elements that cannot be assigned to genus or species remain important for understanding the diversity and distribution of plesiosaurs during this stage.

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The H6 Aarhus meteorite breccia: A new look at an old rock

MAJA C.F. PEDERSEN, TOD E. WAIGHT & JAMES M. SCOTT



Geological Society of Denmark
<https://2dgf.dk>

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On 2 October 1951, a 750 g meteorite fell as two pieces over the Danish city of Aarhus. A sample of Aarhus is examined here using modern in situ analytical methods to reassess the meteorite's history, which was previously investigated in 1963 using petrography, wet chemistry and X-ray diffraction. It is here confirmed to be an H6 ordinary chondrite based on the textural characteristics and the homogenous olivine (olivine ($\#Fa_{19.9\pm0.5}$) and orthorhombic low-Ca pyroxene (enstatite, $Fs_{17.6\pm0.7}$) compositions. The meteorite's pyroxene Mn/Fe ratios align with the trend of those for non-differentiated planetary bodies and thus support the assumption that the parent body largely retained a chondritic composition. Aarhus preserves textural evidence for a phase of brecciation pre-dating the major metamorphic recrystallisation phase and so occurred early on in the parent body history, possibly during the asteroid's construction. The main metamorphic textures are then overprinted by shock fracturing of olivine and pyroxene and the formation of maskelynite after plagioclase, which may relate to the catastrophic disruption of the parent body. Aarhus is similar to the Danish meteorites Ejby (H5/6), which landed on Copenhagen in 2016, and Dueodde (H5), which was recovered from a roof on Bornholm in 2017.

Keywords: Denmark, meteorite, mineral chemistry, olivine, ordinary chondrite

Maja C.F. Pedersen and James M. Scott (jscott@geo.au.dk), Aarhus University, Department of Geoscience, Høegh-Guldbergs Gade 2, 8000 Aarhus C, Denmark. Tod E. Waight, Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen, Denmark.

At 18:15 on 2 October in 1951, a bright fireball was observed over Denmark (Buchwald 1992). This bright meteor dropped two meteorite fragments: Aarhus I and Aarhus II (Fig. 1). Aarhus I, at 300 g, was found in Risskov shortly after the fireball, although it had broken into four fragments (Nørby 2013). The fall was a significant event in the city's history, with scientific and cultural institutions urging people to participate in efforts to locate fragments of meteorite and reconstruct its trajectory (Nielsen 1953). A second stone, Aarhus II at 420 g, was found two weeks later a few kilometres away. The classification of Aarhus as an ordinary chondrite was made by Mason (1963) and although olivine compositions were inspected, the analyses were by X-ray diffraction, only a single Fe/(Fe+Mg)*100 value is reported, and no other minerals were chemically analysed. The H6 classification first reported in Grady (2000) appears to be based upon the van Schmus and Wood (1967) criteria and Mason's (1963) olivine value coupled with thin section images in Callisen *et al.* (1963). Since the 1963 publications, geological interpretations regarding meteorites, and the tools to investigate them, have evolved, which means that a modern look at the mineralogy

could provide new insights. Here, we present new electron beam chemical analyses of Aarhus, assess the existing classification, and compare it with similar Danish meteorites.

Methods

The main masses of Aarhus II and fragments of Aarhus I are housed at the Natural History Museum Denmark in Copenhagen as part of the Danish Meteorite collection. The largest fragment of Aarhus I, however, is stored at the Natural History Museum of Aarhus. With their permission, a small fragment (3×2×1.5 cm) was cut off a corner and mounted in epoxy resin. The sample was then polished and carbon coated for analysis with a TESCAN scanning electron microscope at the Department of Geoscience at Aarhus University. The SEM was used with an energy beam configuration of voltage 20 keV and current of 20 nA at a fixed working distance to measure the mineral compositions and obtain back-scattered electron images and maps. The beam was calibrated regularly with pure copper metal, and the

chemical data standardized against the default factory standards. Measurements were obtained using the Oxford Instruments Aztec software. To confirm that our SEM data are robust, minerals in the same fragment were re-analysed by wavelength dispersive spectrometry using an JEOL JXA-8200 superprobe electron microprobe at the Department of Geosciences and Natural Resource Management at University of Copenhagen. The microprobe was operated with a beam diameter of 5 micrometers, an accelerating voltage of 15 KeV and a beam current of 15 nA. Elements were standardized against in house reference materials including corundum (Al), Marjalathi olivine (Mg), albite (Na), orthoclase (K), rutile (Ti), hematite (Fe), Mn-Ti-oxide (Mn), chromite (Cr), Ni-metal (Ni), and wollastonite (Si and Ca). In-house secondary silicate standards (fayalite and pyrope garnet) were also analysed for quality control. Counting times were 20 s on peak and on backgrounds for all elements excluding Na and K (10 s). Matrix corrections were performed using the phi-rho-z method (Goldstein *et al.* 2017).

Results

Aarhus I has a slightly cracked dark fusion crust and a broken face that exposes the pale interior (Fig. 2a). The pale interior is composed of less than 1 cm-sized angular clasts set within darker areas (Fig. 2b, c). A few relict chondrules can be found in the matrix, which has olivine and low-Ca pyroxene as main phases (Fig. 3a, b, c). The chondrules are slightly elongated and approximately 0.4 by 1 mm in average size, with two displaying a barred texture comprising olivine and plagioclase (likely maskelynite, which is plagioclase glass). The main minerals in the meteorite are olivine and low-Ca pyroxene, accompanied by maskelynite, kamacite and taenite-tetrataenite (Fe-Ni alloys), troilite (FeS), diopside, chromite, merrillite ($\text{Ca}_3\text{NaMg}(\text{PO}_4)_7$) and apatite (Figs 3, 4, 5). Ca-pyroxene is relatively rare and found primarily as smaller skeletal grains ($< 100 \mu\text{m}$), often occurring with maskelynite and fine-grained troilite. Kamacite is up to $500 \mu\text{m}$ in size and is by far the most abun-

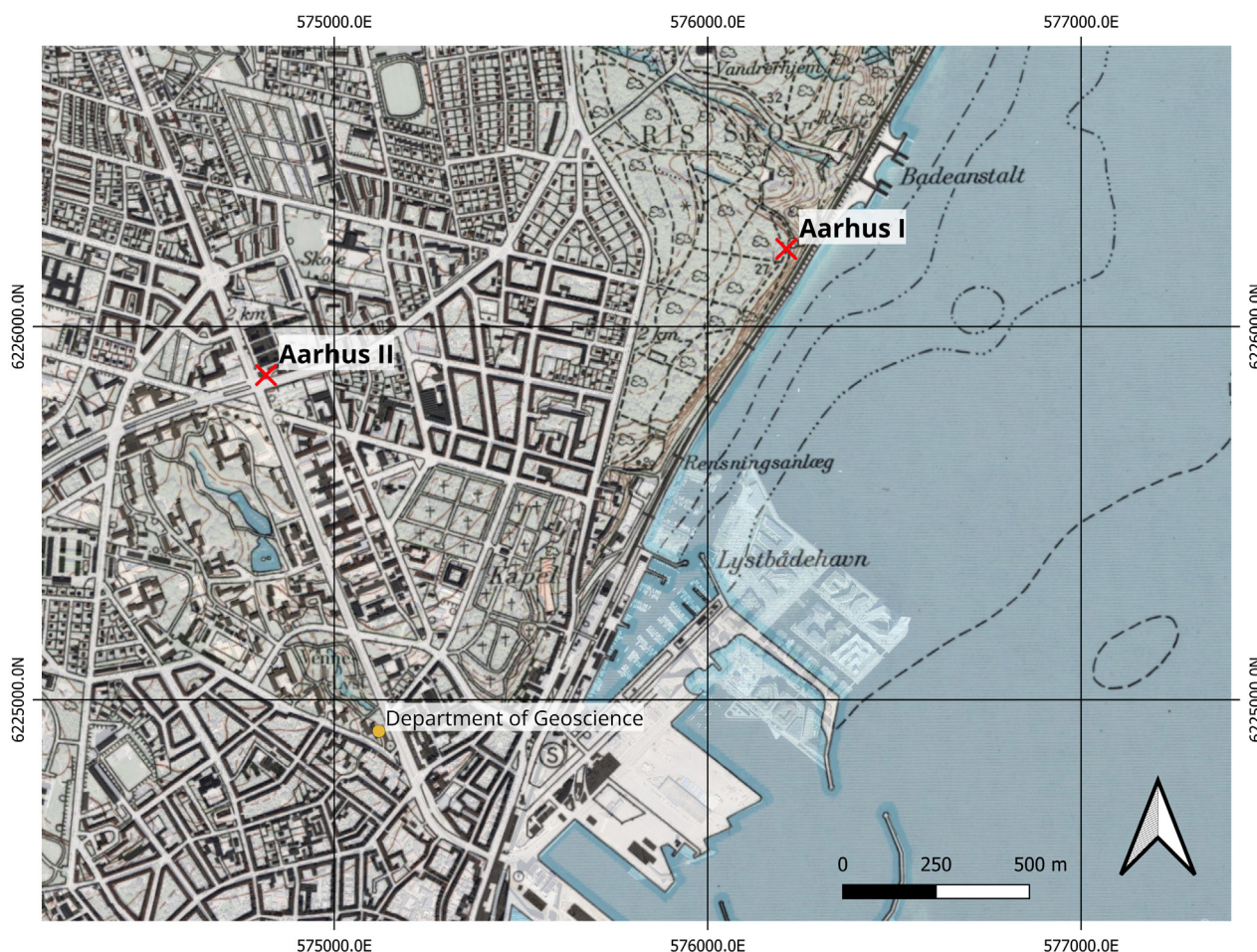


Fig. 1. The fall sites of Aarhus I and II on a map of Aarhus from 1953–1976 with orthophoto from 2024 as background (Klimadatastyrelsen 1953–1976; GeoDanmark 2024). The current location of the Department of Geoscience is marked for reference. The site of Aarhus I marks the location of the memorial stone for Aarhus I, which fell within 100 m.

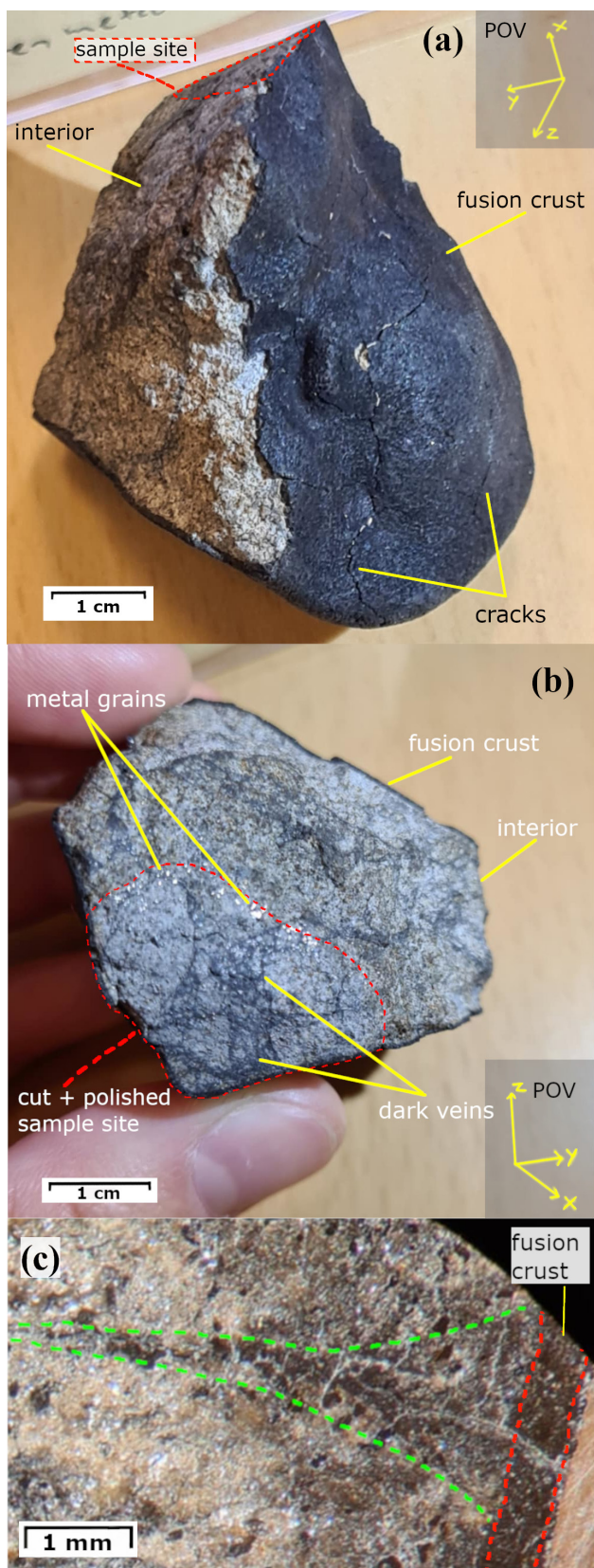


Fig. 2. Images of the Aarhus I meteorite hand specimen (A) and sampled section (B, C). plg, plagioclase glass; tr, troilite.

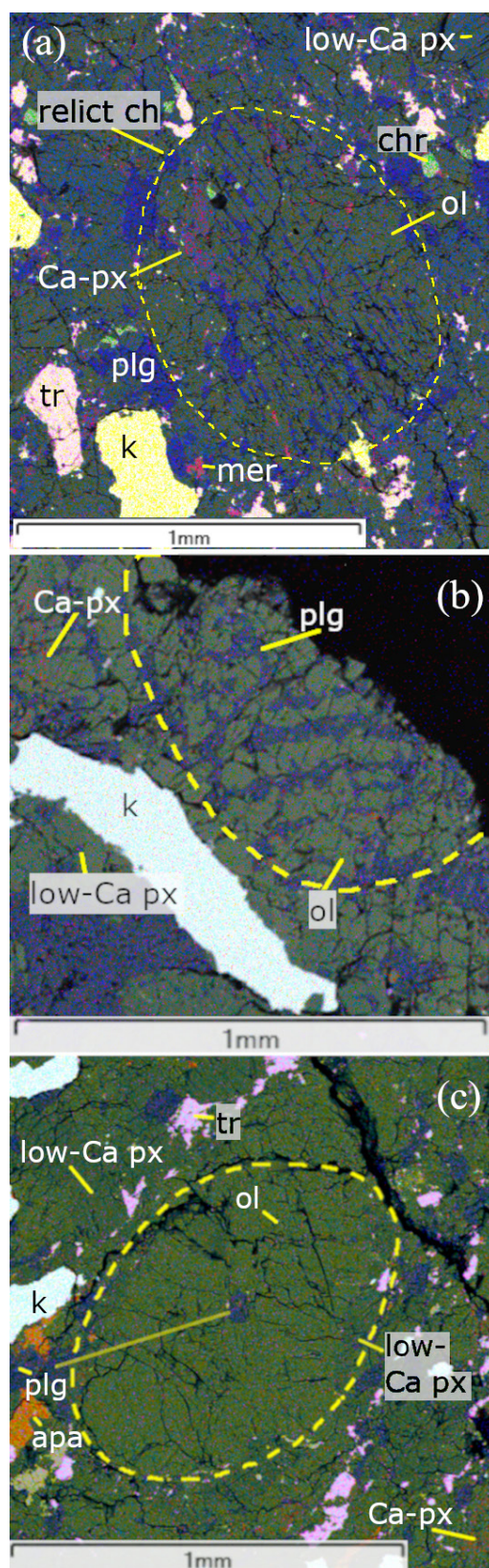


Fig. 3. Examples of relict chondrules in Aarhus. The colours are false-coloured. Px, pyroxene; plg, plagioclase (maskelynite); apa, apatite; ol, olivine; tr, troilite; k, kamacite; Chr, chromite; mer, merrillite; ch, chondrule.

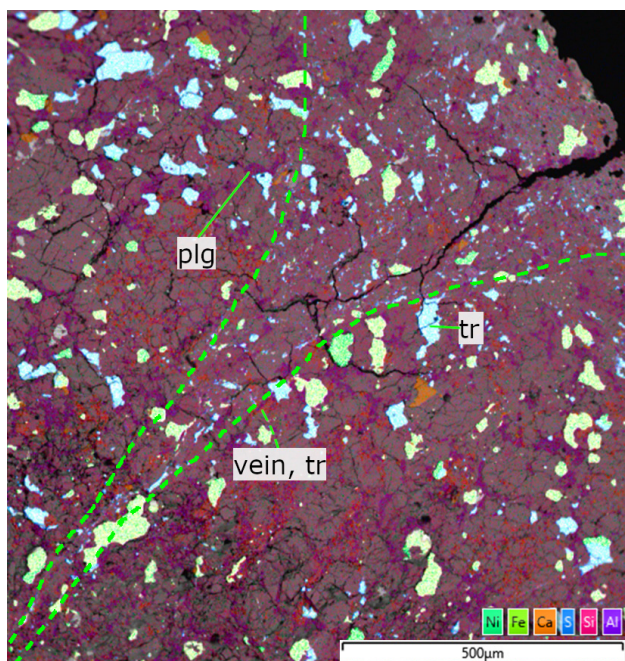


Fig. 4. False-coloured element map of the occurrence of a vein or zone of finer-grained troilite within the meteorite. The dashed green lines correspond with the zone visible in figure 2C.

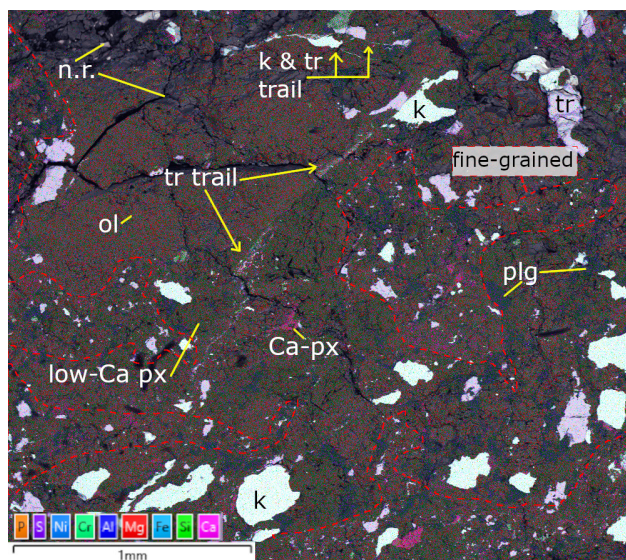


Fig. 5. False-coloured scanning electron microscope EDS map and backscattered electron image showing the different zones of grain size in the meteorite. K, kamacite; tr, troilite; ol, olivine; plg, plagioclase glass; px, pyroxene; n.r., fractures in the polished sample.

dant metal phase (Figs 4, 5). Troilite is also abundant and generally either found as grains up to 200 μm or forming very fine trails ($< 5 \mu\text{m}$; Fig. 5). The fusion crust of the meteorite can be split into three distinct textural domains (Fig. 6a, b, c). The rim is the ~ 0.1 mm thick exterior part of the meteorite that was last

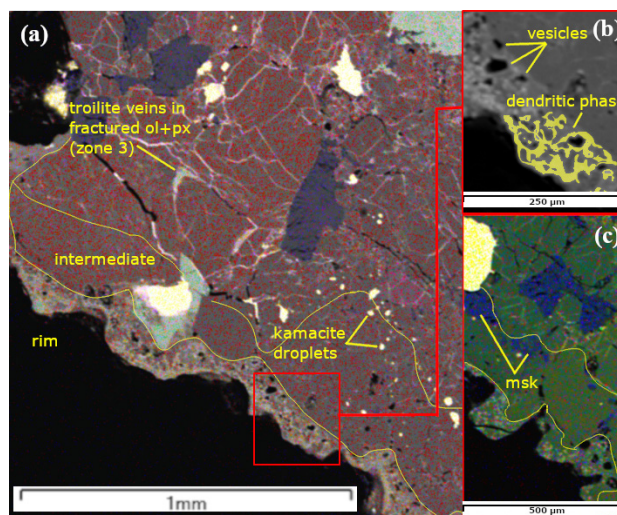


Fig. 6. False-coloured images from the margin of the meteorite showing the occurrence of a fusion crust and consecutive zones of alteration of the meteorite.

melted during its passage through the atmosphere, and is characterized by glass, dendritic olivine and small vesicles ($< 30 \mu\text{m}$ (Fig 6b). The intermediate zone is the ~ 0.3 – 0.4 mm wide area adjacent to the rim and is characterized by sparse droplets of metal phases and some larger maskelynite grains (Fig 6c). Vesicles are also found here to a lesser extent than at the rim. Zone 3 is the third textural position counting from the rim towards the centre of the sample, and contains distinct troilite veins filling fractures in the olivine-pyroxene groundmass (Fig. 6a). The thickness varies from 0.5 to 1.5 mm.

Mineral compositions

The mineral compositions are important for classifying the meteorite in the ordinary chondrite group (H, L, or LL) and are not readily available other than a note that the olivine has a #Fa of '18' (Mason 1963). The olivine chemically varies depending on textural position. Our measurements of dendritic olivine in the fusion crust's outermost zone have a higher content of Fe and are unrepresentative for the original olivine in the rock prior to atmospheric entry. Excluding those data, a total of 35 analyses acquired by scanning electron microscope from further inside the meteorite, from chondrules and matrix, gives a mean composition of #Fa $_{19.9\pm0.5}$ (Table 1), with a range between 18.8 and 22 and a mean deviation of 2%. The microprobe data give #Fa $_{19.8\pm0.7}$, which confirms the SEM results (Supplementary 1).

Of the pyroxenes, the low-Ca pyroxene is enstatite, with SEM data yielding compositions between 15.7 and 19.6 mol% but with an average Fs-content of

Table 1. Mean chemical compositions of the main mineral constituents of Aarhus I

wt%	Olivine (n = 35)	Low-Ca pyroxene (n = 44)	Ca pyroxene (n = 22)	Plagioclase (n = 49)	Apatite (n = 12)	Merrillite (n = 16)	Chromite (n = 13)
SiO ₂	38.6	55.7	53.4	64.5	0.00	0.82	0.00
TiO ₂	0.00	0.20	0.52	0.00	0.00	0.00	1.90
Al ₂ O ₃	0.00	0.24	0.85	21.6	0.00	0.00	6.97
Cr ₂ O ₃	0.00	0.17	1.16	0.09	0.00	0.00	55.2
FeO	18.6	11.8	4.30	0.78	0.79	1.26	29.0
MnO	0.49	0.53	0.22	0.00	0.00	0.00	1.00
MgO	41.9	30.4	16.6	0.00	0.12	3.59	3.13
CaO	0.00	0.69	22.0	2.50	51.9	46.4	0.00
Na ₂ O	0.00	0.10	0.64	8.91	0.44	2.56	0.00
K ₂ O	0.00	0.00	0.00	0.90	0.00	0.00	0.00
P ₂ O ₅	0.00	0.00	0.00	0.00	40.9	45.1	0.00
Total	99.59	99.71	99.69	98.29	94.15	99.80	97.20
Oxygens	4	6	6	8	12.33	56	4
Si	0.99	1.98	1.96	2.86	0.04	0.25	0.00
Ti	0.00	0.01	0.01	0.00	0.00	0.00	0.05
Al	0.00	0.01	0.04	1.13	0.00	0.00	0.29
Cr	0.00	0.00	0.03	0.00	0.00	0.00	1.54
Fe ²⁺	0.40	0.35	0.13	0.03	0.06	0.34	0.86
Mn	0.01	0.02	0.01	0.00	0.00	0.00	0.03
Mg	1.60	1.61	0.91	0.03	0.01	1.87	0.17
Ca	0.00	0.03	0.87	0.12	4.78	18.0	0.00
Na	0.00	0.01	0.05	0.77	0.07	1.73	0.00
K	0.00	0.00	0.00	0.05	0.00	0.00	0.00
P	0.00	0.00	0.00	0.00	2.96	13.7	0.00
Total	3.00	4.02	4.01	4.99	7.92	35.89	2.94
Fa	19.9 ± 0.5						
Fs	17.6 ± 0.7						
Wo	1.3 ± 0.2						
An	6.9 ± 0.7						
Or	45.4 ± 0.1						
	13 ± 1.4						
	5 ± 1.6						

Fa = 100*Fe/(Mg + Fe). Fs = 100* Fe/Fe+Mg+Ca, Wo = 100*Ca/(Fe+Mg+Ca). 100*An = Ca/(Ca+Na+K), 100*Or = K/(Ca+Na+K).

$Fs_{17.6 \pm 0.7}$ (n = 44; Fig. 7a; Table 1). The microprobe data yield an average of $Fs_{17.7 \pm 0.8}$, again confirming the SEM results. The Ca pyroxene is diopside, bordering on augite, and has a mean Fs-content of $Fs_{6.9 \pm 0.7}$ (n = 22; Table 1).

The plagioclase composition phase, which we believe is most likely maskelynite because plagioclase melts at lower temperatures compared to olivine and orthopyroxene (Stöffler *et al.* 2018) and is unfractured compared to the adjacent olivine and orthopyroxene, has a general oligoclase composition of $Ab_{82 \pm 0.8}An_{13 \pm 1.4}Or_{5 \pm 1.6}$ (n = 49; SEM data; Fig. 7b). Microprobe data yield compositions of $Ab_{82 \pm 0.6}An_{12 \pm 2.6}Or_{6 \pm 2.6}$, once again confirming the results obtained by SEM. There is some variation in the An and Or components, but the cause of this is unclear. It does not relate to chondrule versus matrix textural position, and maskelynite can be heterogeneous, probably due to the incomplete mixing of former feldspar zoning during the glass forming stage (Chen & El Goresy 2000; Burgin *et al.* 2023).

The chemical compositions of the minor mineral phases apatite, merrillite and chromite are given in Table 1. Generally, the minor phases occur sparsely either very fine-grained (< 10 µm) or as moderate

grain sizes (50–100 µm), although in one area a large (> 1 mm) chromite and merrillite assemblage bridges the fusion crust rim with the interior of the meteorite sample. Kamacite has a mean Ni-composition of 6.3 wt% (n = 30), taenite a mean of 35.9 wt% Ni (n = 6), and tetrataenite has a mean of 44.9 wt% Ni (n = 2). The analysed tetrataenite is primarily found bordering kamacite or as an exsolution from kamacite.

Discussion

Classification

The existing classification of the Aarhus meteorite is an H6 ordinary chondrite (Gradey 2000), which appears to have been derived from Mason's (1963) unpublished olivine X-ray diffraction analysis and Callisen *et al.*'s (1963) petrographic observations. The H indicates that it is a high iron ordinary chondrite, with the 6 indicates that it displays a very high degree of metamorphic equilibration. Of the ten classification criteria for chondrites based on petrologic type (van Schmus & Wood 1967), the ones deemed most relevant are the composition and homogeneity

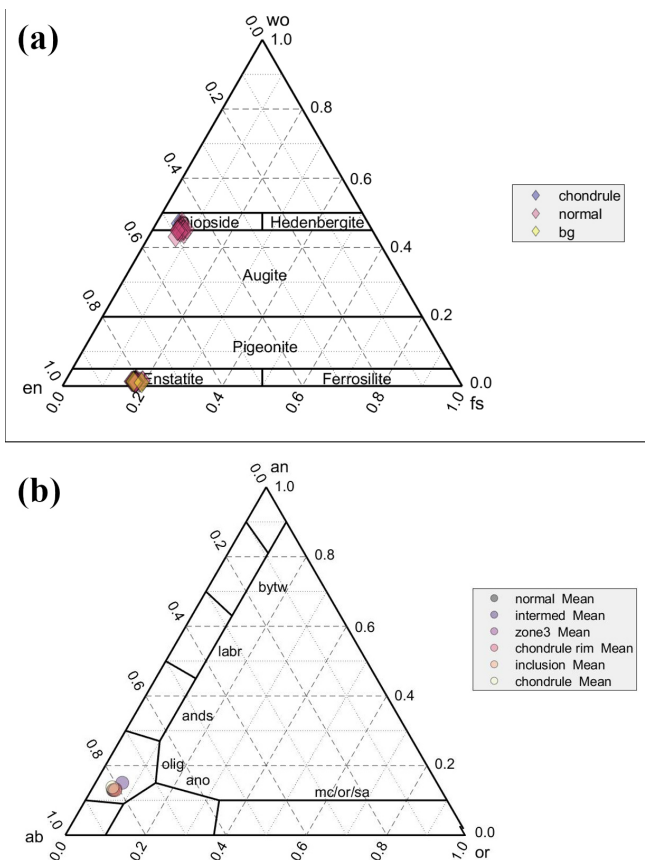


Fig. 7. Classification diagrams of the pyroxene (A) and plagioclase (B) in Aarhus.

of olivine, nature of the feldspar grains, texture of the matrix, and the chondrule-matrix integration. Our olivine data show the mean olivine composition to be $Fa\# = 19.9$ and strongly supports the classification as H-type (Fig. 7). The olivine compositions have a mean deviation of $\sigma_{\mu, 2sd} = 2\%$, which corresponds to petrological type 5 or 6 (Van Schmus & Wood 1967).

The low-Ca pyroxenes analysed are of enstatite composition (Fig 7a) and thus orthorhombic. This low-Ca pyroxene structural state is diagnostic of the petrologic types 6-7 (Hazen 2021). Diopside undergoes coarsening with an increasing grade of thermal metamorphism (Huss *et al.* 2006) and occurs as a minor phase in equilibrated ordinary chondrites, which also supports the classification as a type 6 (Hazen 2021).

The size of the plagioclase (maskelynite) grains is diagnostic of the petrologic type (van Schmus & Wood 1967). For either type 5 or 6, this phase should be found as products of metamorphism rather than relict grains incorporated into the meteorite during assembly. In type 6 chondrites, it should exist abundantly as 50–100 μm sized interstitial grains (van Schmus & Wood 1967), whereas in type 4–5 it is found as 2–50 μm sized grains (Hutchison 2004). In

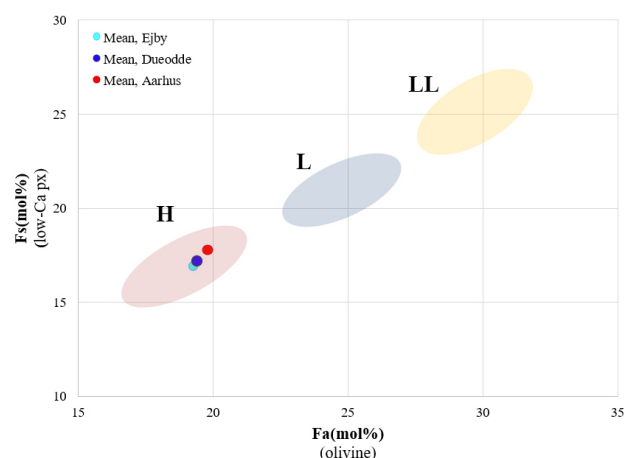


Fig. 8. Classification diagram of the H, L and LL ordinary chondrite fields based upon olivine and orthopyroxene composition. Data for Ejby are from Haack *et al.* (2019), and Dueodde are taken from unpublished results presented on the Meteoritical Bulletin (<https://www.lpi.usra.edu/meteor/metbull.cfm>).

Aarhus, the plagioclase is found in great abundance with large grains of $> 50 \mu\text{m}$ but also smaller grains of 5–25 μm . The occurrence of the larger grains indicates classification as type 6. The coarse-grained texture of the matrix and the poor delineation of the chondrules, which are also diagnostic for the petrologic type 6, were likely caused by thermal heating of the rock caused by radioactive decay of abundant short-lived isotopes whilst in an early Solar System parent body.

Shock effects and brecciation

The Aarhus meteorite has undergone shock metamorphism, as evident from the fractures in olivine and pyroxene, and the occurrence of maskelynite. The occurrence of maskelynite indicates a shock class of S5 and indicates shock pressures of at least 30–45 GPa (Stöffler *et al.* 2018). The shock textures appear to be superimposed upon an earlier phase of brecciation. The darker zones surrounding clasts, seen best macroscopically (Fig. 2b, c), are slightly richer in fine-grained troilite and metal sulphide than the clasts, and have textures indicate there was a degree of healing and grain boundary growth (Fig. 4) prior to the last major shock event. This may mean that this phase of coarse brecciation occurred on the parent body, probably early in the rock's history, and before the rock was statically thermally equilibrated at H6 conditions. Thus, this metamorphosed breccia texture is not related to the shock event that fractured olivine and orthopyroxene and melted plagioclase that may be related to the catastrophic disruption of the parent body.

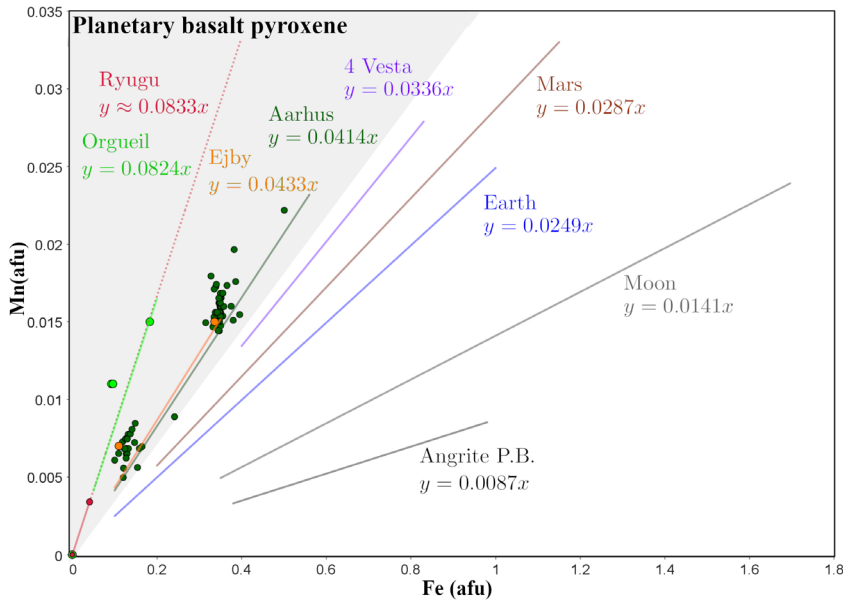


Fig. 8. Mn versus Fe diagram for orthopyroxene and clinopyroxene data in various meteorites. The diagram is modified from Papike *et al.* (2003).

Comparison with Danish H-chondritic meteorites

There are two further known H meteorites in Denmark. The H5/6 Ejby meteorite fell over Copenhagen in 2016 (Haack *et al.* 2019), and Dueodde, an H5, is reported in the Meteoritical Bulletin to have been recovered from Bornholm in 2017 after probably having lain there for several years. There is currently insufficient mineral data for Dueodde to undertake a comparison. However, for the mineral phases stated in Table 1 the residuals, Δ , between Aarhus and Ejby and the relative percentagewise deviation, $\Delta_{\%}$, relative to Aarhus have been calculated by $\Delta = C_{\text{oxide, Aarhus}} - C_{\text{oxide, Ejby}}$ and $\Delta_{\%} = \Delta_{\text{abs}} / C_{\text{oxide, Aarhus}}$ and , where is the wt% of a given oxide. Generally, Aarhus and Ejby are very similar: olivine, low-Ca pyroxene and feldspar, with relative deviations of 0-3% for oxides. An exception is the plagioclase (maskelynite) of Aarhus that contains less Na_2O than Ejby. The metals are similar in Aarhus and Ejby with relative deviations of ~0% for kamacite, taenite and troilite in the substantial elements: Fe and Ni for kamacite and taenite, and Fe and S for troilite. Tetrataenite is somewhat different in Fe and Ni composition between Aarhus and Ejby, although within ~10% relative deviation. The fact that the three known meteorites found thus far in Denmark are similar is consistent with H meteorites being the most commonly found type – not that Denmark especially attracts them!

Origin of the Aarhus meteorite

There are different methods of linking meteorites to an asteroidal parent body. The HED meteorites, for example, are commonly argued on the basis of spec-

tra data to come from the asteroid 4Vesta (McSween *et al.* 2013). For chondrites, most attempts at identifying parent bodies based on astrophysical data will be inconclusive (Sears 2004). An exception is a recent interpretation of the asteroid Ryugu as a C-type asteroid based on near-infrared reflectance observations, which was confirmed from returned material (Yada *et al.* 2022). Although isotopic data such as O isotopes form a common means of estimating the parent body of a meteorite, a less expensive method is the geological comparison of major and minor elemental ratios in mineral phases, such as pyroxene, olivine, and feldspar (e.g., Papike *et al.* 2003). The Fe/Mn ratio, which the change of behaviour in geochemical affinity from lithophile to siderophile for Mn during the core-formation process (Ringwood 1991; Gessmann & Rubie 2000), can be used to differentiate some parent bodies.

The ratio of Mn/Fe in pyroxene in Aarhus are plotted in Figure 9, along with the those for basalt pyroxenes of Earth, Mars, the Moon, 4 Vesta, the angrite parent body from Papike *et al.* (2003), and the carbonaceous chondrites Ryugu (Nakamura *et al.* 2022) and Orgueil (Leshin *et al.* 1997), as well as the Danish H5/6 Ejby (Haack *et al.* 2019). The trend of pyroxene Mn/Fe ratios of Aarhus is and is distinct from any of the differentiated bodies (Vesta, Mars, Earth, the Moon and angrite parent body) but overlaps with that of Ejby (Fig 9). The trends of Aarhus, Ejby, Orgueil and Ryugu are steeper than that of Earth, whose mantle is known to be depleted in Mn, and less depleted than 4 Vesta, Mars, and the angrite parent. The Aarhus and Ejby pyroxene compositions therefore confirm that these meteorites are probably very little modified from their primary composition. This comparison indicates that an area

can be marked on this mineral composition diagram that shows whether or not a parent body of an analysed meteorite has undergone differentiation and/or element mobility and could be usefully employed in cases where there is very little volume of material available for geochemical analyses.

Conclusions

The Aarhus meteorite has been analysed for the first time since 1963 and now has a comprehensive suite of mineral analyses. The mineral assemblage confirms it to be an ordinary chondrite, with the olivine and orthopyroxene compositions supporting a 'H' (high iron) classification. The petrologic type 6 is indicated by the homogeneous olivine compositions, orthorhombic low-Ca pyroxene, large feldspar grains, a recrystallized matrix, and poor chondrule delineation. Aarhus originates from an undifferentiated parent body, which is supported by the Fe/Mn trend found in pyroxenes. Texturally, brecciation predates metamorphism, and thus was probably brecciated very early on in the Solar System history. The shock metamorphic history later was later superimposed on this rock. These results upscale the transmitted light microscope observations made by Callisen *et al.* (1963) and thus provide new insights into this old rock.

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An early Neoglacial moraine at Sanddalen, NE Greenland

JASON P. BRINER & OLE BENNIKE



Geological Society of Denmark
<https://2dgd.dk>

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The Greenland Ice Sheet experienced a minimum ice volume phase in the middle Holocene. The timing and footprint of this minimum ice configuration remain poorly constrained. This minimum configuration, along with ice-sheet recession into and re-growth out of this minimum ice phase, provide critical constraints of the ice sheet's response to Holocene climate forcing. With few exceptions, the late Holocene expansion across the entire ice-sheet perimeter culminated during the last millennium – a period that encompasses the Little Ice Age. Here we focus on a rare moraine in North-East Greenland to which we assign an age of $\sim 4600 \pm 400$ cal. yr BP via correlation with local sea level curves. Thus, the moraine post-dates the middle Holocene minimum ice phase yet pre-dates the Little Ice Age by thousands of years. The early Neoglacial age of the moraine attests to this sector of the ice sheet reaching modern day ice-margin configuration as early as ~ 4.6 ka, which is consistent with findings elsewhere in North-East Greenland.

Keywords: Greenland Ice Sheet, Inland Ice, Holocene, Quaternary, climate change

Jason P. Briner [jbriner@buffalo.edu], Department of Earth Sciences, University at Buffalo, Buffalo, NY, USA. Ole Bennike [obe@geus.dk], Geological Survey of Denmark and Greenland (GEUS), Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

The Greenland Ice Sheet has been losing mass every year this century and is significantly contributing to global sea level rise (Mankoff *et al.* 2021). Even at present global temperature, it has been argued that meters of sea level rise from Greenland is inevitable, leaving ‘how long will it take’ and not ‘how much will sea level rise’ as the more relevant question (Stokes *et al.* 2025). Characterizing ice-sheet response to past interglacials is one approach for revealing centennial-scale rates of ice-sheet change under a given climate forcing. The Holocene, when the Greenland Ice Sheet became smaller than it is today, provides the most data-constrained interglacial to target in this quest.

Despite ample geologic evidence revealing a minimal size of the Greenland Ice Sheet during the middle Holocene, the minimum size achieved and the spatiotemporal pattern of its recession and regrowth remain poorly constrained (Larsen *et al.*, 2015; Briner *et al.* 2016). The timing of deglaciation around the present-day ice margin constrains the initiation of smaller-than-present interval. This generally occurred around 7000 yr but is spatially variable (Bennike & Björck 2002; Leger *et al.* 2024). Limited data exist to constrain timing of minimum ice, which is generally 6000–3000 yr (Larsen *et al.* 2016). Some evidence points to spatial heterogeneity in the ice sheet's

minimum phase, for example it is thought to have occurred 5000–3000 yr in west-central Greenland (e.g., Cronauer *et al.* 2016), 4000–2000 yr in southwestern Greenland (Young & Briner 2015; Larsen *et al.* 2015) but 8000–4000 yr in North-East Greenland (Larsen *et al.* 2018; Smith *et al.* 2023). The timing of when ice reappears near the present-day ice margin constrains the end of the smaller-than-present interval, which is similarly temporally variable. One challenge in further constraining the end of the minimum ice phase is that there are few moraines demarcating the advance towards the present ice configuration because they were removed during the historic maximum extent during the Little Ice Age (~ 1250 – 1900 AD; Kjær *et al.* 2022) with few exceptions (Bennike & Sparrenbom 2007). Thus, instead, the timing of ice approaching present margins is usually based on re-worked organic material amenable to radiocarbon dating, such as overrun vegetation or re-worked material (e.g., Briner *et al.* 2014; Kjær *et al.* 2022) or sedimentary sequences in pro-glacial lakes (e.g., Briner *et al.* 2010; Larsen *et al.* 2011) or ice-dammed lakes (e.g., Smith *et al.* 2023).

Here, we explore a previously described candidate for a pre-LIA moraine at Sanddalen, North-East Greenland (Fig. 1), that post-dates the middle Holo-

cene minimum ice phase (Bennike & Weidick 2001). We map glacial outwash terraces that we interpret to be associated with the moraine of interest and extract their elevations using the Arctic DEM. Finally, we relate these outwash terraces to previously dated relative sea level datasets to derive an age estimate for the Sanddalen moraine.

Glacial geomorphology of Sanddalen

Sanddalen lies between the major distributary outlets of the NE Greenland Ice Stream (Fig. 1). To the south lies Storstrømmen, which bifurcates into

southern and northern ocean-calving margins. To the north of Sanddalen lie Zachariae Isstrøm and Nioghalvfjærdsfjorden. At Sanddalen, a smaller outlet glacier is one among a few glaciers draped across a north-south strip of rolling terrain that exists directly downflow of an over-deepening, that when ice free, would contain an inland sound (Morlighem *et al.* 2017). The present ice margin fronts a zone of fresh, unvegetated moraines, the historical moraines deposited during the Little Ice Age. The north terminus of Storstrømmen ended in a floating tongue that extended 24 km beyond the present glacier (2024) margin. Post-Little-Ice-Age recession elsewhere in the region is not as significant, and at Sanddalen it is merely a few 10s of meters. It can be challenging to map the Little Ice Age ice extent around Sanddalen,

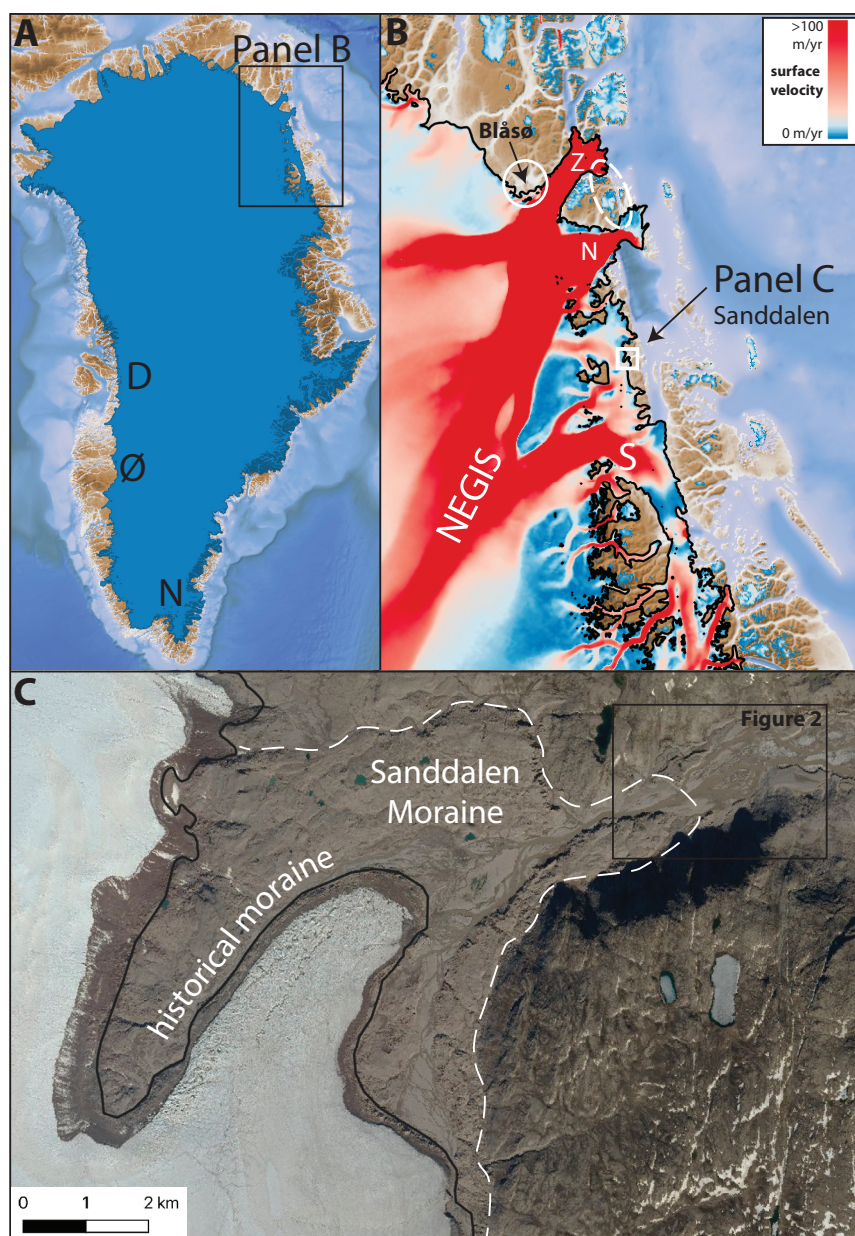


Fig. 1. A. Map of Greenland showing locations discussed in the text; D: Drygalski Moraines; Ø: Ørkendalen; N: Narsarsuak. B. NE Greenland showing sites mentioned in text; Z= Zachariae Isstrøm; N= Nioghalvfjærdsbrae; S=Storstrømmen. White circles are sites of relative sea-level curves from Bennike & Weidick (2001) that are discussed in the text. Color represents surface velocity; red: high velocity (Gardner *et al.* 2019). C. Satellite image of the historical moraine and the drift sheet of the Sanddalen Moraine at Sanddalen, NE Greenland.

however, because there is a second unvegetated drift sheet that extends farther than the Little Ice Age drift sheet (Fig. 1).

Bennike & Weidick (2001) described the drift as largely unvegetated, ice-cored hummocky moraine covering ~15 km² and containing shell fragments up to 200 m a.s.l. which we herein informally name the ‘Sanddalen Moraine’. Between the down-valley drift limit (end moraine) and the sea is a narrow valley with small remnants of outwash terraces above the modern river plain preserved on the northern and southern sides of the modern braid plain (Fig. 2). Where the Sanddalen Moraine crosses the valley bottom, it appears connected with an outwash terrace. Based on mapping the surface geomorphology using the Arctic DEM product (Porter *et al.* 2023), it appears that the terrace is an outwash head that grades di-

rectly to the Sanddalen Moraine, and if so, reveals that the deposition of the outwash terraces and the moraine were contemporaneous (Fig. 2). The terrace elevations can be plotted in longitudinal profile, as can the modern river. The profiles of the terraces and river closely parallel each other, with the terraces consistently lying 15 to 18 meters higher than the modern river, including at the present-day coastline fan-delta (Fig. 3).

The relative sea level at the time of the last deglaciation at Sanddalen can be estimated from a raised marine delta that formed at the base of a now-head-less glacial meltwater channel. During the last deglaciation, while an ice lobe filled the lower valley, it fed a meltwater channel that spilled southward across a topographic divide, down a ~4-km-long channel ending at a marine delta with a surface that is ~35

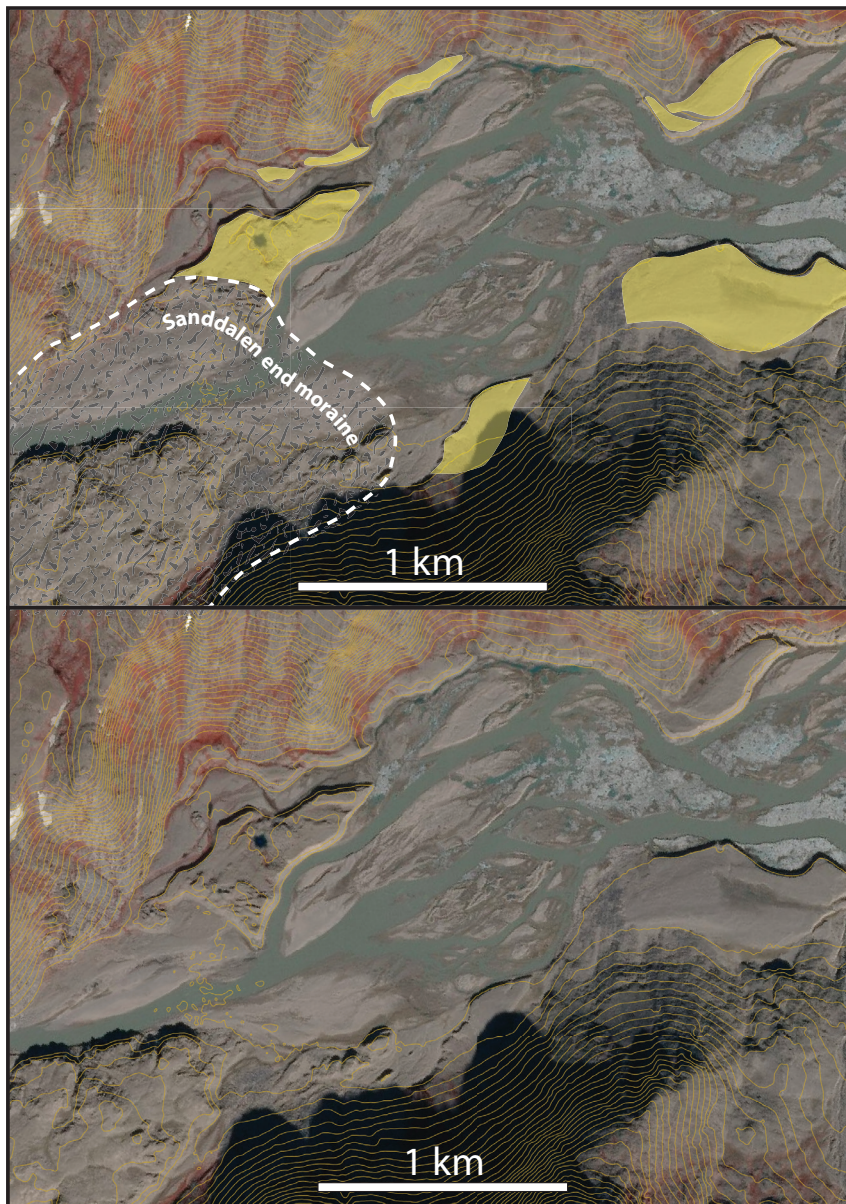


Fig. 2. Top: Sanddalen end moraine and mapped outwash terrace remnants (shown in yellow) the north and south sides of the modern braid plane sourced from the present ice-margin at Sanddalen. Bottom: Uninterpreted image. Contour spacing is 10 m and is used here to clarify topography. North is up in both images. Base image is a mosaic from Sentinel2 (10 m resolution) and Spot (1.6 m resolution) imagery. Map location shown in Figure 1.

m above sea level. This elevation is slightly lower than the marine limit recorded from a location ~10 km south of Sanddalen of 40 m, which connects to other areas with similar marine limit values around the present ice margin to form a 40 m isobase trending north-northeast (Bennike & Weidick 2001).

Age of the Sanddalen Moraine

Bennike & Weidick (2001) obtained six radiocarbon ages from bivalves re-worked into the Sanddalen

Moraine. Their ages, ranging from 6100–5500 cal. yr BP, provide a maximum age for the moraine of ~5500 cal. yr BP. Relative sea-level curves allow for dating of events not otherwise directly dated if their relation to sea level is known (e.g., Mangerud *et al.* 2019). Bennike & Weidick (2001) constructed several relative sea level curves for the terminus areas of Zachariae Isstrøm and Nioghalvfjærdsfjorden. These relative sea level histories are constrained by radiocarbon ages of uplifted marine sediments not always with a direct tie to sea level and thus are not based on sea level index points. Nevertheless, the curves are drawn to

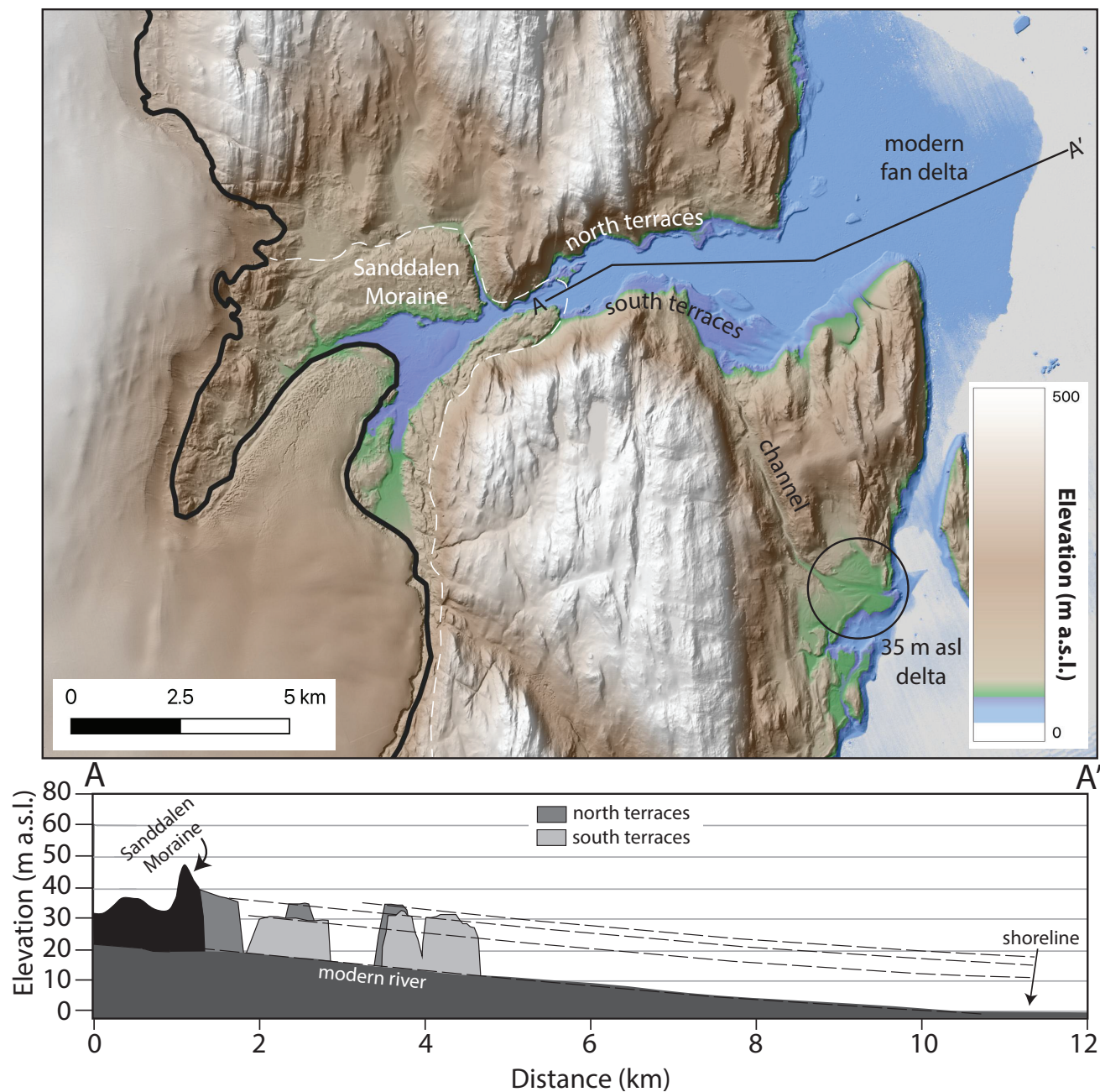


Fig. 3. Map showing elevation of Sanddalen region, location of Sanddalen Moraine and terraces in the outflow valley between the glacier at Sanddalen and the sea. Bottom shows topographic profiles of the modern river and raised outwash terraces.

encompass the radiocarbon ages from raised marine material and thus provide useful approximations for the shape and history of relative sea level. Bennike & Weidick (2001) also provide nine radiocarbon ages from uplifted marine sediments closer to Sanddalen, ranging in elevation from 2 to 40 m a.s.l., but did not formulate them into a relative sea level curve. We also do not use these ages to formulate a relative sea level curve, but plot them alongside the curves from Blåsø and Nioghalvfjerdsfjorden (Fig. 1), which reveals a close correspondence and indicates that the relative sea level curves from farther north generally apply to the Sanddalen region (Fig. 4).

Collectively, the relative sea level histories can be used to constrain the age of the 35 m a.s.l. delta and the outwash terraces between the Sanddalen Moraine and the coast. Using the relative sea level curve from inner Nioghalvfjerdsfjorden that lies along the same 40 m isobase but from slightly north of Sanddalen (Bennike & Weidick 2001), we estimate the 35 m a.s.l. delta to be ~7000 cal. yr BP. When considering the other relative sea level histories from Bennike & Weidick (2001), the age could be as young as ~6500 cal. yr BP. The Sanddalen Moraine outwash terraces, which lie 15–18 m a.s.l., intercepts the inner Blåsø sea level curve from 5000 to 4200 cal. yr BP, with an average intercept age of 4600 ± 400 cal. yr. BP (Fig. 4). Radiocarbon ages from raised marine fauna at Sanddalen support the use of the Blåsø relative sea level curve (radiocarbon ages have been recalibrated using Marine20; Heaton *et al.* 2020). Using the broader collection of relative sea level curves, the age could

be as young as ~3500 cal. yr BP. Such an age assignment of 4600 ± 400 cal. yr BP for the Sanddalen Moraine is consistent with its maximum age based on the reworked bivalves of ~5500 cal. yr BP.

Discussion

The proposed ~4600-year-old Sanddalen Moraine would be the oldest Neoglacial moraine yet identified from the Greenland Ice Sheet. Several moraines previously thought to be Neoglacial have since been directly dated to be from the last deglaciation. These include the Drygalski Moraines near Disko Bugt thought to be ~3000 yr old (Weidick 1968; Kelly 1980). They have since been dated to ~8600–7600 yr with ^{10}Be dating (Cronauer *et al.* 2016). The Ørkendalen Moraine System east of Kangerlussuaq, suggested by Forman *et al.* (2007) to contain a 2000-year-old moraine, have since been more directly dated with ^{10}Be dating to ~6800 yr (Levy *et al.* 2012). The Narsarsuaq moraines, South Greenland, remain the exception. Radiocarbon dated lake sediments and direct ^{10}Be dating consistently date the moraines to ~1500 yr (Bennike *et al.* 2007; Winsor *et al.* 2014; Larsen *et al.* 2016). In west central Greenland, directly dated local glacier moraines have ages between ~1500 and ~1000 yr, not too dissimilar in age from the Narsarsuaq moraines (e.g., Young *et al.* 2015; Schweinsberg *et al.* 2019).

Evidence that the Greenland Ice Sheet reached the approximate location of the present margin as early as ~4600 cal. yr BP is consistent with other findings in North-East Greenland. Bennike & Weidick (2001) presented radiocarbon ages from the inner and central parts of Nioghalvfjerdsfjorden (up-valley from the present terminus) based on mollusc shells, bones of marine mammals and driftwood from raised marine deposits adjacent to the fjord. The ages range from ~7700–4400 cal. yr BP, revealing a smaller-than-present ice configuration spanning that interval. The older end of this age range (a close constraint for deglaciation timing) was later bolstered by ^{10}Be dating deglaciation in this region, first by Larsen *et al.* (2018) who reported ages of 9.3 ± 0.4 ka, and later by Roberts *et al.* (2024) who reported an age range of 9.0 to 8.2 ka; these ages supported earlier radiocarbon ages that provided minimum constraints on deglaciation of ~9700–7700 cal yr BP (Bennike & Weidick 2001). Smith *et al.* (2023) reconstructed the Holocene dynamics of the Nioghalvfjerdsfjorden ice shelf via radiocarbon dating raised glaciomarine sediments and sediment core analysis from Blåsø, a large epishelf lake up-valley of the present grounding line. Their reconstructions suggest that the ice shelf experienced a minimum phase between 8.5 and 4.4 cal. ka BP leaving open marine conditions where

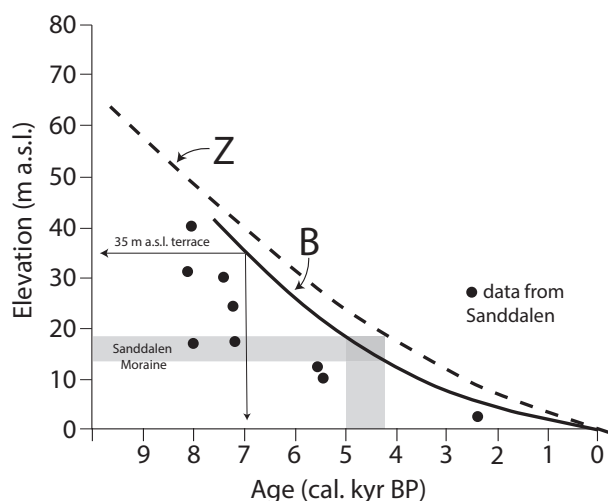


Fig. 4. Relative sea level curves (B: Blåsø; Z: from near the Zachariae Isstrøm terminus) from Bennike & Weidick (2001); locations of sites where these curves are derived is shown in Fig. 1. Black data points are radiocarbon dated marine samples in the Sanddalen area (from Bennike & Weidick 2001). Gray shading demarcates the elevation range of outwash terraces that grade to the Sanddalen Moraine.

Nioghalvfjerdsbræ currently resides. The ice shelf reformed at Blåsø after 4.4 cal. ka BP, reaching a thickness similar to present by 4.0 cal. ka BP. The history of the ice margin at Sanddalen is highly consistent with the findings of Smith *et al.* (2023).

The 35 m a.s.l. ice-fed delta down-valley from the present ice margin at Sanddalen is suggestive of an ice advance farther down valley than the advance that deposited the Sanddalen Moraine. The elevation is ~5 m lower than the local marine limit, which is dated to ~8000 cal. yr BP (Bennike & Weidick 2001). The estimated age of ~7400 cal. yr BP (7475 yr before today) is similar to a mode of moraine deposition in areas around Baffin Bay (Young *et al.* 2021) and may be related. Regardless, if a glacier around the present margin existed ~7400 cal. yr BP, and then again ~4300 yr BP, it constrains the smaller-than-present ice phase to between these two ages.

There is some surging glacier behavior in northern Greenland (Hill *et al.* 2017; Andersen *et al.* 2025), and it is possible that the Sanddalen Moraine is the result of a surge, hence its unusual occurrence. Andersen *et al.* (2025) suggest that Storstrømmen is one of the largest surging glaciers in the world, and its surge lengths in the 20th century were ~10 km. We thus infer that a surge of the glacier at Sanddalen, if any, would likely have been initiated from a position relatively nearby, likely much less than 10 km away. Surge or no surge, we suggest that the Greenland Ice Sheet had attained a near-present-day ice configuration following a period of reduced size by ~4600 cal. yr BP.

Conclusion

The NE Greenland Ice Sheet margin experienced a minimum ice phase between ~7400 and 4600 cal. yr BP. The Sanddalen Moraine provides evidence for expansion of ice slightly beyond the present-day ice configuration ~4600 cal. yr BP, the earliest moraine yet identified that post-dates the Holocene minimum ice phase. It is possible that a surge is partly the reason why the ice margin may have been so extensive at this time. Even so, such a surge would likely have initiated from a baseline position near-present-day ice configuration at ~4600 cal. yr BP. The timing of when NE Greenland Ice Stream outlets experienced a minimum ice phase from ~7.7 to ~4.3 cal. ka BP differs from the ice-sheet minimum phase elsewhere, for example ~5.0–3.0 cal. ka BP in central-west Greenland (Larsen *et al.* 2015; Young *et al.* 2015; Cronauer *et al.* 2016). Such spatiotemporal variability likely stems from both differing climate-forcing and ice-sheet behavior, and should be the focus of future investigations.

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Geochemical characterisation of the Danish subsurface ash series for carbon mineralisation potential

ANNA BUHL PEDERSEN, NIELS HEMMINGSEN SCHOVBO, STÉPHANE BODIN, ARKA RUDRA, DAVID LUNDBEK EGHOLM, OLE RØNØ CLAUSEN, CHRISTIAN TEGNER & HAMED SANEI



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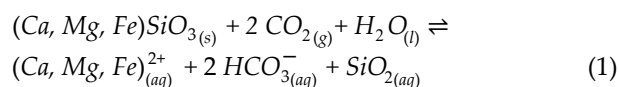
The Danish subsurface ash series within the Eocene-aged Fur and Ølst Formations has a large theoretical CO₂ storage capacity through carbon mineralisation, a potential that is the main motivation behind the C-ASH project initiated by researchers from the Department of Geoscience, Aarhus University. The potential carbon storage is achieved by injection of CO₂ into the closely spaced volcanic ash beds in the Danish subsurface to accelerate silicate dissolution, leading to carbon fixation by mineralisation of CO₂ as carbonate minerals. This provides a valuable alternative to conventional CO₂ storage technologies that typically aim to store CO₂ as a supercritical phase in deep porous aquifers. One of the essential requirements for the mineralisation technology is the identification of ash beds that contain enough reactive divalent cations (Ca²⁺, Fe²⁺, Mg²⁺) to sustain the silicate dissolution – carbonate precipitation reactions. This study aims to provide a geochemical proxy to identify and locate suitable ash beds with high CO₂ sequestration potential. For this purpose, the shallow Harre borehole drilled in 1980 in northwestern Denmark is analysed using high-resolution XRF and SEM-EDS. In the Harre well the ash beds are most abundant within a five meters thick interval in the uppermost part of the Ølst Formation between 191 and 196 meters below surface. The XRF data show that titanium (Ti) is the most reliable elemental proxy for identifying the volcanic ash beds and that calcium (Ca), which is an important divalent cation for carbon mineralisation, is mostly enriched in the volcanic ash beds within the five meters interval. However, Ca may also be associated with gypsum (CaSO₄·2H₂O) and carbonates (CaCO₃), suggesting that part of the Ca have already leached from silicates within the ash beds. This fraction is believed to be low and that the ash beds' suitability for carbon mineralisation remain high.

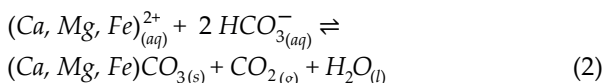
Keywords: Carbon mineralisation, volcanic ash, geochemical proxy, XRF, SEM-EDS.

Anna Buhl Pedersen [abp@geo.au.dk], Department of Geoscience, Aarhus University, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C, Denmark. Niels Hemmingsen Schovbo [nsc@geus.dk], Geological Survey of Denmark and Greenland (GEUS), Øster Voldgade 10, DK-1350 Copenhagen K, Denmark. Stéphane Bodin [stephane.bodin@geo.au.dk], Arka Rudra [arudra@geo.au.dk], David Lundbek Egholm [egholm@geo.au.dk], Ole Rønø Clausen [ole.r.clausen@geo.au.dk] and Hamed Sanei [sanei.geo.au.dk], Department of Geoscience, Aarhus University, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C, Denmark.

Promising mechanisms for Carbon Capture and Storage (CCS) has been known for many decades and play a vital role in the continuous efforts to achieve net zero CO₂ emissions (IPCC 2005). Conventional carbon storage, where supercritical CO₂ is injected into deep, permeable geological reservoirs sealed by an impermeable caprock, is considered important in managing the effects of climate change (Baklid *et al.* 1996; Torp & Gale 2004; IPCC 2005, 2018, 2023). However, other alternatives are needed to diversify the possibility of carbon storage. One such alternative is carbon mineralisation through silicate disso-

lution, where carbon is stored permanently as carbonate minerals by accelerating the natural process of the carbon-silicate cycle (Seifritz 1990; Lackner *et al.* 1995; Snæbjörnsdóttir *et al.* 2020). By injecting aqueous-dissolved or liquid CO₂ into reactive rocks like basalts, divalent cations are leached out through silicate dissolution, which eventually results in the precipitation of carbonate minerals (Eq. 1–2).





As an addition to a more permanent way to store CO_2 , mineralisation through silicate dissolution significantly reduces the time it takes for CO_2 to be mineralised, which is no more than a few years (Snæbjörnsdóttir *et al.* 2017). The process has been successfully demonstrated in Iceland through the CarbFix project, which since 2012 continues to store CO_2 in a basaltic subsurface (Aradóttir *et al.* 2011;

Gíslason *et al.* 2018; Snæbjörnsdóttir *et al.* 2020). The Carbfix injection site at Hellisheiði is ideal for carbon mineralisation due to the basaltic subsurface together with a well-documented hydrothermal system providing the optimal permeability and temperature to quickly mineralise the CO_2 (Snæbjörnsdóttir *et al.* 2020). A basalt-rich geology of this character and setting is, however, not accessible everywhere in the world and to maximise the potential utilisation of carbon mineralisation globally, further research is needed to identify suitable rock types in the subsurface with similar reactive character.

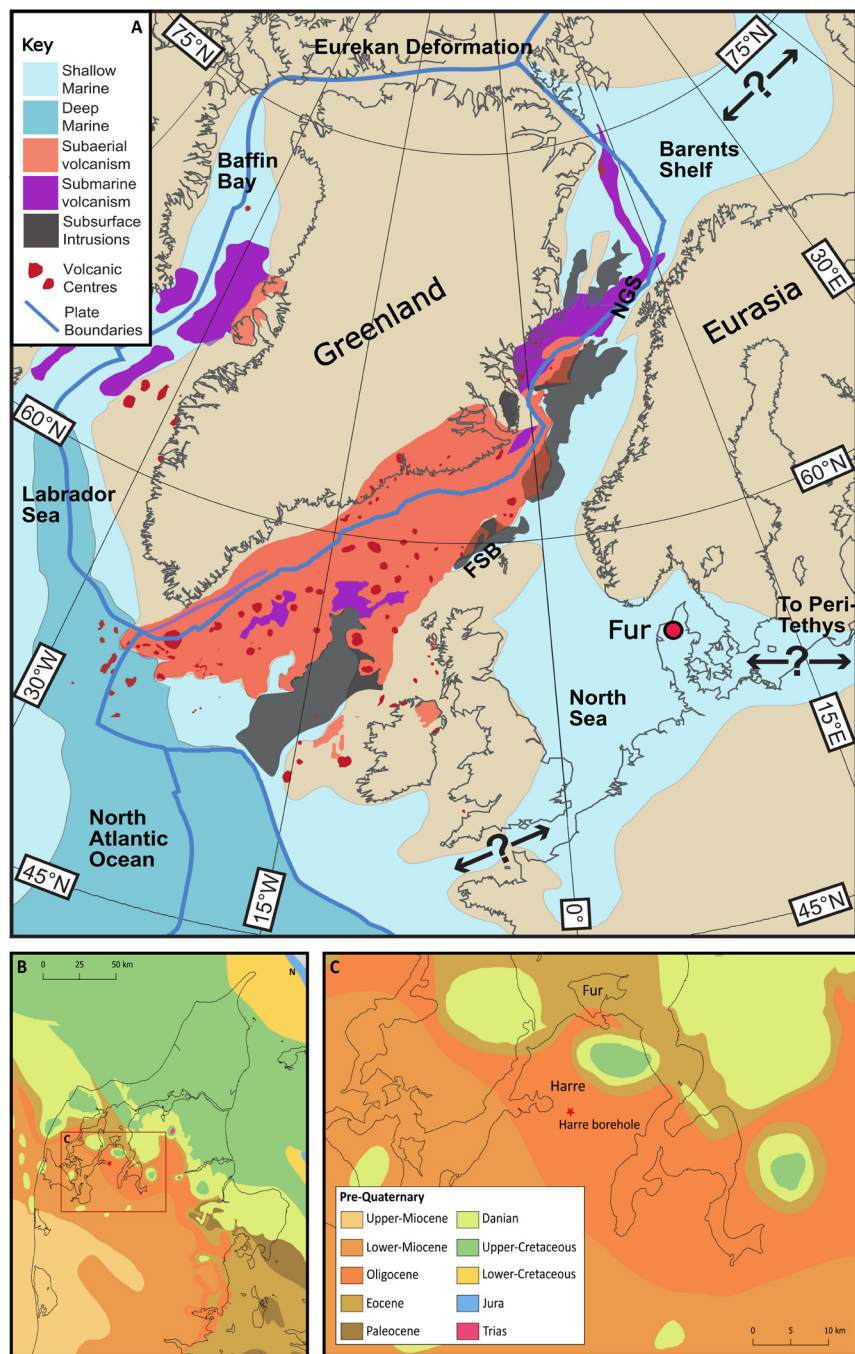


Fig. 1. Paleogeographic reconstruction of Early Eocene (A; adapted from Jones *et al.* 2023) and the pre-Quaternary surface of the region in northwestern Denmark (B, C). A. The map shows the extent of the inland sea with a narrow opening to the north defining the North Sea during the Early Eocene. The red, yellow and dark grey areas represent the different types of volcanism (see legend). The dark and light blue areas represent deep and shallow marine areas, respectively. FSB: Faroe-Shetland Basin; NGS: Norwegian–Greenland Seaway. B. Northern part of Denmark. Salt structures in the area are represented by the circular structures defined by older formations from the Danian and the Upper Cretaceous. The study area is marked by the red rectangle. C. Closer look at the study area dominated by Palaeogene sediments. The location of the Harre borehole is marked by a red star south of Fur island.

During the Late Paleocene/Early Eocene, more than 180 volcanic ash beds with a basaltic to rhyolitic composition (Larsen *et al.* 2003) were deposited in the North Sea area in connection with the opening of the Atlantic Ocean and creation of the North Atlantic Igneous Province (NAIP; Knox *et al.* 2010; Stokke *et al.* 2020, 2021). In the northwestern part of Denmark, ash beds are found in the Fur and Ølst formations (Bøggild 1918; Pedersen 1981; Pedersen & Surlyk 1983; Heilmann-Clausen 1995). Farther south in Denmark, the volcanic ash beds are found 200–300 m below the surface (Nielsen *et al.* 1994). The majority of the ash has a composition akin to the basalts in Iceland and exhibit primary textures including glassy fragments (Larsen *et al.* 2003) and thus has the potential to store large amounts of CO₂ via the carbon mineralisation process. This concept is the main idea behind the C-ASH project (Carbon Fixing by Volcanic Ash) initiated by researchers from the Department of Geoscience, Aarhus University and Climate Foundation Skive (Climate Foundation Skive 2025).

The aim of this study is to explore and analyse the whole-rock geochemistry of the Danish subsurface Ash Series present in the Harre drill core obtained in 1980 (GEUS 1980; Nielsen *et al.* 1994; Heilmann-Clausen 1995). By using high-resolution X-Ray fluorescence (XRF) analyses and Scanning Electron Microscopy – Energy Dispersive X-ray Spectrometry (SEM-EDS), new geochemical proxies can be used in combination with conventional lithological description to quickly recognize the presence of the Danish subsurface Ash Series in future boreholes. In the case of carbon mineralisation, potential target zones as well as zones of geochemical and lithological importance can also be distinguished.

Geological setting

During the Early Eocene, the Danish area and the rest of the North Sea Basin were covered by an inland sea, which for a brief period of 1 million years only had a connection to open water through the narrow Norwegian–Greenland Sea (Fig. 1A; Knox *et al.* 2010). During that time, deposition of thick packages of shales and mudstones dominated in the Danish area (Dinesen *et al.* 1977; Nielsen *et al.* 1986; Heilmann-Clausen 1995; Pedersen *et al.* 2011). In conjunction to the volcanic activity as well as the early rifting of the North Atlantic Ocean, volcanic ash beds spread widely over the region and can be tracked as far away from the NAIP as Austria (Andersen 1937; Larsen *et al.* 1999; Egger *et al.* 2000). These ash beds define Sequence 1.2 of the Danish area and contain the Fur and Ølst formations (Heilmann-Clausen *et al.* 1985; Michelsen *et al.* 1999). They constitute excellent stratigraphical markers to correlate the sediments of

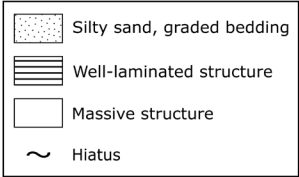
the North Sea and means to estimate the volume and frequency of different stages of volcanism associated with the rifting and creation of NAIP (Pedersen 1981; Pedersen & Surlyk 1983; Morton & Evans 1988; Schmitz & Asaro 1996; Larsen *et al.* 2003; Jones *et al.* 2019; Stokke *et al.* 2020; Stokke *et al.* 2021; Jones *et al.* 2023).

In most of the North Sea and onshore Denmark, the volcanic ash beds are situated in mudstones and clay formations known as Balder and Sele formations in the central North Sea and the Ølst Formation onshore (Heilmann-Clausen *et al.* 1985; Nielsen *et al.* 1986; Danielsen & Thomsen 1997; Schiøler *et al.* 2007). However, in the northwestern part of Denmark the ash beds can be found interbedded with diatomite, locally known as ‘Moler’, defining the Fur Formation (Pedersen & Surlyk 1983). This diatomite interval can be tracked along a narrow belt stretching northwest along the Norwegian coast, believed to represent a narrow upwelling zone driven by northern winds (Bonde 1973, 1974, 1979; Thomsen & Danielsen 1995; Danielsen & Thomsen 1997). The upwelling would cause the bottom waters to become poor in oxygen, reflected by well-laminated diatomite (Pedersen 1981; Pedersen & Surlyk 1983).

The Harre borehole

In May 1980, the drilling of the Harre borehole was completed. The borehole is located close to the village of Harre located south of the island of Fur (Fig. 1B, C). During the drilling, core sections in plastic core liners of 1.5 m in length and 10 cm in diameter were retrieved (GEUS 1980; Nielsen 1994a). The present part of the ash layers in the Harre borehole is recognized from 190.88–222.00 meters below surface (m b.s.), with a total thickness of 31.12 m. The facies of the Fur and Ølst formations interfinger in a characteristic way, where the diatomitic Fur Formation is interbedded between an upper and lower clay interval belonging to the Ølst Formation with gradual transitions (Fig. 2). The interfingering stratigraphy contrasts with most of the Danish area, where the two formations are geographically separated (Heilmann-Clausen *et al.* 1985; Nielsen 1994b). More importantly, the majority of the ash beds in the borehole occurs in the upper clay interval of the Ølst Formation. These ash beds mainly represent the positive series in the Ash Series as established by Bøggild (1918) and Gry (1940). From the Harre core sections, strata are missing from the transition from Fur Formation to the upper part of the Ølst Formation and at the transition between the lower part of the Ølst Formation and Holmehus Formation (Nielsen *et al.* 1994; Nielsen 1994b).

The upper part of the Ølst Formation is present



Positive
ash series

Negative
ash series

from 190.88–196.5 m b.s. in the Harre borehole and consists of non-diatomaceous, greenish grey clay. At the bottom of the interval, the clay gradually becomes less dense and appears similar to the underlying diatomite. The volcanic ash beds vary between black and dark grey in color with a sandy silt grain size (Nielsen 1994b; Nielsen *et al.* 1994). Occasionally, burrows and signs of reworked material are present (Nielsen *et al.* 1994). Based on grain size analyses, the sand content increases in the upper part of the Ølst Formation, likely caused by mixing of the ash beds and silt due to bioturbation (Nielsen 1994b). The following interval (196.5–218.5 m b.s.) is recognized as the diatomite belonging to the Fur Formation. Within the Fur Formation, three different types of clay have been distinguished based on changes in lamination from well-laminated to poorly laminated or massive structures. The positions of the three types of clay within the Fur Formation show complex and inter-fingering relations due to fluctuations in the diatom/clay ratio (Nielsen *et al.* 1994). The Fur Formation contains a few ash beds widely spaced from each other, which contrasts with the overlying Ølst Formation. The ash beds in the present part of the Fur Formation in the Harre borehole mostly belong to the negative series of the ash bed stratigraphy of Bøggild (1918) and Gry (1940). The lowest clay interval (218.5–222 m b.s.) belongs to the Stolleklint Clay of the Ølst Formation and consists of non-diatomaceous clay, similar to the clay in the upper part of the Ølst Formation. It contains few thin ash beds. In contrast to the upper clay interval in the Ølst Formation, lamination is present (Nielsen *et al.* 1994).

Material, methods and data analysis

The methods used in this study consist of handheld X-ray fluorescence (HH-XRF) measurements, Scanning Electron Microscopy - Energy Dispersive X-ray Spectrometry (SEM-EDS), micro-X-ray fluorescence spectrometry (μ -XRF) and pyrolysis, as well as a range of data analysis such as normalisation and multivariate statistical analysis. The measurements and analyses were conducted at the Department of

Geoscience and at the Interdisciplinary Nanoscience Centre (iNANO) at Aarhus University. From the Harre drill core, nineteen core sections approximately 1.5 m long each were selected. The core sections numbered 128–148 constitute the interval of 190.5 to 222.0 m b.s. in the borehole. The core sections were chosen to include the ash beds of the Ash Series in the units corresponding to the Ølst and Fur formations. Core sections 141 and 144 (depth intervals 210.0–211.5 and 214.5–216.0 m b.s.) were not available for analysis.

Handheld (HH) XRF analysis

A Bruker SI TITAN handheld XRF device was used to establish elemental variation. The depth of penetration is around 1 cm with a spot size of ~8 mm. The procedure was as follows: the plastic core liners were opened with a saw and the surface was scraped clean of drill mud to provide a clean, relatively flat surface. Each sample was analysed for 60 seconds for every cm as continuously along the cores as possible.

For every core section, three standard measurements were performed before and after the measurements on the core. Furthermore, the standard was measured for every sixth measurement in average to control the stability of the instrument. The standard used was the CS-M2 GEO/SOIL sample available at the Department of Geoscience. Reproducibility of the standard measurements revealed precision to be better than 10% for most of the analysed elements with the exceptions of S (33%) and P (17%; Table 1). Standard averages were only available for a selection of elements, and accuracy calculations were therefore limited. However, for the available averages, accuracies remain better than 10% except for K regarding the concentrations of the standard (Table 1).

Quality of the Harre drill core

Ideally, the geochemical variations in a sediment core would be obtained using an XRF core scanner. The reason for using a HH-XRF instrument for this study

Table 1. Descriptive statistics of HH XRF standard measurements

Element	Al	Si	P	S	K	Ca	Ti	Mn	Fe	Ni	Cu	Zn	As	Sr	Zr	Pb
Mean	6.283	32.160	0.034	0.171	3.763	0.662	0.153	0.096	1.651	0.004	0.020	0.073	0.007	0.016	0.023	0.086
Median	6.352	32.471	0.033	0.161	3.789	0.663	0.152	0.097	1.654	0.004	0.020	0.073	0.007	0.016	0.023	0.086
St.dev.	0.542	1.896	0.006	0.056	0.290	0.046	0.009	0.009	0.125	0.001	0.002	0.005	0.001	0.001	0.001	0.003
Max	7.399	35.826	0.052	0.440	4.446	0.770	0.178	0.124	1.920	0.006	0.024	0.085	0.010	0.018	0.027	0.094
Min	3.791	22.233	0.011	0.070	2.842	0.499	0.121	0.068	1.269	0.002	0.015	0.057	0.003	0.014	0.020	0.077
n	266	266	266	266	266	266	266	266	266	266	266	266	266	266	266	86
Precision (%)	8.6	5.9	16.9	32.5	7.7	7.0	6.0	9.3	7.5	16.1	8.1	6.2	19.0	3.7	4.6	3.8
Accuracy (%)	9.0	7.2	–	–	12.3	–	–	1.7	2.9	6.6	1.0	–	–	–	–	3.0
MOE	0.077	0.271	0.001	0.008	0.041	0.007	0.001	0.001	0.018	0.000	0.000	0.001	0.000	0.000	0.000	0.001
Standard (average)	6.900	34.660	–	–	4.292	–	–	0.098	1.700	0.004	0.020	–	–	–	–	0.083

is based on the overall state of the core sections. The cores had dried out and are intensively fractured, posing challenges to measure continuously along the sections. The core had not been halved either, which meant that a flat measurement surface was not readily available for the analysis. Samples from previous studies of the core were occasionally present in small plastic bags. In some intervals the volcanic ash beds were completely unconsolidated and mixed with pieces of clay and diatomite, which made it challenging to provide a representable result for the ash beds in question. It is, however, not uncommon for deep drill cores to be in a similar condition. An available drill core is still far more superior to well cuttings and outcrops in terms of coherent stratigraphy and determination of details such as formation boundaries and sedimentary structures. Regarding the geochemical variations and sampling it also provides a more accurate estimation, as e.g. well cuttings can be compromised by drilling mud contamination and alteration (Sanei *et al.* 2020). A HH-XRF instrument was therefore considered the most suitable approach, as the measurable surfaces can be determined manually. Furthermore, the XRF data obtained in this study have successfully reflected the lithologies in the Harre drill core as established by Nielsen *et al.* (1994), revealing distinct trends related to the volcanic ash as well as the diatomite. The trends will be discussed in the following.

Centred log ratio (clr) transformation and Principal Component Analysis (PCA)

Since this study deals with compositional data, normalisation is needed before multivariate statistical analyses can be performed on the data to eliminate any spurious relationships between the components (Aitchison 1984). Centred log ratio (clr) transformation is commonly used on geochemical data and is therefore used for the normalisation of the HH-XRF data. The clr transformation normalises the data by taking the natural logarithm of the ratio of each data value divided by the geometric mean of all parts of the analysis point. In this way misinterpretations can be avoided during further statistical analysis of the

data. To use the clr transformation, false zeros such as values measured below detection limit need to be handled. Therefore, the corresponding standard error value divided by two was used (Schovsbo & Petersen 2024). Variables that are dominated by measurements below detection limit are deemed unsuitable and excluded from the dataset before normalisation and further analysis. Of the elements and oxides deemed suitable for analysis, 15.3% of the data consist of measurements below detection limit (supplementary file A). The clr normalised data have further been auto-scaled and centred.

To identify any hidden patterns or correlations within the clr normalised XRF data, Principal Component Analysis (PCA) was used. PCA is a widely used statistical tool to reduce high-dimensional geochemical data into linearly uncorrelated variables called principal components; a set of vectors that explain the variance in the dataset. By reducing the high-dimensional dataset, it is possible to visualise the data in a two-dimensional space (Kherif & Latypova 2020). The data matrix of the HH-XRF data defines the elements and oxides as variables and the depth point compositional values as observations. This is used to analyse correlations between the occurrences of the elements and oxides with regards to the different lithologies and secondary deposits present.

Scanning Electron Microscopy – Energy Dispersive X-ray Spectrometry (SEM-EDS)

Based on the HH-XRF measurements, seven samples were chosen at different depths in different lithologies for further analysis using SEM-EDS (Table 2). To mount the samples on the sample stubs, a conducting carbon cement (Leit-C) was used. Before performing SEM-EDS, the samples were coated with platinum (Pt) using the LEICA EM SCD 500 sputter coater. The mounting and coating were performed at iNANO, Aarhus University. For SEM-EDS, the TESCAN VEGA scanning electron microscope sourced by tungsten filament electrons and with integrated EDS was used; it is housed at the Department of Geoscience, Aarhus University. The used accelerator voltage was set to 15 kV. The SEM images were obtained using the TESCAN Essence™ software and the elemental analysis of the chosen samples were obtained using the Aztec software from Oxford Instruments.

Pyrolysis analysis

Pyrolysis analysis was performed using a HAWK Pyrolyser and Total Organic Carbon (TOC) analyser

Table 2. Samples analysed with SEM-EDS, μ -XRF and pyrolysis

Sample ID	Sample depth (m b.s.) uncorrected	Lithology
HA-2	191.12	Volcanic ash (+118)
HA-1	191.27	Clay layer (upper clay interval)
HA-3	192.90	Volcanic ash (+90D)
HA-7	196.79	Diatomite
HA-5	207.82	Diatomite
HA-6	208.98	Diatomite
HA-4	220.24	Clay layer (lower clay interval)

+118 and +90D refer to the respective volcanic ash beds from which the samples were taken. Depths are uncorrected according to Nielsen *et al.* (1994).

(Wildcat Technologies, U.S.A.). Approximately 50 mg of sample was initially purged to 300 °C (resulting in the S0 peak), then pyrolysed at 300 °C for 3 minutes, producing the S1 peak, which represents free hydrocarbons (HC). Following this, a temperature ramp of 25 °C/min was applied up to 650 °C, during which hydrocarbons (S2 peak), CO (S3 CO peak), and CO₂ (S3 CO₂ peak) were continuously measured. These measurements correspond to the labile organic carbon. In this study, the value of S1 (free HC) is considered as the sum of S0 + S1 (expressed in mg HC/g rock; Rudra *et al.* 2024). After the pyrolysis phase, the sample was purged under an oxygen atmosphere and reheated from 150 °C to 850 °C (25 °C/min). The CO and CO₂ released during this step represent the residual carbon fraction (Lafargue *et al.* 1998) until 700 °C, beyond which the CO₂ released is calculated as mineral carbon. The total organic carbon (TOC) content is the sum of the labile (reactive) and residual (inert) organic carbon (see supplementary file A).

Micro-X-ray Fluorescence Spectrometry (μ-XRF)

Seven samples used for SEM-EDS were further analysed using μ-XRF. The purpose of using μ-XRF was

to support and semi-quantify the findings of the SEM-EDS analysis as well as to determine the geochemical compositions and distribution of elements in the samples. For this purpose, area scans were obtained, where average element and oxide quantifications of the samples were measured (supplementary file B). The μ-XRF data is produced based on a standardless quantification using the M-Quant software provided by the instrument. Based on earlier studies, the quantification of the elements and oxides wt.% have shown good long-term consistency and reliability of instrument performance (Birch *et al.* 2019; Hrnjić *et al.* 2020; Orfanou *et al.* 2020; Orfanou *et al.* 2021; Barfod *et al.* 2024). The samples were mounted on thin glass plates using Blu Tack to make the measurement surfaces as even as possible. The samples remained unpolished during the analysis. The instrument used was the M4 Tornado from Bruker located at the Department of Geoscience, Aarhus University. The X-ray source consists of a rhodium X-ray tube. For the scans, an energy of 50 kV and a current of 600 μA were used. The spot size was set to 20 μm with a measurement time of 25 ms/pixel. The lightest element that can be detected by the instrument is sodium (Na).

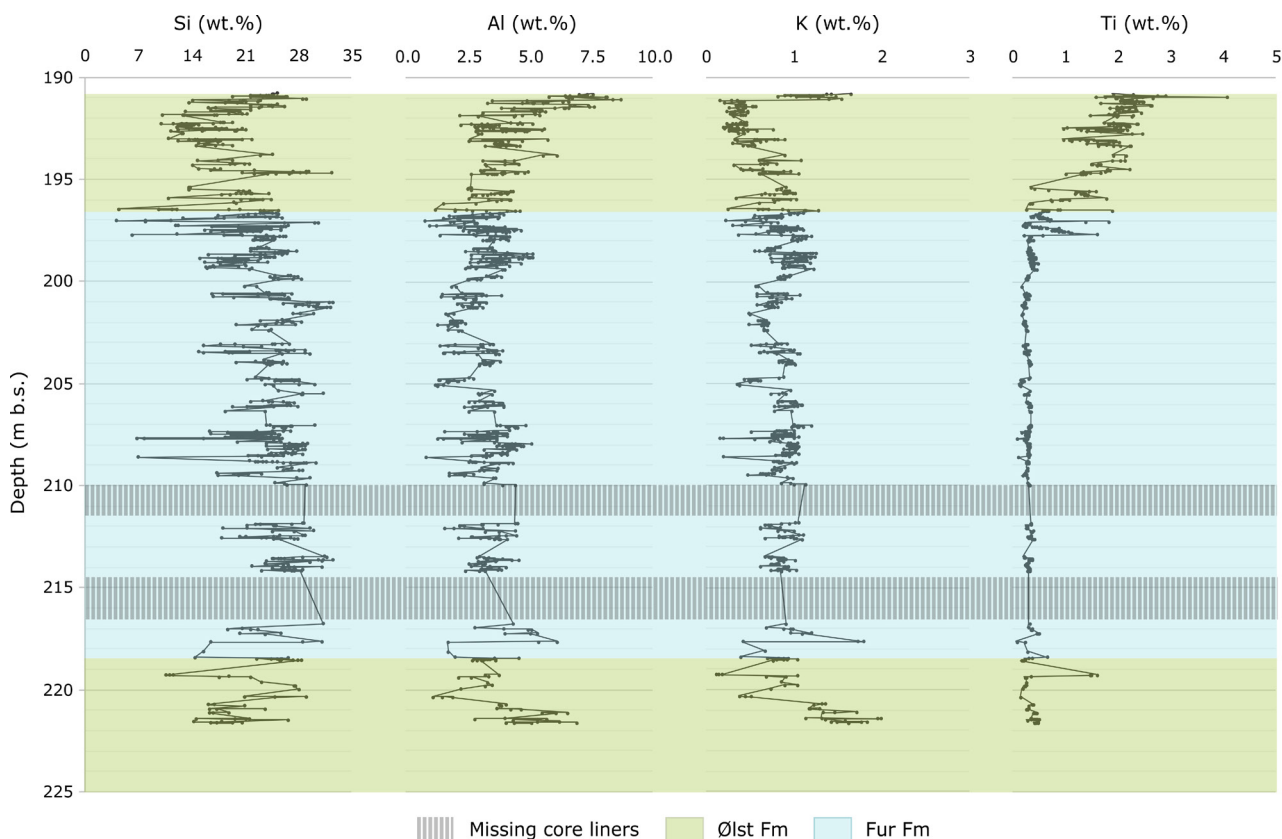


Fig. 3. Depth profiles of the measured concentrations of Si, Al, K, and Ti in wt.%. Missing core liners are marked with grey striped bars. The blue and green intervals indicate the Fur and Ølst Formations defined by Nielsen *et al.* (1994). The depths are uncorrected. The error bars are smaller than the symbols. Precisions remain under 10% for all the elements.

Results

Stratigraphic variations of element concentrations

After processing the HH-XRF data, selected elements were plotted against depth (Figs 3, 4). The concentrations of Si, Al and K oscillate without any major depth trend. However, in the uppermost 5 m within the upper part of the Ølst Formation, an increasing and decreasing trend towards the top can be seen for Al and K, respectively. Conversely, Si exhibits a decreasing trend followed by an increasing trend towards the top. No distinguishable trends are evident in the Fur Formation. In the bottom 3 m in the lower part of the Ølst Formation, despite the relatively few data points, Al and K appear to decrease from bottom to top.

Out of all the elements, Ti shows the most distinct pattern when plotted against depth. The Ti concentrations are near constant from the bottom of the core section at 222 until 198 m b.s. except one outlier between 219 and 220 m b.s., where there is a small peak in concentration. The most notable pattern is the significant variability in Ti concentrations in the upper part of the Ølst Formation with an overall increase in concentration towards the top of the analysed inter-

val. Here, the Ti concentrations are more than 4 folds higher than seen in the base of the section (Fig. 3). A drop in concentration is seen around 195.5 m b.s.

The S, Ca, Fe and Mn content fluctuate significantly (Fig. 4). The S concentrations are highest within the Fur Formation and decrease significantly in the upper part of the Ølst Formation. Between 196 and 198 m b.s. three distinct peaks are visible in the S and Ca profiles. Further down between 207 and 210 m b.s. a pair of peaks can be seen again in both profiles. Distinctive peaks in Mn content are present in this depth interval as well. Between the two missing core liners, the Mn profile exhibits an increase in concentration, which is not as visible in the S and Ca profiles. The Fe depth profile shows fluctuating concentrations overall. However, it can be argued that there is a general increase in Fe from around 200 m b.s. towards the uppermost part of the section. Ca generally seems to increase gradually in the upper part of the Ølst Formation in a similar manner as Ti, Fe and Al.

Geochemical screening and data normalisation

The element depth profiles are highly fluctuating due to the influence of different secondary phases present

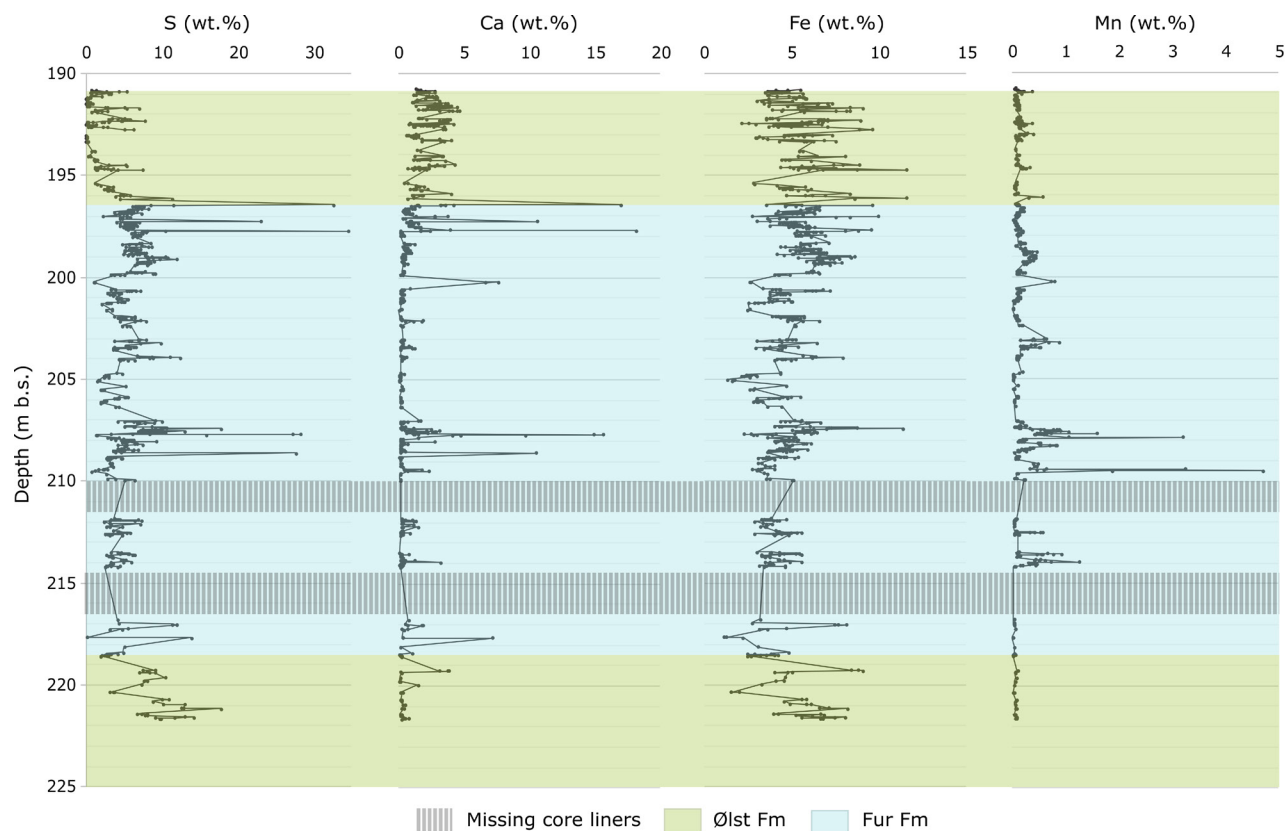


Fig. 4. Depth profiles of the measured concentrations of S, Ca, Fe, and Mn in wt.%. Missing core liners are marked with grey striped bars. The blue and green intervals indicate the Fur and Ølst Formations defined by Nielsen *et al.* (1994). The depths are uncorrected. The error bars are smaller than the symbols. Precisions remain under 10% for all the elements except for S (32.5%).

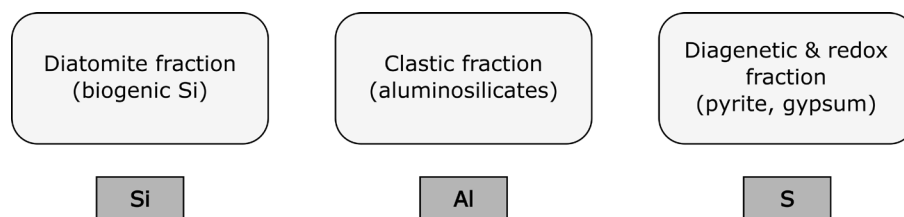


Fig. 5. Schematic diagram of the three normalisations used for the geochemical screening method inspired by Sanei *et al.* (2001). Normalisation to Si is chosen to eliminate the biogenic Si fraction from the bulk data. Normalisation to Al is used to eliminate the clastic fraction (clay). Normalisation to S is used to eliminate the diagenetic and redox fraction caused by the presence of secondary deposits.

in the sediment, which impact the ratios between the elements (Sanei *et al.* 2001). To account for the matrix effect, a geochemical screening method inspired by Sanei *et al.* (2001) was used (Fig. 5), where different normalisations representing their respective fraction are used to eliminate that specific fraction from the data profile, leaving behind the ash signal. In this study, three normalisations are considered to extract hidden patterns as well as the volcanic ash signal in the profiles. Since most of the selected core sections are influenced by the presence of diatomite, a dilution effect caused by biogenic silica needs to be considered, which is accounted for by normalising the XRF data to Si (Fig. 6; Pedersen & Surlyk 1983). The presence of clastic material is also an important fraction to consider, as two clay intervals as well as clay interbedded in the diatomite constitute major parts of the stratigraphy. To eliminate the influence of clastic material from the bulk data, a normalisation to Al

is chosen, as Al is a main constituent of aluminosilicates (Fig. 7; Roulet *et al.* 2000; Rimmer 2004). The S depth profile reveals relatively high concentrations of S throughout most of the stratigraphy, except the upper clay interval in the Ølst Formation (Fig. 4). It has long been known that pyrite (FeS_2) and gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) are frequent in the Fur and Ølst formations (Pedersen *et al.* 1975; Pedersen 2008). Therefore, normalisations of Fe and Ca to S are used to account for diagenetic and redox deposits (Fig. 8). The resulting patterns of the normalisations will be described further below.

Normalisation to Si

For Al/Si and K/Si the normalisations revealed similar patterns within the Fur Formation, where the clastic content fluctuates towards the beginning of

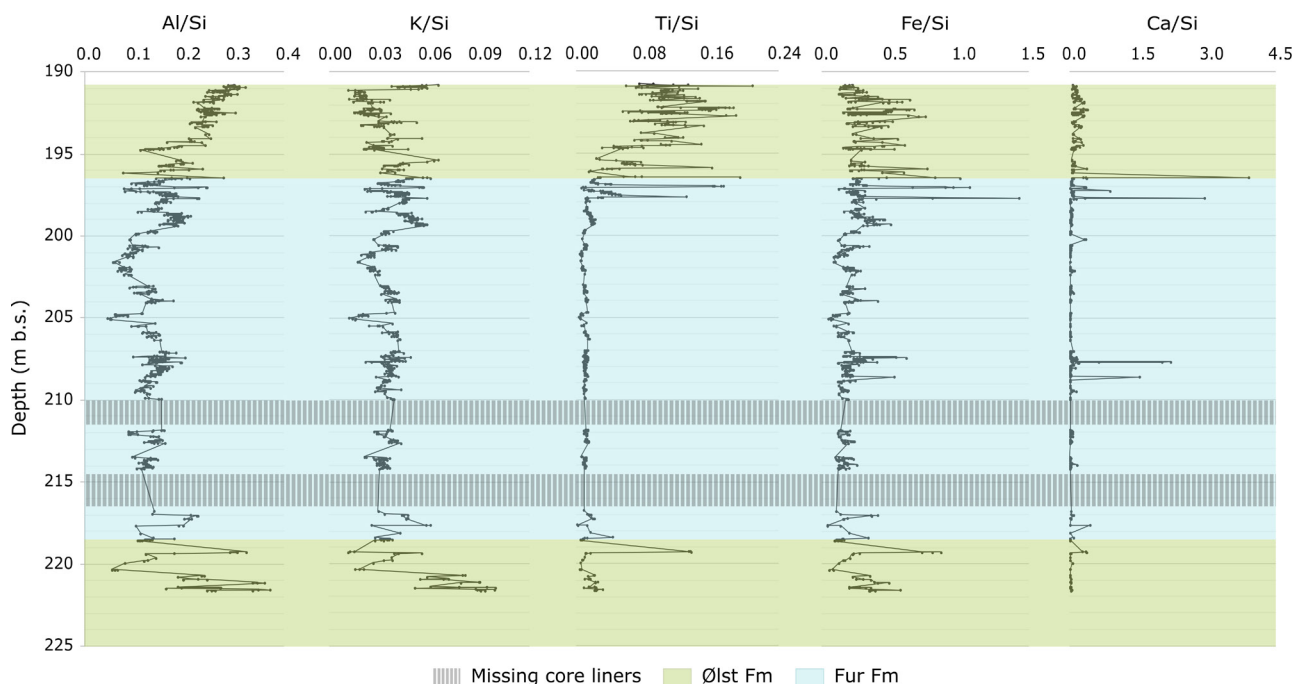


Fig. 6. Normalisation to Si. By normalising to Si, the biogenic silica signals are eliminated from the bulk data. Missing core liners are marked with grey striped bars. The blue and green intervals indicate the Fur and Ølst Formations defined by Nielsen *et al.* (1994). The depths are uncorrected.

the upper part of the Ølst Formation. In the base of the upper part of the Ølst Formation around 196.5 m b.s., the two normalisations show opposite trends, where an increase in the Al/Si ratio and a decrease in K/Si can be seen towards the top of the formation. In the lower part of the Ølst Formation, the compounds show a similar pattern with a decrease in concentration just beneath 220 m b.s., which is instantly replaced by a large increase in both ratios.

The Ti/Si normalisation shows more clearly the increase in Ti concentrations in the upper part of the Ølst Formation where the volcanic ash beds dominate. Four peaks between 195 and 198 m b.s. are even more distinguishable after the normalisation, showing ratios higher than most in the depth profile.

The Fe/Si and Ca/Si normalisations exhibit similar patterns to the Ti/Si profile in the upper part of the Ølst Formation, where they show increasing trends from around 195.5 m b.s. until 193 m b.s., followed by decreasing trends towards the top of the interval. Both Fe/Si and Ca/Si show three-four peaks similar to those seen in Ti and Ti/Si between 195 and 198 m.b.s (Figs 3 and 6). The peaks are absent in the Al/Si and K/Si ratios (Fig. 6). Between 207 and 209 m b.s., two correlating peaks are present in the Fe/Si and Ca/Si ratios, though more prominent in the Ca/Si depth

profile. Those peaks are absent in the depth profiles of Al/Si, K/Si, and Ti/Si. In the lower part of the Ølst Formation, a peak is present in the Fe/Si and Ca/Si ratios equal to the one seen in the Ti/Si plot.

Normalisation to Al

The Si/Al depth profile exhibits more clearly the variations in the diatom/clay ratio within the Fur Formation (Fig. 7). This profile particularly illustrates a higher diatom/clay ratio in the 200–203 m b.s. depth interval, as well as at 205 m b.s. Si/Al appears to be constant from approximately 194 m b.s. to the top of the section. Additionally, a significant increase in the ratio is observed at 220 m b.s.

The Ti/Al ratio shows the same increasing trend in the uppermost part of the Ølst Formation. The peaks with relatively high ratios between 195 and 198 m b.s. as well as between 207 and 209 m b.s. reappear in the Fe/Al and Ca/Al depth profiles. The Fe/Al depth profile is otherwise more erratic compared to the Fe/Si ratio and shows no distinct patterns besides a general increase upwards in the depth profile before decreasing again from 195 m b.s. and to the top. The Ca/Al ratio remains close to constant throughout the depth

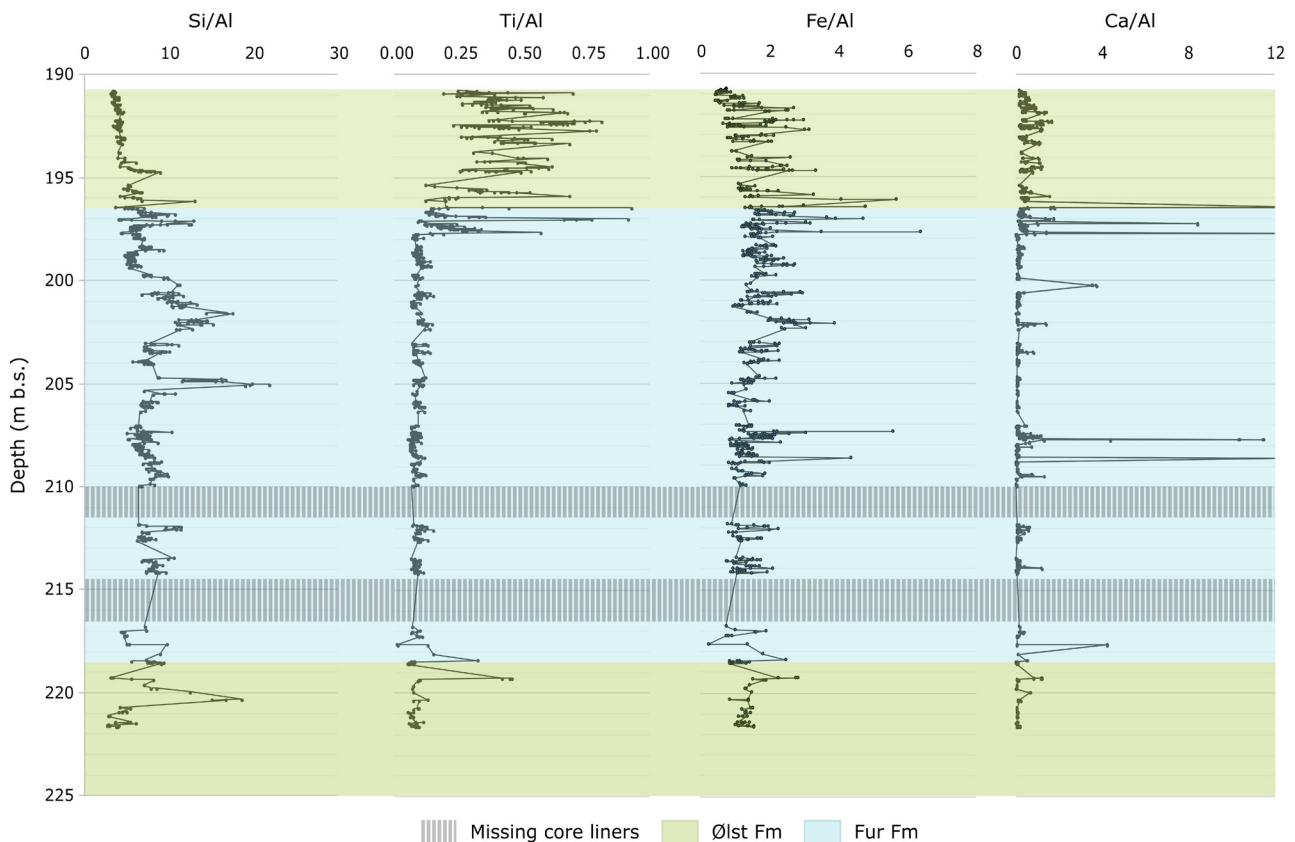


Fig. 7. Normalisation to Al. By normalising to Al, signals caused by the clastic (clay) fraction such as aluminosilicates are eliminated from the bulk data. Missing core liners are marked with grey striped bars. The blue and green intervals indicate the Fur and Ølst Formations defined by Nielsen *et al.* (1994). The depths are uncorrected.

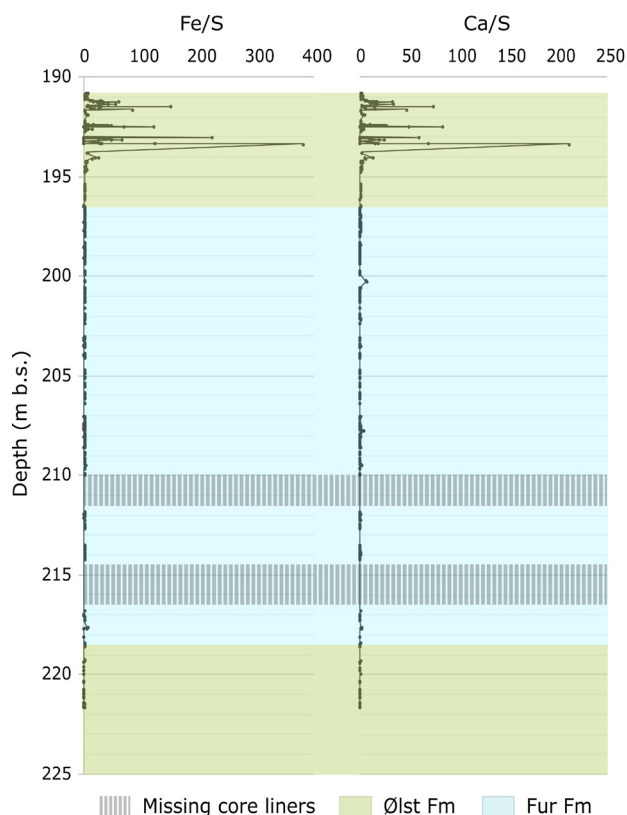


Fig. 8. Normalisation to S. By normalising to S, signals caused by the diagenetic or redox fraction (pyrite and gypsum) are eliminated from the bulk data. Missing core liners are marked with grey striped bars. The blue and green intervals indicate the Fur and Ølst Formations defined by Nielsen *et al.* (1994). The depths are uncorrected..

profile except for the peaks with high increases. In the upper part of Ølst Formation, the Ca/Al ratio displays a similar increase as the Ca/Si ratio.

Normalisation to S

The Fe/S and Ca/S normalisations show similar patterns. Most of the distinct peaks in concentration seen in the Fe/Si, Ca/Si, Fe/Al and Ca/Al normalisations are now eliminated, confirming the presence of diagenetic deposits related to S. From 194 m b.s. and to the top of the section both ratios increase significantly, confirming that most of the Fe and Ca related to other phases such as the volcanic ash are situated in the top of the core section. No such increase is seen in the lower part of the Ølst Formation, suggesting

that the increasing content at the uppermost part of the Ølst Formation can be explained by the abundance of volcanic ash beds present here.

Carbon fractionation

The results of the carbon analysis indicate that the total carbon content (TC) in the uppermost part of the Ølst Formation with closely spaced ash intervals ranges between 0.6 and 0.8 wt.%. In contrast, the highest TC content is measured in the lowermost part of the Ølst Formation at 220.24 m b.s., where it reaches a maximum of 3.6 wt.% (Fig. 9A). This depth interval also contains the highest fraction of reactive organic carbon (Fig. 9B).

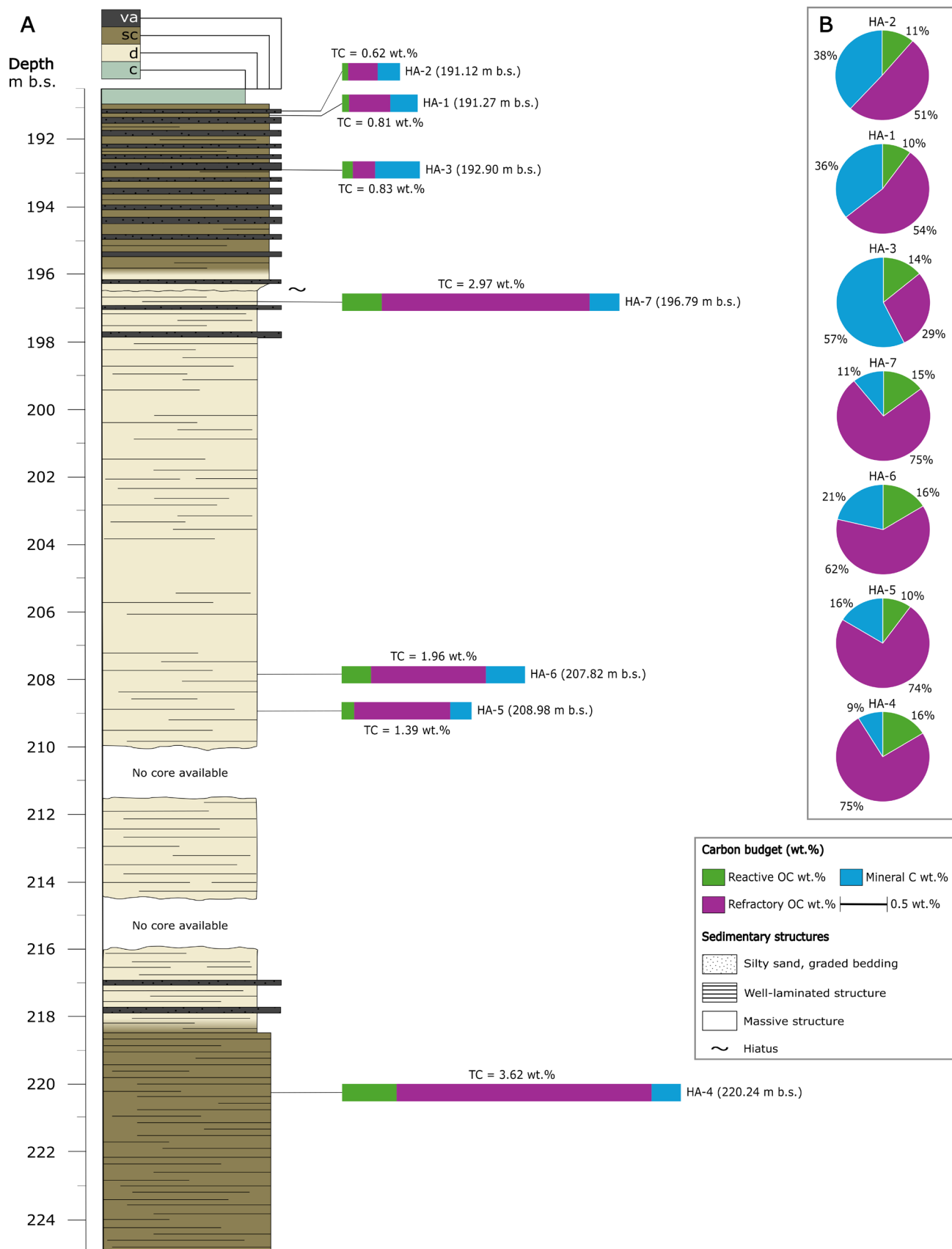
At 208.98 m b.s., within the Fur Formation, there is a significant decline in both TC and its reactive fraction due to the dilution effect caused by the diatomite. The two intervals above 207.82 m b.s. and 196.79 m b.s. exhibit a progressive increase in TC, particularly in organic and reactive carbon fractions. The highest organic carbon content in the diatomite interval is observed at 196.79 m b.s. at the transition to the upper clay interval with closely packed ash layers. The three uppermost samples in the upper part of the Ølst Formation are characterised by a sharp decline in the TC content and the reactive carbon fraction. In this interval, organic carbon is almost entirely refractory and is likely dominated by detrital organic material.

To further investigate the distribution of different carbon fractions, pie charts are used to represent the respective fraction of the different carbon phases, i.e., reactive organic carbon, refractory organic carbon, and mineral carbon (Fig. 9B). The results show that the samples from the upper part of the Ølst Formation exhibit the highest proportions of mineral carbon relative to the rest of the section, which comprises more than 35% of the TC in the samples taken from 191.12 and 191.27 m b.s. and 57% from the sample at 192.90 m b.s.

Mode of occurrence of elements (elemental affinities)

The PCA of the clr normalised XRF data show that the first three principal components (PCs) model 58.42% of the data variance (PC1: 36.60%, PC2: 13.38%, PC3: 8.44%). The score plots of PC1 vs. PC2

Fig. 9. Sedimentary log and carbon analysis results. **A.** The carbon budgets are given in wt.% of the seven samples at the assigned depths in the stratigraphy (see scale in the legend). The budget is divided into reactive OC, refractory OC, and mineral C. **B.** Pie charts of the carbon fractionation of the seven samples. The samples are shown in order of depth from top to bottom. Depths are uncorrected according to Nielsen *et al.* (1994). The top three samples from the ash-containing interval show the highest fractions of mineral C, while the samples belonging to the Fur Formation and the lower part of the Ølst Formation show higher fractions of reactive and refractory carbon.



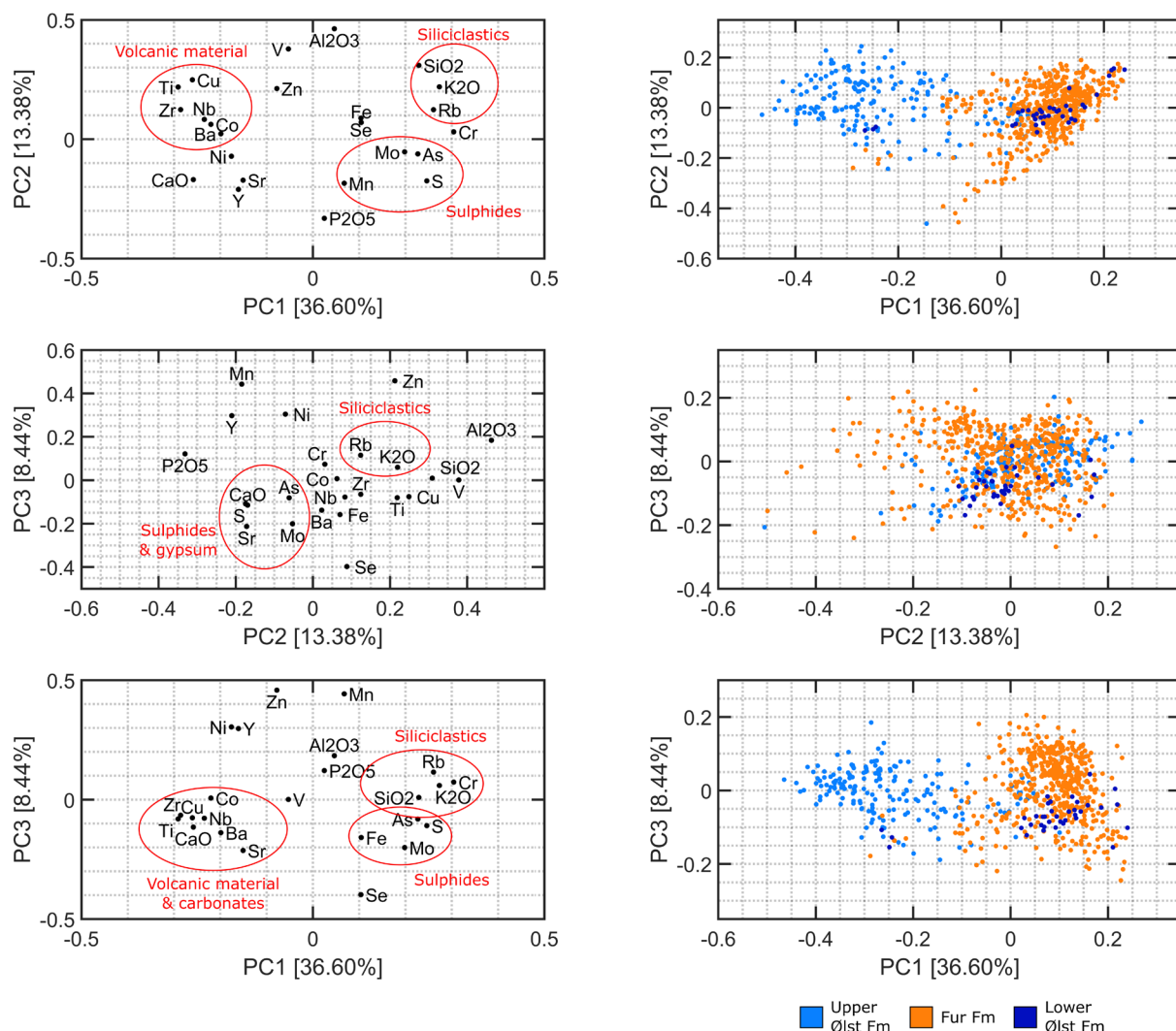


Fig. 10. Principal component analysis (PCA) of the clr normalised, scaled and centred XRF data. The top three principal components of the PCA are plotted against each other in the following order: PC1 vs. PC2, PC2 vs. PC3, and PC1 vs. PC3. The variables and their contributions to the principal components are represented in the left side, while the scores are represented in the right side of the figure. The scores are coloured according to their respective lithological interval as defined by Nielsen *et al.* (1994) (see legend).

and PC1 vs. PC3 show a distinction between samples from the upper part of the Ølst Formation with clay and volcanic ash and the samples of diatomite from the Fur Formation, while the scores belonging to the samples of clay from the lower part of the Ølst Formation plot together with the diatomite from the Fur Formation (Fig. 10). The samples containing clay and volcanic ash within the upper part of the Ølst Formation are characterised by a generally negative PC1, while the diatomite interval from the Fur Formation is distinguished by a positive PC1. In all score plots, a few scores from the Fur Formation plot further away from the general grouping and closer to the scores belonging to the upper part of the Ølst Formation with clay and ash. This is also the case for a few scores belonging to the lower part of the Ølst Formation.

The variables show a clear grouping of Mo, As, and S characterised by a positive PC1, indicating the presence of sulphides. In the PC1-PC3 plot, Fe is also associated with the elements, supporting the occurrence of pyrite. In the PC2-PC3 plot, where the dominating factor is removed, CaO plots together with this grouping, suggesting the presence of gypsum associated with the sulphides. Sr plots close to CaO in all plots characterised by the same negative PC1, suggesting the presence of carbonate minerals as well (Brand *et al.* 1998). Ti, Cu, Zr, Nb, Ba, and Co exhibit another grouping characterised by a negative PC1, which is the same for the scores belonging to the interval rich in volcanic ash. SiO₂ is associated with K₂O, Rb and Cr in all plots defined by a positive PC1 and PC2, indicating mostly siliciclastic or clay-rich material. Compared to the groupings previously

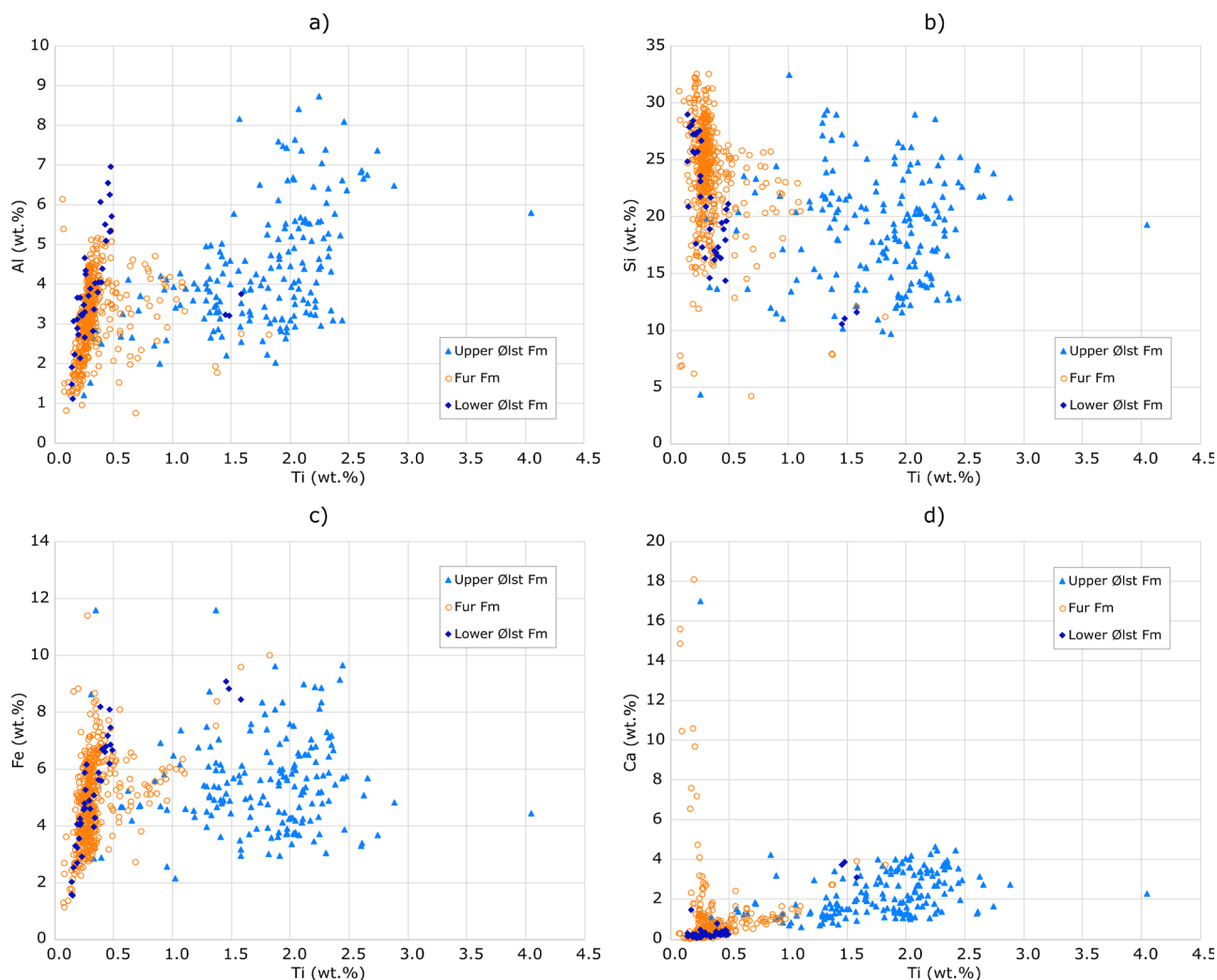


Fig. 11. Cross plots of chosen elements plotted against Ti. a) Al vs. Ti. b) Si vs. Ti. c) Fe vs. Ti. d) Ca vs. Ti. The data have been divided into the intervals of known lithologies, consisting of the upper part of Ølst Formation with volcanic ash beds (light blue triangles), the Fur Formation (orange circles) and the lower part of Ølst Formation (dark blue diamonds). Distinctive trends are most predominant in the Fur Formation and lower part of Ølst Formation with a Ti content below 0.5 wt.%, while the upper part of Ølst Formation shows scattered data points with an elevated Ti content above 0.5 wt.%. The error bars are smaller than the symbols.

mentioned, Al_2O_3 is situated in between and characterised by a positive PC2, showing associations with both the volcanic and siliciclastic materials.

Geochemical facies

For further correlations, selected elements were plotted against Ti, as the results presented above have shown a close relation between Ti and the ash bearing interval. The data have been divided into the same three lithology classes as described earlier in the text (Fig. 11). Ti is a conservative, lithophilic element, while the selected elements can participate in various geochemical reactions (Goldschmidt 1937). Therefore, the cross plots can be used to reveal addi-

tional patterns within the dataset, most importantly regarding the volcanic ash.

Common to all four cross plots in Fig. 11 is a clustering of most of the data points situated in the Fur Formation with a Ti content below 0.5 wt.%. For Al and Fe there are positive linear correlations with Ti (Figs 11a and 11c). A positive linear trend between Ca and Ti is also present, though an inverse relationship applies for the data points with a Ca content over 5 wt.% and a Ti content below 0.5 wt.% (Fig. 11d). For Si a negative linear correlation can be seen within the Fur Formation (Fig. 11b). The present data points from the lower part of the Ølst Formation appear to follow the same trends as those within the Fur Formation in all cross plots. A smaller but distinct group of data points within the Fur Formation

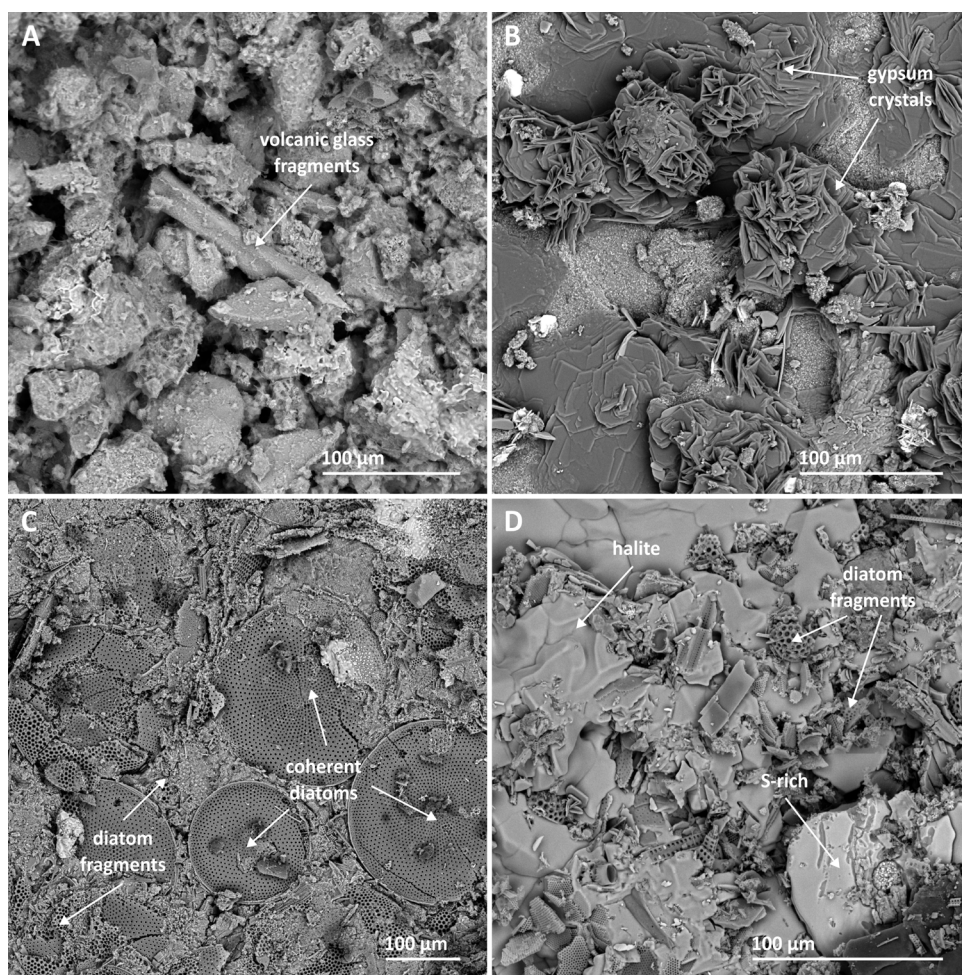


Fig. 12. Backscattered electron images of four of the seven samples taken. **A.** Sample HA-3 from volcanic ash layer +90D showing volcanic glass fragments. **B.** Sample HA-4 from the lower part of the Ølst Formation showing well-developed gypsum crystals. **C.** Sample HA-5 from the Fur Formation showing coherent diatoms and diatom fragments. **D.** Sample HA-7 close to the boundary between the upper part of the Ølst Formation with ash beds and the Fur Formation. The sample shows fragments of diatoms as well as S-rich secondary deposits.

interval appears in the cross plots characterised by elevated Ti varying between 0.5 and 2 wt.%. These outlying data points correspond to a transition into the group of data points belonging to the upper part of the Ølst Formation.

The data points positioned in the upper part of the Ølst Formation appear more scattered and follow no certain type of correlation except in the Ca-Ti cross plot, where most of the data points arguably follow a positive linear trend (Fig. 11d). The most important characteristic is the enrichment in the Ti content; however, the responding contents of the elements vary. The upper part of the Ølst Formation is enriched in Al as well as Fe and Ca (Fig. 11a and Fig. 11c, d). Si decreases in concentration, as the Ti content increases (Fig. 11b). A few data points belonging to the lower part of the Ølst Formation display Ti contents around 1.5 wt.%.

SEM-EDS and μ -XRF results

Common for nearly all samples is the presence of halite (NaCl), which is evident on both the electron im-

ages and μ -XRF area scans. However, sample HA-4 appears not to be influenced by the salt. The halite is believed to be a result of the pore water evaporating from the core during storage. Supplementary descriptions and pictures of the SEM-EDS and μ -XRF results can be found in supplementary file B.

Upper part of the Ølst Formation

Under the SEM, the volcanic ash beds +118 (191.12 m b.s.) and +90D (192.90 m b.s.) (samples HA-2 and HA-3, respectively) show chaotic distributions of volcanic glass fragments characterised by conchoidal fracture planes. The fragments vary in grain size between very fine- and fine-grained sand, and the samples show an overall porous texture (Fig. 12A). Based on the μ -XRF area scans, the volcanic ash shows elevated contents of SiO_2 , Al_2O_3 , Fe_2O_3 , and TiO_2 . In layer +118 (HA-2), both CaO and MgO are relatively low compared to layer +90D (HA-3). Besides halite, both ash beds also exhibit phases elevated in S indicating the presence of secondary phases (Fig. 13B).

Sample HA-1, which is taken from a clay layer next

to +118 (191.27 m b.s.), exhibits a lighter and darker phase of which the latter is adjacent to the ash layer. Under the SEM, the sample surface is clearly dominated by halite, however, in the gaps the material consists of unorganized fragments with a plated texture. While the lighter phase of the sample is dominated by halite, the μ -XRF area scan reveals elevated contents of SiO_2 , Al_2O_3 , Fe_2O_3 , and TiO_2 in the darker phase. However, it also exhibits individual phases consisting almost entirely of SO_3 and CaO , suggesting the occurrence of gypsum (Fig. 13A).

Fur Formation

Three samples (HA-5-7) were taken from the Fur Formation at different depths. HA-7, which is taken close to the boundary between the Fur Formation and the upper part of the Ølst Formation (196.79 m b.s.), is chosen based on the peaks seen in the Ca/Si and S/Si depth profiles, which could indicate secondary deposits. The SEM reveals a fragmented matrix

consisting of diatoms. In between the diatom fragments, secondary occurrences are present rich in S (Fig. 12D). Samples HA-5 and HA-6 are taken to represent 'clean' diatomite (207.82 and 208.98 m b.s., respectively). Under the SEM, circular coherent diatoms are more frequent (Fig. 12C). The diatomite matrix for all three samples is well defined by the μ -XRF area scans by a high SiO_2 content (Fig. 13D). The secondary phases consist mostly of equal amounts of CaO and SO_3 indicating gypsum, while others are dominated by either Ca or S (Figs 13D-E). HA-7 is more elevated in Fe compared to HA-5 and HA-6.

Lower part of the Ølst Formation

Sample HA-4 originates from the lower part of the Ølst Formation, where volcanic ash beds are very limited (220.24 m b.s.). The SEM has revealed distinct rose-shaped crystals throughout the sample surface, a well-known characteristic for gypsum crystals (Fig. 12B; Ralph *et al.* 2025). The matrix of the sample is more compact compared to the clay layer in sample HA-1

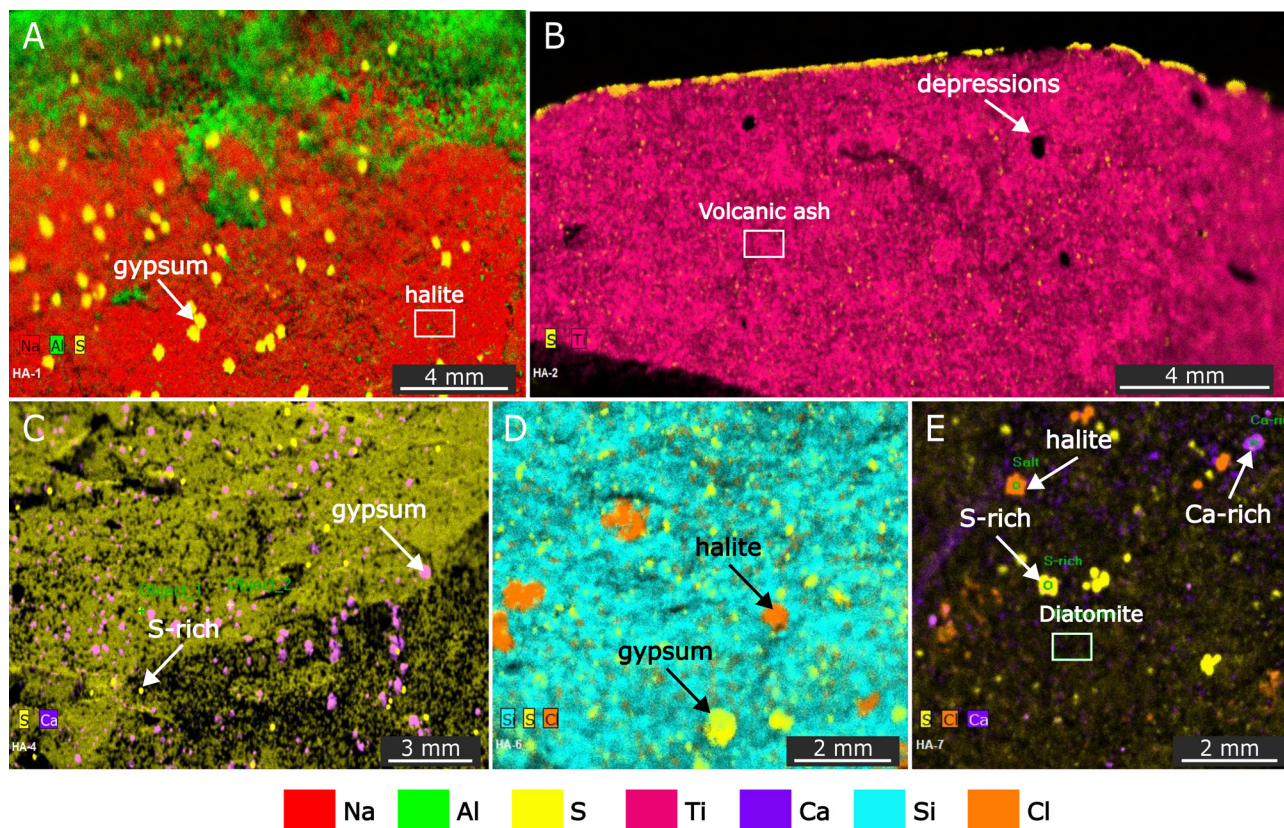


Fig. 13. μ -XRF area scans of five of the seven samples taken. **A.** Sample HA-1 from a clay layer in between ash beds in the upper part of the Ølst Formation. The area scan reveals gypsum occurrences in the pore spaces of the sample. **B.** Sample HA-2 from volcanic ash layer +118. While the area scan shows elevated concentrations of Ti, it also reveals secondary deposits rich in S. **C.** Sample HA-4 from the lower part of the Ølst formation. S dominates the sample, confirming the occurrences of pyrite and gypsum. **D, E.** Samples HA-6 and HA-7 from the Fur Formation. Among the diatom matrix secondary deposits like gypsum and halite are present.

and show very low porosity. The μ -XRF area scan reveals that the sample contains little SiO_2 and is dominated by S, Fe_2O_3 , Al_2O_3 and Na_2O (Fig. 13C). Smaller phases equally rich in CaO and SO_3 confirm the presence of the gypsum crystals, while other phases contain mostly S. The high contents of S and Fe indicate that the presence of pyrite dominates the sample.

Discussion

Geochemical proxy for volcanic ash

The depth profile of Ti shows the most distinct geochemical trends for the normalised XRF data, separating the upper part of the Ølst Formation with volcanic ash from the rest of the core section. The PCA and cross plots have further supported the distinction of the upper part of the Ølst Formation with volcanic ash from the Fur Formation and lower part of the Ølst Formation. Ti is well known to be incorporated in marine sediments (Calvert & Pedersen 2007), and it is therefore essential to determine whether the elevation in Ti is a consequence of a change in clay mineral assemblage or caused by the volcanic ash beds. This can be accomplished by calculating enrichment factors (EF) of Ti. The enrichment factors will be based on Al ratios of the XRF measurements with reference to the average composition of deep-sea sediment (Eq. 3) (Turekian & Wedepohl 1961; Taylor & McLennan 2003; Calvert & Pedersen 2007).

$$EF(Ti) = \frac{\frac{Ti}{Al}}{\frac{Ti_{ref}}{Al_{ref}}} \quad (3)$$

Depth variations of the estimated EFs of chosen elements have been calculated in this study (Fig. 14). The EF(Ti) profile shows enrichment of greater than seven times relative to the average pelagic sediment. This high enrichment of Ti coincides with the upper part of the Ølst Formation containing volcanic ash beds, which clearly indicates that the enrichment in Ti is due to the presence of volcanic ash rather than normal sedimentary processes. Titanium is known to be a conservative, lithophilic element, which is relatively immobile in surface environments due to the 4+ valence (Winchester & Floyd 1977; MacLean & Barrett 1993).

The geochemical compositions of the volcanic ash beds also need to be considered, as the origins of the individual beds are related to different stages of volcanism (Pedersen *et al.* 1975; Morton & Evans 1988; Morton & Knox 1990; Larsen *et al.* 1999; Larsen *et al.* 2003; Stokke *et al.* 2020; Stokke *et al.* 2021; Jones *et al.* 2023). The ash beds of the positive series are especial-

ly known to differ from the older beds of the negative series. Besides a few beds of rhyolitic composition, the positive series mainly consists of ferrobasalts with a Fe-Ti-rich tholeiitic composition (Larsen *et al.* 2003) reflected in our data by the elevated concentrations in Ti in the top of the core section, where the ash beds of the positive series are situated. The ash beds of the negative series have widely different compositions (trachyte, rhyolite and alkaline basalts) and are often heavily altered, based on the amount of volatile contents present (Larsen *et al.* 2003). Since the Ti concentrations in the negative series are generally low compared to the positive series due to Ti fractionation, Ti is not necessarily the best indicator for identifying the older ash beds.

The presence of divalent cations in the Harre borehole

The most important factor for the possibility of carbon mineralisation is the presence of free divalent cations (Ca^{2+} , Mg^{2+} , Fe^{2+}) necessary for reacting with dissolved CO_2 (carbonic acid) and precipitating carbonate minerals (Snæbjörnsdóttir *et al.* 2020). Contrary to Ti, which is a relatively immobile element, divalent cations can be leached out of the ash due to alteration processes (Pedersen & Buchardt 1996; Larsen *et al.* 2003; Longman *et al.* 2021). Compared to the Fur Formation, where the ash beds are known to be well-preserved in diatomite, the same ash beds are recognized as heavily altered in the clay-rich Balder and Sele formations from the North Sea as well as in the onshore Ølst Formation of equal age (Heilmann-Clausen *et al.* 1985; Huggett 1993). Since the volcanic ash beds are mostly situated within a clay interval equal to the Ølst Formation in the Harre borehole, there is a possibility that the beds have undergone alteration in contrast to the well-preserved ash beds imbedded in diatomite farther north (Güven & Grim 1978; Pedersen *et al.* 2011). It is therefore crucial to determine whether the divalent cations are still present or have been leached out of the subsurface volcanic ash beds.

Magnesium measurements have proved unsuitable for evaluating the presence of divalent cations in the Harre drill core, as most of the measured concentrations were below the detection limit (supplementary file A). Calcium is an important cation in terms of carbon mineralisation, and the enrichment of Ca in the upper part of the Ølst Formation is therefore a key piece of information for further development of a potential carbon mineralisation facility in the area. The depth variations of Ca and Fe both show a gradual increase in the upper part of the Ølst Formation similar to Ti normalised to S, which suggests that the increase of Ca and Fe in the uppermost part

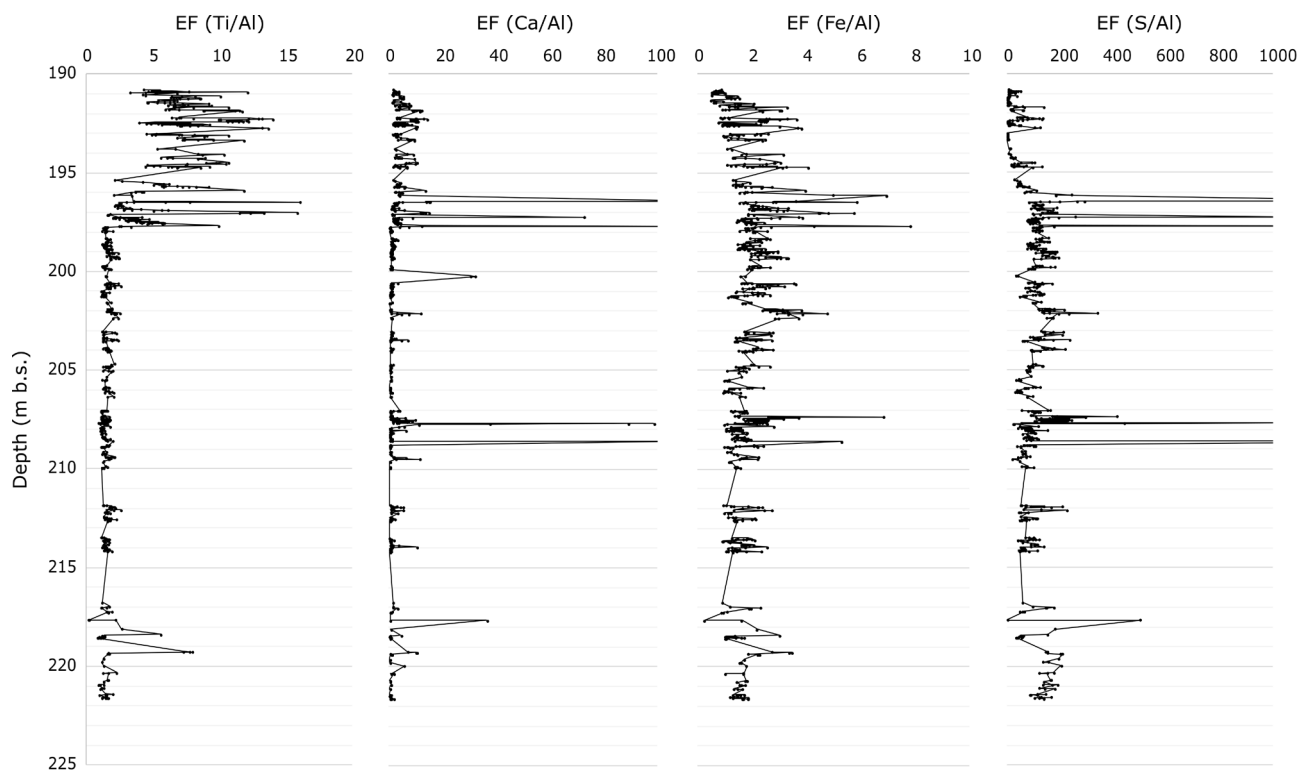


Fig. 14. Chosen Enrichment Factors (EF) based on chosen Al ratios. The reference values used for the EF calculations are based on the elemental concentrations in pelagic sediments from Taylor & McLennan (2003). The most significant enrichments are seen in Ti and Ca, which are mostly limited to the ash-containing interval in the top of the core section.

of the Ølst Formation is related to non-diagenetic deposits, likely associated with volcanic ash. Despite the extreme enrichments of Ca associated with the gypsum horizons within the Fur Formation, the ratio is more uniformly enriched in the upper part of the Ølst Formation with volcanic ash. This is not the case for the lower part of the Ølst Formation, where the enrichment is limited (Fig. 14). The enrichment seen in the upper part of the Ølst Formation therefore indicates the influence of Ca in the volcanic ash. The EF(Fe) shows an overall increasing trend towards the top of the core section; however, it is difficult to assign the enrichment to any specific phases as the pattern fluctuates significantly. Since Fe is a common constituent in clay-rich sediments as well as in diagenetic phases like pyrite, this may influence on the general Fe trends (Stucki 2013). HH-XRF determines total Fe, and therefore it is uncertain which oxidation level defines the present Fe in the core.

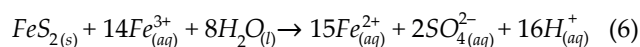
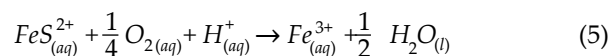
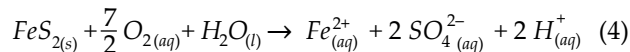
Gypsum deposits – potential mapping of Ca mobility

Gypsum and pyrite are commonly found in outcrops of the Fur Formation and the underlying Stolleklint Clay (Pedersen *et al.* 1975; Pedersen 2008; Pedersen *et al.* 2011). In the Harre borehole, this is the case as

well. Especially gypsum has been found throughout the analysed core section, which is best demonstrated by the SEM-EDS and μ -XRF data. The gypsum found in most of the samples are visible on the μ -XRF area scans, while sample HA-4 from the lower part of the Ølst Formation clearly illustrates coherent gypsum crystals with SEM-EDS (Fig. 12B). The occurrences of gypsum reflect the mobility of Ca within the present Ash Series and is further discussed in the text below.

Pyrite oxidation

Studies of diatomite outcrops on the island of Fur indicate that gypsum deposits can be explained by the oxidation of pyrite (Pedersen *et al.* 1975; Pedersen 2008). Above the redox level, pyrite is oxidized primarily by O_2 , producing sulphate ions (SO_4^{2-} ; Eq. 4–6; Moses & Herman 1991; Chandra & Gerson 2010). This leads to the precipitation of minerals such as jarosite ($KFe_3(SO_4)_2(OH)_6$) and gypsum ($CaSO_4 \cdot 2 H_2O$; Pedersen 2008).



For the sulphate ions to precipitate as gypsum, Ca^{2+} ions need to be available, which is happening naturally by the weathering and alteration of Ca bearing phases (Berner *et al.* 1983; Berner 1999, 2004). A possible source of Ca in the Harre core could be the volcanic ash beds. The altered ash beds found in the clay-rich formations in the North Sea and in the onshore Ølst Formation lead to the suspicion that the volcanic ash in the Harre core might have experienced alteration as well, given that they are mostly situated in clay instead of diatomite. It is, however, evident from earlier studies of the volcanic ash beds within the Harre core that many of them remain unaltered (Hansen 2018). Additionally, the Ca participating in the formation of calcareous concretions in the Fur Formation has partly been attributed to blooms of calcareous plankton, dissolution of skeletal material from fish and invertebrates, and volcanic dust dispersed in the diatomite (Pedersen & Buchardt 1996). The above-mentioned serve as additional possible sources of Ca for the precipitation of gypsum and more likely, as they are more abundant than the ash.

Sample HA-4 comes from the lower part of the Ølst Formation. This interval shows high content of pyrite and organic matter, resulting in a relatively high gamma ray signal, and can be attributed to the Stolleklint Clay (Nielsen *et al.* 1994; Heilmann-Clausen 1995; Schiøler *et al.* 2007). The results of the SEM-EDS and μ -XRF analyses of sample HA-4 reveal high contents of both pyrite and gypsum. We suggest that the gypsum occurrences seen throughout the Harre core, and particularly in sample HA-4, are a result of pyrite oxidation occurring in the lower part of the Ølst Formation. From there, it is possible that the released sulphate ions have been transported by the formation fluid farther up in the stratigraphy due to the high porosity of the diatomite (~70%; Pedersen *et al.* 2011).

The older volcanic ash beds (–28 to –34) present at the bottom of the Fur Formation are also of basaltic origin, however heavily altered and less enriched in TiO_2 , K_2O , and P_2O_5 compared to the younger ferro-basaltic beds in the upper part of the Ølst Formation (Larsen *et al.* 2003). It is possible that the Ca has leached out of the older ash beds and thereby contributing to the precipitation of gypsum as well, which will be discussed below.

Potential leaching and mineralisation of Ca

The relatively low S content in the upper part of the Ølst Formation shows a trend of significant meaning. The EF(S) profile indicates depletion in S in this interval compared to the average pelagic sediment (Fig. 14). This could indicate that the precipitation front of gypsum has not yet reached the top interval with the

volcanic ash beds. This is further supported by the SEM-EDS and μ -XRF findings, where halite is clearly dominating the pore spaces.

The positioning of positive peaks between 196 and 198 m b.s. in the Ca and S profiles, as well as their respective Si normalisation profiles occur between the peaks seen in the Ti/Si profile (Fig. 15). Some of the volcanic ash beds in this interval (–11 to –13) are known to exhibit similar geochemical trends to the ash beds of the positive series above, however, more enriched in Si and Ti (Larsen *et al.* 2003). This could explain the peaks seen in the Ti normalisations from this interval. The peaks in the S/Si and Ca/Si ratios as well as in the EF(Ca) and EF(S) located in between the Ti peaks could therefore indicate the leaching and reprecipitation of Ca from the surrounding volcanic ash beds.

Pyrolysis analysis has further revealed the presence of mineral-stored carbon, suggesting that carbonates have formed. This is especially the case for the ash bearing interval in the upper part of the Ølst Formation, which exhibits mineral carbon fractions above 35% of the total carbon contents (Fig. 9). These results provide strong evidence for past mineralisation within the volcanic ash. The potential leaching of Ca from the volcanic ash could be of concern for the potential of carbon mineralisation. The Ca^{2+} is considered one of the important cations for the mineralisation of CO_2 , and it is therefore crucial that as much Ca as possible remains available. Though the established gypsum occurrences show evidence of leaching of Ca, it is also obvious that the Ca content remains high among the volcanic ash beds in the top relative to the rest of the core section (Fig. 16). It is also important to address that the total carbon content measured throughout the core section is low (Fig. 9). Especially in the ash bearing interval in the upper part of the Ølst Formation, the TOC content is relatively low due to dilution by siliciclastic volcanic materials. These findings suggest that a significant potential for further mineralisation remains, despite the findings of past mineralisation in the ash.

It is equally important to consider the fact that the core sections have been stored for many years and dried out completely. During storage, it is likely that most of the pyrite present in the core has been oxidized and reprecipitated as gypsum over time. Additionally, the previous studies of the Harre drill core by Nielsen *et al.* (1994) report no occurrences of gypsum in the ash-bearing interval from the fresh core samples. It is therefore likely that most of the gypsum precipitated during storage of the core.

Since the HH-XRF measurement error of the S standard is high (33%), there is a risk of over interpreting the elevated peaks in the S depth profile. However, the Ca standard HH-XRF measurements show a relatively low measurement error (precision=7%).

Since the Ca depth profile shows the same trends as in S, it is evident that the peaks are not simply errors in the handling of the HH-XRF instrument. As the average Ca concentration of the used standard was unavailable, it is difficult to estimate the accuracy of the HH-XRF measurements. It is emphasized that the geochemical data presented in this study were created to provide an overview of the distribution of elements and compounds throughout the analysed core sections. They should therefore not be considered presentable of the actual quantities of Ca, especially regarding the volcanic ash beds. In the future, it will be crucial to examine the amount of free divalent cations in the volcanic ash to provide a better estimate of the quantity of CO₂ that can be stored through carbon mineralisation in the region.

Implications – carbon storage potential of the ash beds

Based on the results of this study, the ash beds show a large potential for carbon mineralisation. The ash beds are closely spaced in the top 5 m of the analysed core interval, which therefore defines the main target zone for the process to take place. A reservoir of this

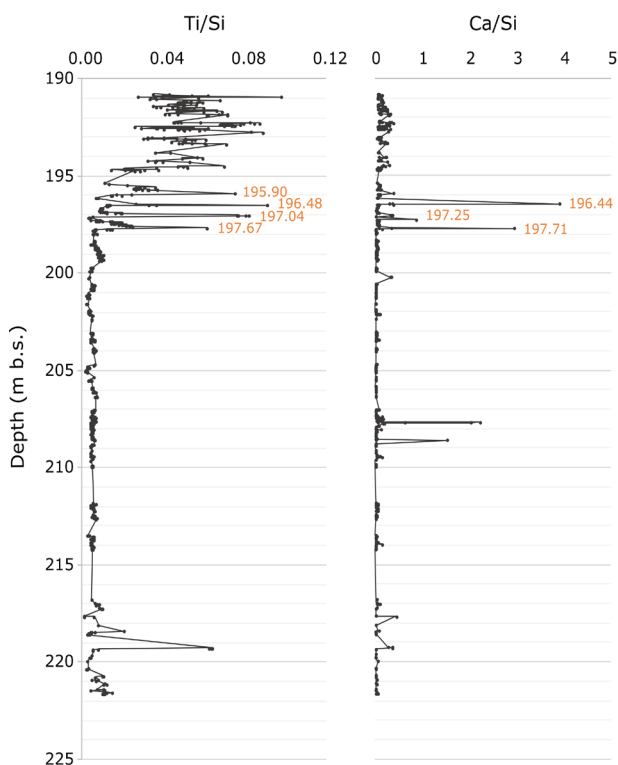


Fig. 15. Ti/Si and Ca/Si depth profiles. The depths of the elevated ratios between 196 and 198 m b.s. in both profiles are provided. It is evident from the depth points that the peaks in Ca/Si are situated in between the peaks in Ti/Si, suggesting leaching and redeposition of Ca as gypsum.

thickness with widespread geographical coverage in a large area in Jylland has significant mineralisation potential. The vision of the C-ASH project is to utilise the large geographical coverage of the ash beds to connect distributed local sources of CO₂ from smaller capture facilities like biogas. Thereby a larger number of CO₂ sources may potentially be directly integrated with mineralisation in the future. The fact that

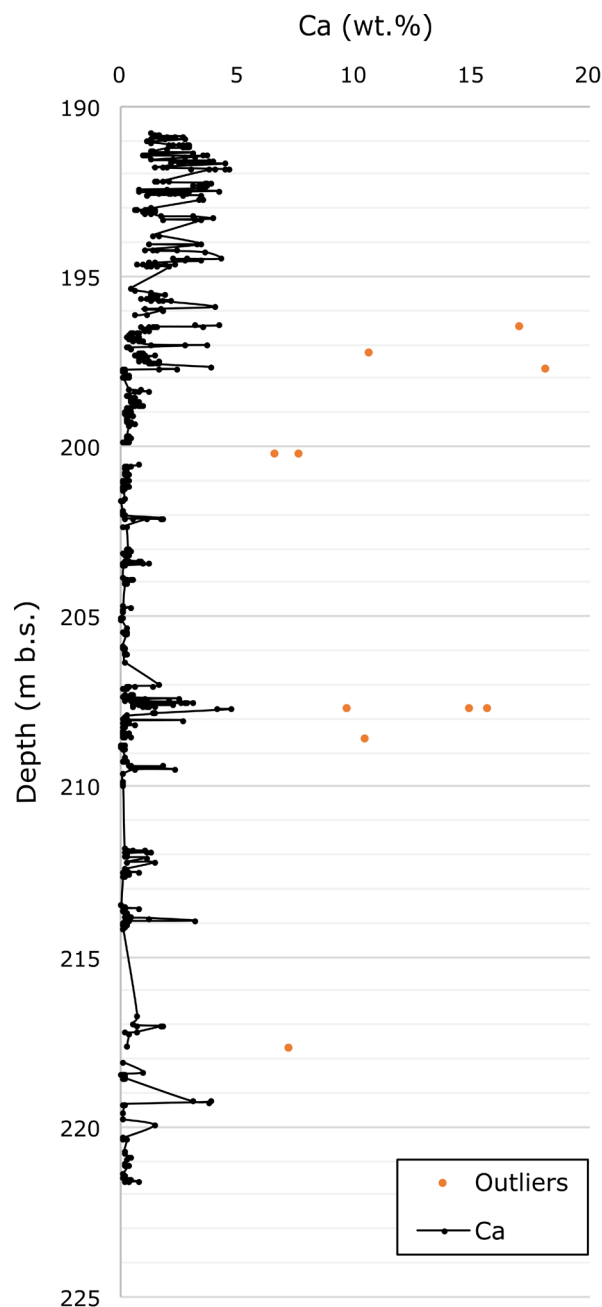


Fig. 16. Profile showing the distribution of Ca throughout the core section. Outliers identified as gypsum are presented with orange dots to better illustrate the increase of Ca associated with volcanic ash in the upper part of the Ølst Formation. The error bars are smaller than the symbols. The precision for Ca is 7%.

the ash beds are more closely packed in the Harre borehole compared to the outcrops on Fur could prove to be advantageous, as a more focused target zone may support more efficient water flow and mineralization. The results of this study show that the Ti-Fe basalts situated in the target zone clearly have a higher content of Ca compared to the rest of the ash beds, making the target zone even more suitable for carbon mineralisation. The analysed ash beds (+90D and +118) furthermore exhibit low degrees of weathering, even though they are situated in clay instead of diatomite. However, important questions related to the hydrological properties of the target zone remain to be answered, which requires further studies regarding the permeability and porosity of the sediments and ash.

Conclusion

Through the selected geochemical analyses of the core section, Ti has proven to be the best elemental proxy for volcanic ash due to a distinct association with the ash beds of the positive series identified in the core. The high content of the highly conservative element Ti is a signature of the positive series. It is therefore considered a stable indicator of the Ti-Fe basaltic ash beds. The results show that the majority of the present ash beds are situated in the top 5 to 6 m of the core section, where they are interbedding with clay from the Ølst Formation instead of diatomite from the Fur Formation, contrasting to the outcrops seen on the island of Fur. Previous studies of the Harre borehole by Nielsen *et al.* (1994) also revealed an interfingering stratigraphy between the Fur and Ølst formations.

The divalent cation of calcium (Ca^{2+}) is an essential driver of the carbon mineralisation reaction, which is evidently enriched in the uppermost part of the Ølst Formation, associated with volcanic ash from the positive series. However, this study also shows that Ca can be incorporated in authigenic minerals such as carbonates and gypsum. We suggest that these secondary minerals reveal the mobility of Ca and possibly some degree of leaching from the volcanic ash. Based on the results of this study and previous studies, the fraction of secondary minerals is believed to be minimal, as the degree of alteration in the ash layers remains low. The ash layers are therefore still considered highly suitable for carbon sequestration, a key asset for the C-ASH project.

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The stromateiform fish *Parapropercarina multispinata* gen. et sp. nov. from the Eocene Fur Formation of Denmark

ANE ELISE SCHRØDER, TOMÁŠ PŘIKRYL & GIORGIO CARNEVALE



Geological Society of Denmark
<https://2dgd.dk>

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A new stromateiform fish from the earliest Eocene Fur Formation, northwestern Denmark, is described as *Parapropercarina multispinata* gen. et sp. nov. by using non-destructive μ XRF-element mapping and standard comparative osteology. The new genus and species is diagnosed by a distinctive combination of characters: a moderately elongate, laterally compressed body; six branchiostegal rays, a single deeply notched dorsal fin with 15 spines and 18 rays; three supraneurals; anal fin with two or three spines and 24 soft rays; pectoral fin with 18 rays extending posteriorly approximately at the level of the 10th abdominal vertebra; pelvic fin containing one spine and five rays; 36 (15+21) vertebrae; well-developed parapophyses on posterior abdominal vertebrae; caudal skeleton comprising fused hypurals 1+2, partially fused hypurals 3+4, autogenous hypural 5, autogenous parhypural lacking parhypurapophysis, two uroneurals, and three epurals; oral jaw dentition uniserially arranged; body densely covered with thin, cycloid scales. *Parapropercarina multispinata* gen. et sp. nov. thus shows a mosaic of features, that clearly aligns it within the Stromateiformes (Stromateoidei). This new fossil extends the occurrence of a body plan similar to that of propercarinids back to the early Eocene of the eastern North Sea Basin.

Keywords: Stromateiformes, Stromateoidei, Propercarinidae, Nomeidae, North Sea realm.

Ane Elise Schröder [aes@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark; also Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy [aneelise.schröder@unito.it]. <https://orcid.org/0000-0001-9371-400X>. Tomáš Přikryl [prikryl@gli.cas.cz], Department of Paleobiology and Paleocology, Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, 165 00 Praha 6 - Lysolaje, Czech Republic. <https://orcid.org/0000-0002-7939-3622>. Giorgio Carnevale [giorgio.carnevale@unito.it], Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy <http://orcid.org/0000-0002-3433-4127>.

<https://zoobank.org/urn:lsid:zoobank.org:pub:A96AD4C0-A884-4537-836E-4E5C44655AC7>

The Fur Formation of Denmark is an early Eocene (Ypresian) offshore marine deposit within the eastern North Sea Basin. It is a world-famous Konservat-Lagerstätte renowned for the exceptional preservation of delicate organic remains, comprising both terrestrial and marine organisms, such as birds, insects, reptiles, plants, bony fishes, sharks, crustaceans, echinoderms, molluscs, and diatoms (for comprehensive overviews, see Larsson 1975; Homann 1991; Wilmsen 2004; Schultz *et al.* 2011; Kristensen *et al.* 2012;

Karl & Madsen 2012; Pedersen *et al.* 2012; Bourdon *et al.* 2016; Schröder *et al.* 2023a). The diatom-rich sediments and intercalated volcanic ash layers characteristic of the formation have long been recognised as conducive to rapid burial and low-oxygen conditions, which allowed the preservation of remarkable details of both hard and soft tissues and the frequent occurrences of articulated skeletons (e.g. Gren *et al.* 2017; Lindgren *et al.* 2017; Schröder *et al.* 2023b).

The ichthyofauna is notably diverse and in-

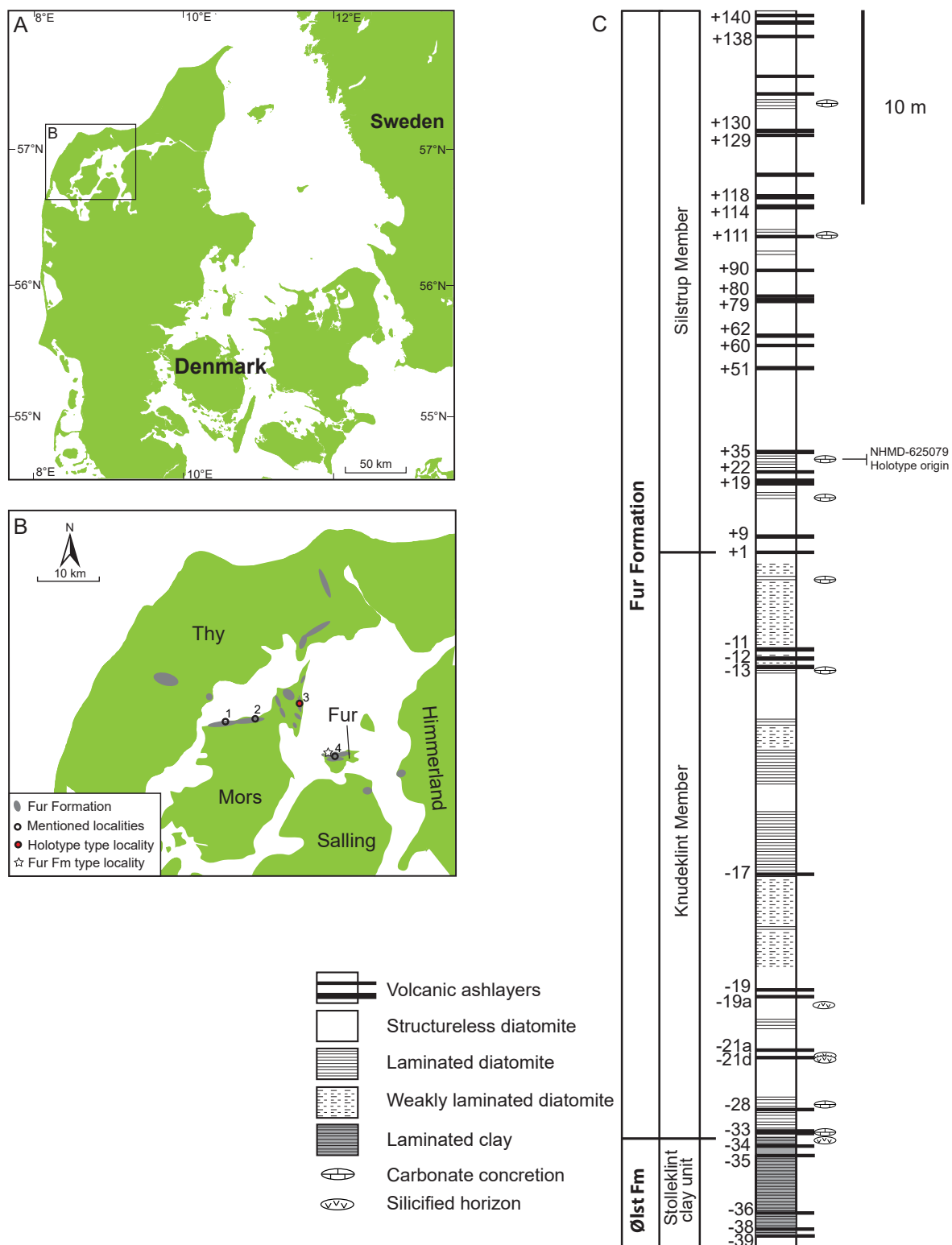


Fig. 1. **A:** Map of Denmark. The western Limfjord area where the Fur Formation is present. **B:** Outcrop localities and near-surface occurrences of the Fur Formation marked in grey. The localities from where the studied specimens originate are marked by circles designated with numbers: 1 = Klitgård Klint (NHMD-1351141); 2 = Bjørneborg (MM-9628); 3 = Ejerslev moclay pit, which is also the type locality of the holotype (NHMD-625079, FUM-N-10535); 4 = Graven at Stendal Høje. 'Graven' refers to the centrally located moclay pit at the locality. The white star indicates the type locality of the Fur Formation. **C:** Sedimentological log comprising the lowermost negative series of the Stolleklint clay unit, and the negative and positive ash series throughout the Fur Formation in northwestern Denmark. The stratigraphic position of the holotype is indicated. Modified from Schröder and Carnevale (2023).

formative for early Eocene vertebrate evolution and diversification. The fish assemblage includes, among others, osteoglossiforms, argentiniforms, polymixiiforms, stromateiforms, zeiforms, lampridiiforms, and syngnathiforms (e.g. Kuhne 1941; Tyler *et al.* 2000; Baciú *et al.* 2005; Bonde 2008; Schröder *et al.* 2022, 2023a, 2025; Schröder & Carnevale 2023, 2025a, 2025b), with bony fishes being the most abundant group of macrofossils. The fish assemblage exhibits a broad ecological spectrum, ranging from pelagic to demersal taxa, and provides a valuable high-latitude complement to the otherwise better-known, broadly coeval Tethyan faunas. In addition to their taxonomic breadth, the bony fishes of the Fur Formation preserve anatomical details that illuminate functional morphology, trophic strategies, and patterns of early Eocene teleost diversification.

Among the acanthomorph contingent, several stromateiforms have been recognised in Danish museums' collections by one of us (AES). The oldest known stromateiform fish, based on skeletal remains, was described by Schröder *et al.* (2023a), and it is now accompanied by material reminiscent of the extinct stromateiform family Propercarinidae. The presence of a fish reminiscent of the propercarinids in the Fur Formation is significant because members of this stromateiform group are relatively rare in the fossil record, and their occurrences were previously restricted to the Oligocene deposits of the Paratethys. The material from Denmark thus provides an opportunity to reassess stromateiform diversity in the early Eocene.

The aim of the present paper is to 1) describe a new genus and species of stromateiform fish, *Parapropercarina multispinata* gen. et sp. nov., based on material housed in three natural history museums' collections in Denmark, and 2) discuss the potential systematic affinities of these propercarinid-like stromateiform remains from the earliest Eocene Fur Formation of Denmark.

Geological setting

The exposed formation localities and near surface occurrences of the earliest Eocene Fur Formation cover the region from the western part of Himmerland to the northern part of Salling, the islands of Fur and Mors, to the area of Thy (Fig. 1A). The Fur Formation is particularly exposed on Fur and Mors, and the sites include coastal cliff exposures and old digging

pits around the two islands (Fig. 1B). It comprises a 60 m thick fossil-rich, marine diatomite, interbedded with ca. 180 and up to 200 ash layers (Bøggild 1918; Pedersen & Surlyk 1983) originating from the volcanic activity triggered by the opening of the North-east Atlantic (e.g. Storey *et al.* 2007). The ash layer sequences were separated into a numbered negative and a numbered positive series by Bøggild (1918). The Knudeklint Member encompasses the negative sequence, and the Silstrup Member reflect the positive sequence. Later officially recognised ash layers have been assigned letters together with the original ash layer number (Fig. 1C, see also Pedersen & Surlyk 1983; Larsen *et al.* 2003). Calcareous carbonate concretions are present in certain horizons of the formation (Fig. 1C). They formed immediately below the sea-floor surface by precipitation of calcite before compaction of the surrounding sediment, commonly forming and growing around remains of dead organisms.

The Fur Formation largely replaces the Ølst Formation in this area of Denmark. Just the lowermost part of the Haslund Member, the Stolleklint clay unit, is exposed in the area. The section comprising ash layers around -39 to -34 belongs to this unit (Heilmann-Clausen *et al.* 1985; Heilmann-Clausen 1995). Radiometric dating of ash layers -17 and +19 of the Fur Formation, yielded $^{39}\text{Ar}/^{40}\text{Ar}$ age determinations of ~55.6 Ma and ~54.4 Ma, respectively (Westerhold *et al.* 2009). The Paleogene–Eocene boundary (P/E) is furthermore evident in the Stolleklint clay unit, based on the onset of the CIE (e.g. Heilmann-Clausen & Schmitz 2000; Schmitz *et al.* 2004; Stokke *et al.* 2020, 2021).

Material and methods

This study is based on material collected from the Ypresian, earliest Eocene, Fur Formation in north-western Denmark. The fossil specimens have been collected at outcrop localities exposed on the islands of Mors and Fur in the western Limfjord area. The fossils are repositied in three Danish museums, namely the collections of Fur Museum and Museum Mors in northern Denmark, and in the Vertebrate palaeontology and Danekræ collections, respectively, of the Natural History Museum of Denmark. The holotype, NHMD-625079 (designated herein), was declared Danekræ fossil trope in 2008 (fossil trope no. DK-540) and thus kept in the Danekræ collection.

For an overview of the unique Danekræ fossil trove legislation pertaining to Denmark, see Schröder *et al.* (2022) and Consolidated Act on Museums (2006).

All specimens were subjected to non-destructive μ XRF-element mapping following the procedures of Schröder and Carnevale (2023), applying a Bruker M4 Tornado Plus Amics at the Department of Geosciences and Natural Resource Management, Copenhagen University. The benchtop device was set to a maximum acceleration of 50 kV and an anode current of either 250 or 600 μ A. The specimens were furthermore studied by conventional methods, using a Leica M80 equipped with a camera lucida drawing arm and by a Leica MZ75. Measurements were obtained on high-resolution specimen photos, applying ImageJ (Rasband 2018). Mapping of strontium and phosphorous reveals anatomical details of the body morphology not accessible by conventional methods; the strontium map exposes the intricate details of the body skeleton counting minute bone structures and skeletal parts hidden by scales on the fossils, whereas phosphorous commonly exposes and greatly enhances less strongly ossified or soft tissue elements, including soft rays and scales – even scales that may not be visible on the physical fossils (see also Schröder *et al.* 2023b). The strontium maps were also directly applied for the interpretative reconstruction drawings along with the fossils.

Institutional abbreviations: FUM-N, Fur Museum, a division of Museum Salling; MM, Fossil and Moclavey Museum, Museum Mors; NHMD, Natural History Museum of Denmark; DK, specimens declared Danekræ fossil trove, and kept in the Danekræ collection of the Natural History Museum of Denmark, University of Copenhagen.

Anatomical abbreviations: aa = anguloarticular; br = branchiostegal rays; cc = compound centrum; cl = cleithrum; co = coracoid; dn = dentary; ect = ectopterygoid; endt = endopterygoid; ep = epural; ffn = foramen of the facialis nerve; fr = frontal; hspu = hae-

mal spine of preural; hyo = hyomandibula; hyp = hypural; le = lateral ethmoid; mtp = metapterygoid; mx = maxilla; ns = neural spine; op = opercle; pal = palatine; par = parietal; pas = parasphenoid; per = pectoral-fin radials; pcl = postcleithrum; phy = parhypural; pmx = premaxilla; pop = preopercle; ptm = posttemporal; pu = preural vertebra; qu = quadrate; ra = retroarticular; sc = scapula; scl = supracleithrum; scos = sclerotic ossicle; smx = supramaxilla; sn = supraneural; sph = sphenotic; soc = supraoccipital; sop = subopercle; sym = symplectic; uh = urohyal; un = uroneural

Morphometric abbreviations: AFB = anal-fin base; CPD = caudal peduncle depth; CPL = caudal peduncle length; DFB = dorsal-fin base; HD = head depth; HL = head length; MBD = maximum body depth; OD = orbit diameter (measured horizontally); PAD = preanal distance; PDD = predorsal distance; POD = preorbital distance; SL = standard length.

Systematic palaeontology

Division Percomorphacea *sensu* Wiley & Johnson, 2010

Order Stromateiformes *sensu* Pastana, Johnson & Datovo, 2022

Suborder Stromateoidei *sensu* Pastana, Johnson & Datovo, 2022

Genus *Parapropercarina* gen. nov.

Type species. *Parapropercarina multispinata* gen. et sp. nov. NHMD-625079A+B

Etymology. The name is derived from the prefix ‘para’ (from Greek ‘παρά’) meaning ‘beside’, ‘at’, ‘together’, ‘alongside’, ‘against’ or ‘through’, and the generic name ‘*Propercarina*’, due to the numerous characteristics shared between the two genera.

Table 1. Type series, referred material and relevant collection data

Catalogue number	Type status	Formation	Member	Lithology	Ash-series	Locality
FUM-N-16161A+B	Paratype, p+cp	Fur Fm	Knudeklint?	Soft diatomite, laminated	N/A	Graven at Stendal Høje, Fur
FUM-N-10535	Paratype	Fur Fm	N/A	Carbonate concretion	N/A	Ejerslev moclavey pit, Mors
FUM-N-17356	Paratype	Fur Fm	N/A	Carbonate concretion	N/A	Fur, no specific locality
NHMD-625079A+B (DK-540)	Holotype, p+cp	Fur Fm	Silstrup	Carbonate concretion	+26 or +27	Ejerslev moclavey pit, Mors
NHMD-1351141	Referred specimen p+cp	Fur Fm	N/A	Carbonate concretion	N/A	Klitgård Klint, Mors
MM-9628	Referred specimen	Fur Fm	Silstrup	Carbonate concretion	+25 to +30	Bjørneborg, Mors

p = part, cp = counterpart

Stratigraphic and geographic range. Ypresian (earliest Eocene), Fur Formation, northwestern Denmark (Fig. 1).

Diagnosis. Stromateoid genus unique in having the following combination of characters: body moderately elongate; jaws with strong conical, uniserially arranged teeth; six branchiostegal rays; sclerotic ossicles present; ventral limb of preopercle with small, short spines; a single dorsal fin with a deep notch, long-based (~42% of SL) with 15 spines and 18 soft rays; three supraneurals, predorsal formula 0/0+0/2/1; anal fin with two or three spines and 24 rays; caudal fin forked with 17 (I,8+7,I) principal rays; procurent spur absent; pectoral fin with 18 relatively long rays, reaching approximately the 10th abdominal vertebra; pelvic fin with a single spine and five rays; 36 vertebrae (15+21); posterior abdominal vertebrae bearing well-developed parapophyses; caudal-fin skeleton with fused hypurals 1 and 2, and partially fused hypurals 3 and 4, autogenous hypural 5, autogenous parhypural, parhypurapophysis absent, two uroneurals, and three epurals; cycloid scales thin, covering nearly the entire body.

***Parapropercarina multispinata* sp. nov.**

Figs 2, 3, 4, 5, 6, 7, 8, 9, Tables 1–2

2011 Fish of unknown affinity, Schultz *et al.*, p. 75, fig. 15A

Holotype. NHMD-625079. Well-preserved and nearly complete articulated skeleton preserved in a carbonate concretion, in part (A) and counterpart (B), 70.1 mm SL. (Fig. 2). The specimen has not been prepared with or coated by protective chemical substances.

Etymology. The name is derived from the Latin words ‘multi’ meaning many and ‘spina’ meaning spine, due to the notable high number of spines in the dorsal fin.

Type locality of holotype. Fur Formation, lowermost Eocene. Collected from the Ejerslev moclay pit locality, northern part of the island of Mors, northwestern Limfjord area, Denmark (Fig. 1A–B). The stratigraphic level is around ash layer +26 or +27 (Fig. 1C).

Paratypes. FUM-N-16161A+B, well-preserved superficial three-dimensional impression in soft diatomite, in part and counterpart, 49.7 mm SL. The impression of the part (FUM-N-16161A) is nearly complete, whereas the area of the head anterior and ventral to the orbit is missing in the counterpart (FUM-N-16161B). The anal fin is also missing; FUM-N-10535, preserved in a single slab of carbonate concretion. Nearly the entire head is missing, but other characters, particularly those related to the squamation pattern, including the intricate organisation of different scale types, are preserved. The lateral-line scales are also evident in this specimen; FUM-17356, well-preserved nearly complete articulated skeleton in a single slab of carbonate concretion, 60.5 mm SL. The Sr-map of this specimen suggests it has undergone some kind of chemical preparation – however, the specimen is an old find and data to conclusively confirm this is not available (Fig. 3).

Referred material. NHMD-1351141, incompletely preserved specimen, in part and counterpart; MM-9628, moderately preserved specimen, missing major parts of the median fins, scales and the epaxial part of the caudal-fin skeleton (Fig. 4).

Table 2. Synopses of morphometric values of *Parapropercarina multispinata* gen. et sp. nov.

Morphometric characters	Holotype NHMD-625079			Paratype FUM-N-16161			Paratype FUM-N-17536		
	Measurements (mm)	% of SL	% of HL	Measurements (mm)	% of SL	% of HL	Measurements (mm)	% of SL	% of HL
SL	70.1	–	–	49.7	–	–	60.5	–	–
HL	22.0	31.4	–	14.1	28.4	–	16.3	26.9	–
HD	18.1	25.8	82.3	11.9	23.9	84.4	14.3	23.6	87.7
POD	5.9	8.4	26.8	3.9	7.8	27.7	4.7	7.8	28.8
OD	4.9	7.0	22.3	3.6	7.2	25.5	4.3	7.1	26.4
MBD	19.6	28.0	–	11.2	22.5	–	15.1	25.0	–
DFB	28.9	41.2	–	20.7	41.6	–	23.3	38.5	–
AFB	16.1	23.0	–	12.2	24.5	–	13.8	22.8	–
CPL	11.6	16.5	–	7.5	15.1	–	10.2	16.9	–
CPD	6.3	9.0	–	3.9	7.8	–	5.6	9.3	–
PDD	26.8	38.2	–	17.4	35.0	–	23.5	38.8	–
PAD	44.3	63.2	–	30.7	61.8	–	36.7	60.7	–

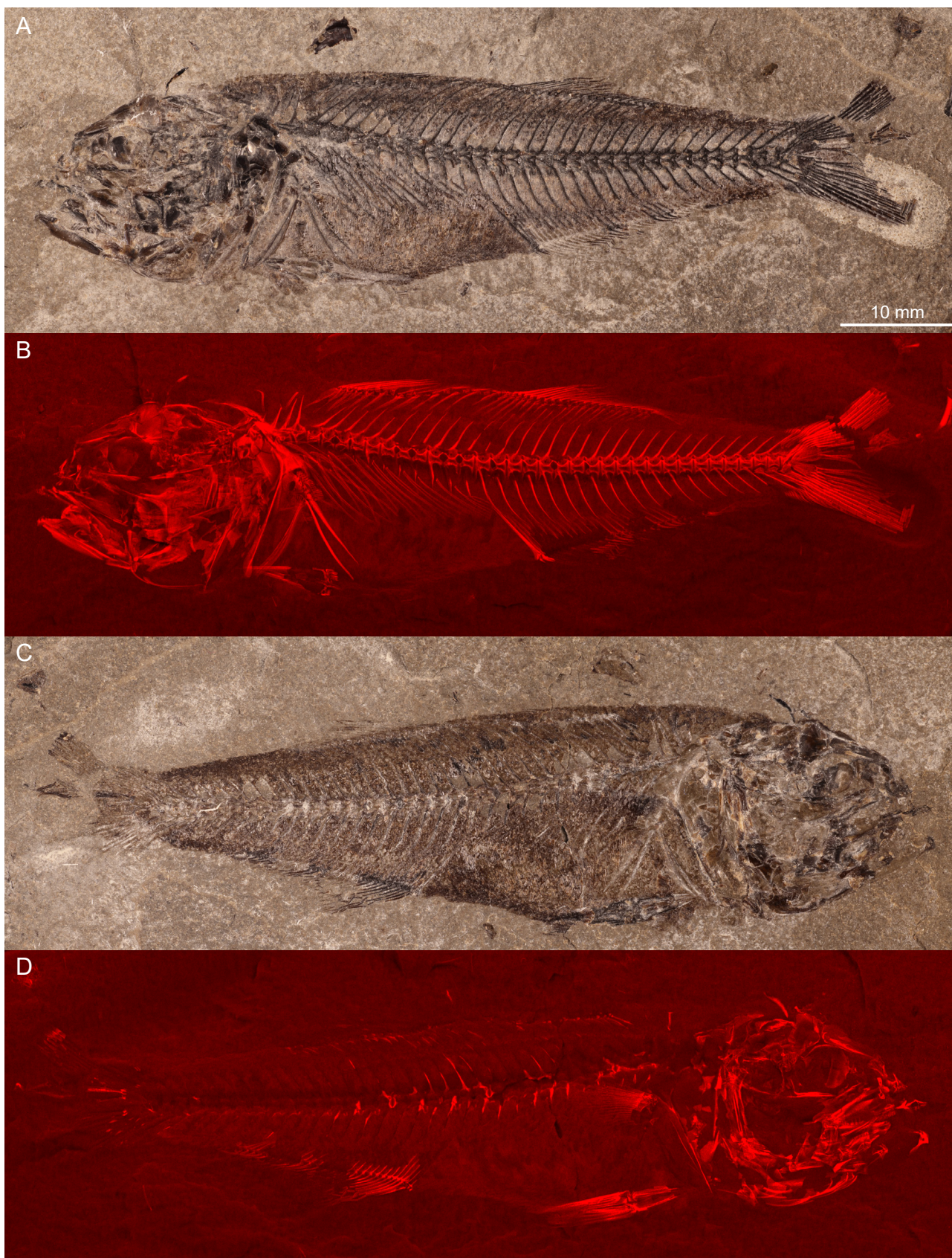


Fig. 2. *Parapropercarina multispinata* gen. et sp. nov., holotype NHMD-625079 (DK-540). A–D: High-resolution photo images and strontium element maps, respectively, of the holotypic part (A–B, NHMD-625079A) and counterpart (C–D, NHMD-625079B). Note particularly the rounded vertebral foramen, located slightly above each centrum (B).

Diagnosis. As for the genus.

Description. The body is elongate, relatively slender and laterally compressed, SL about 70 mm. The head is moderately large, representing nearly 29% of SL. The maximum body depth is contained about four times in SL, measured between the head and the first spines of the dorsal fin; the minimum depth is just in front of the caudal fin. The predorsal distance represents slightly less than 40% of SL. The preanal distance represents slightly more than 60% of SL. The head is nearly triangular in shape with the dorsal margin either straight or slightly convex, and the ventral margin convex. The mouth is terminal, slight-

ly dorsally oriented. The orbit is large, representing about one-fourth of the head length, and is nearly the same size as the preorbital distance. The caudal peduncle is relatively short, representing slightly more than 15% of SL and caudal peduncle depth about 10% of SL (Table 2).

Neurocranium. The neurocranium is moderately deep. The ethmoid region in lateral view is rhomboid-shaped. What appears to be the vomer articulates with the ventral surface of the ethmoid region. The vomer bears several tiny teeth. The lateral ethmoid bears a clear concavity posterolaterally. The frontals are narrow in the anterior part, while about three times wid-

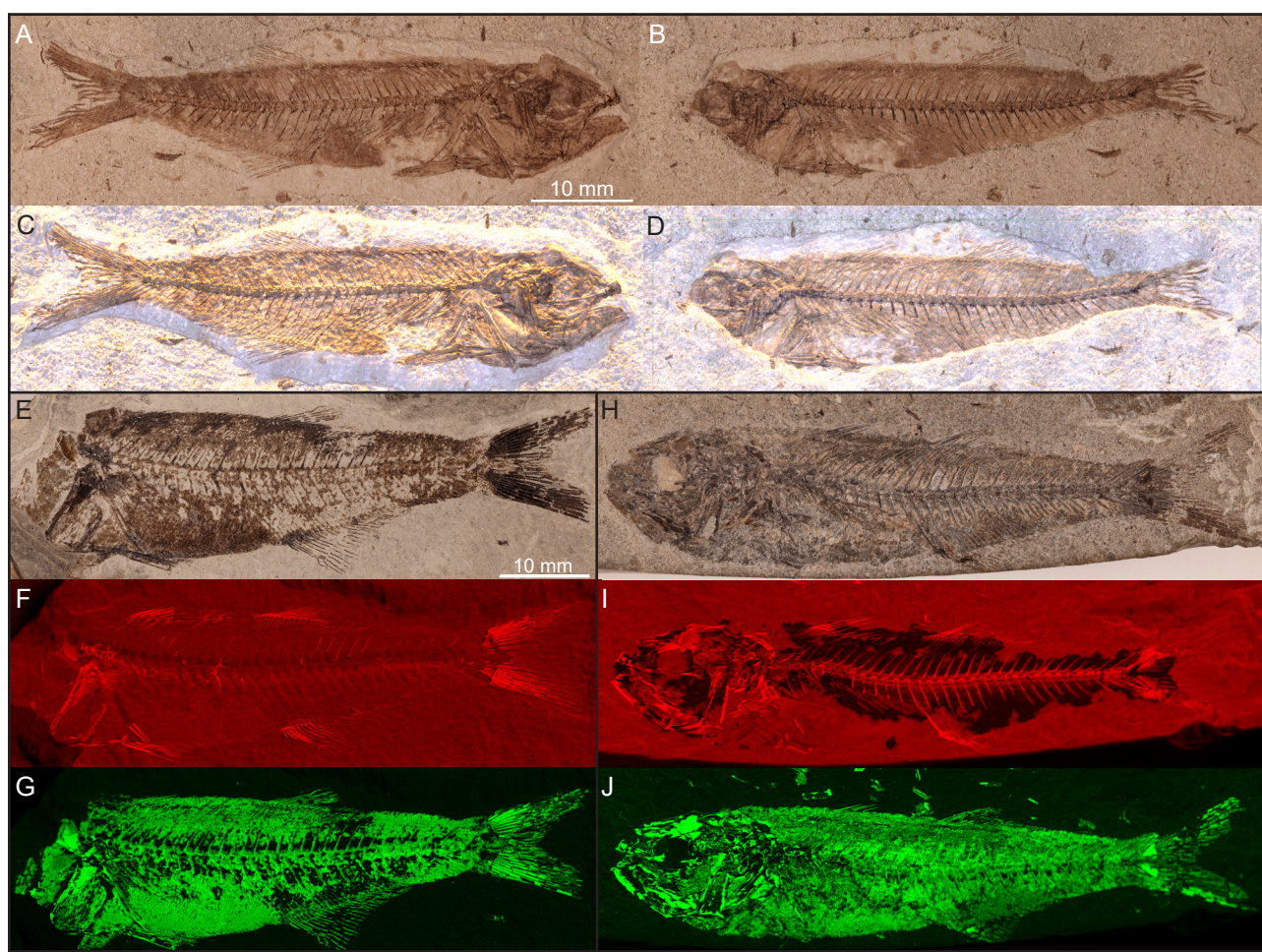


Fig. 3. *Parapropcarina multispinata* gen. et sp. nov. Paratypes. **A–D:** Paratype FUM-N-16161, the scale bar in A applies also to B, C and D. **A:** High-resolution photo image of the part FUM-N-16161A. **B:** High-resolution photo image of the counterpart FUM-N-16161B. **C–D:** Mosaic image of FUM-N-16161A (C) and FUM-N-16161B (D) in different illumination to make the bone imprints appear inverted, thereby enhancing the visibility of the individual bone element morphologies. **E–G:** Paratype FUM-N-10535, high-resolution image (E), strontium element map, note the lack of Sr-signals as the bones are mostly preserved as imprints with exception of the paired and median fins (F), whereas the scales are preserved and clearly visible in the phosphorous map (G). The scale bar in E applies also to F, G, H, I, J. **H–J:** Paratype FUM-N-17356, high-resolution photo image (H), strontium element map (I), note the taphonomic modification of the postcranial portion of the body, including the supraneurals where only two of the three are visible, and the dislocated anteriormost vertebrae, where several are now visible in anterior view.

er in the postorbital region. The posterodorsal corner of the orbit is delimited by the sphenotic; it articulates with the posterolateral margin of the frontal. The frontals articulate with the parietals posteriorly. The supraoccipital crest is short and low. The otic part of the neurocranium is about twice as deep as the ethmoid part. The ventral margin of the neurocranium is occupied by the parasphenoid, which is ventrally curved in the central part; there are well recognisable lateral processes at the postorbital section of the bone (e.g. FUM-N-17356, NHMD-1351141, Figs 2–3). Other parts of the neurocranium are not recognisable.

Infraorbital series and sclerotic bones. None of the circumorbital bones is recognisable. The sclerotic ossicles are large, bowl-shaped and located in the anterior and posterior parts of the orbit. The anterior sclerotic ossicle seems to be slightly larger than the posterior one (compare NHMD-625079 and NHMD-1351141, Figs 2, 4, 5, 6).

Jaws. The oral jaws are strong and massive. The alveolar process of the premaxilla is relatively straight, bearing a single row of small conical teeth. It is not possible to determine the precise number of teeth in any of the examined specimens. Both the ascending and articular processes are short and blunt (NHMD-625079, Fig. 2). Posteriorly, the premaxilla seems to be in close connection with the posterior section of the maxilla. Anterodorsally, the maxilla exhibits a

slight curvature and has well-developed ethmoid and premaxillary processes; just above the posterior margin of the maxilla, there are feebly ossified skeletal remains that are tentatively interpreted herein as a partially preserved supramaxilla (NHMD-625079, MM-9628, Figs 2, 4, 6). The lower jaw articulation is located at the level of the posterior half of the orbit. The dentary is relatively deep, V-shaped and with a straight alveolar margin and a single row of relatively large and spaced conical teeth; at least 12 teeth can be recognised in the paratype FUM-N-16161 (Fig. 3A–D). The anterodorsal corner of the symphysis is slightly curved ventrally, whereas the ventral margin is somewhat convex; its posterior margin reaches the level of the central part of the orbit. There is a large foramen at midheight of the symphysis, probably for the facialis nerve (Fig. 6). The anguloarticular is rhomboid in shape, anteriorly articulating with the dentary and posterodorsally with the quadrate. There seems to be a small retroarticular in the posteroventral corner of the anguloarticular.

Suspensorium. The hyomandibula is elongated with a straight shaft exhibiting an anteriorly developed lamina that is in contact with the metapterygoid. The articular head is massive with a rounded margin and appears to be inclined slightly forward (FUM-N-17536, Fig. 3H–J) bearing a relatively short opercular process. The maximum width of the artic-

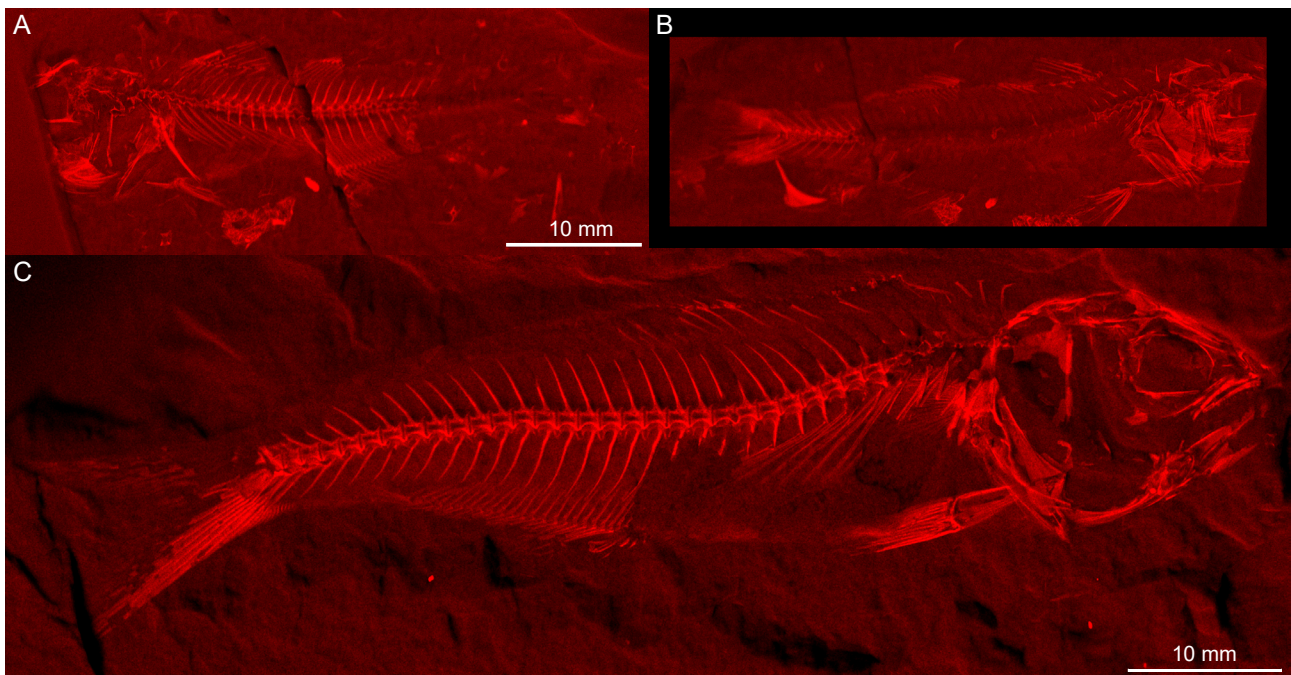


Fig. 4. *Parapropercarina multispinata* gen. et sp. nov. Referred material shown in their strontium element maps. A–B: NHMD-1351141, part (A) and counterpart (B). C: MM-9628.

ular head is contained about 3.5 times in the shaft of the bone. The palatine articulates dorsally with what appears to be the lateral ethmoid and posteroventrally with the ectopterygoid. Several tiny teeth are recognisable along the medial surface of the palatine in

the holotype (Fig. 2). The ectopterygoid is L-shaped, with the horizontal limb being slightly longer than the vertical one; posteriorly, it contacts the anterior margins of the quadrate and the metapterygoid. The endopterygoid articulates with the dorsal margin

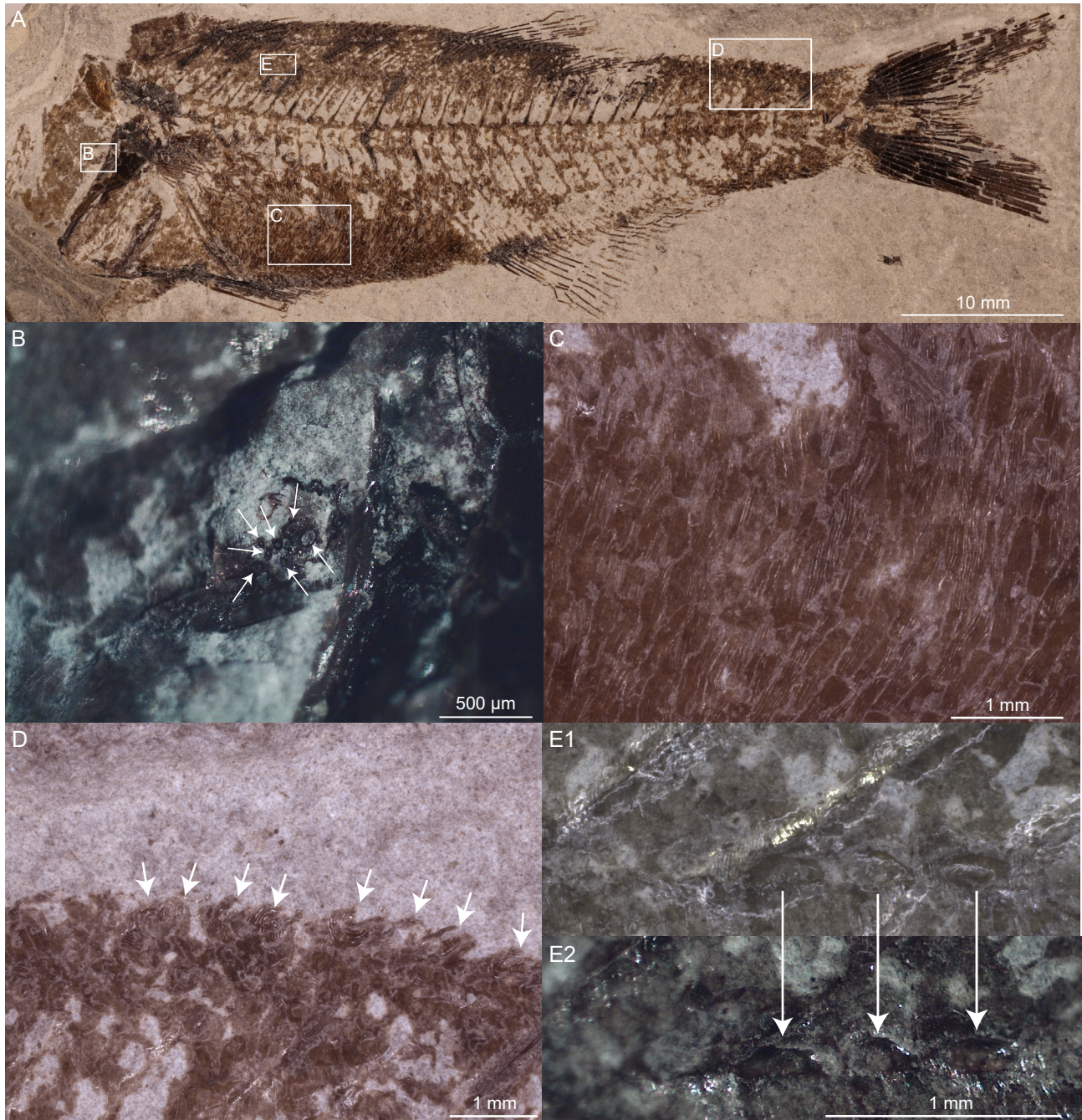


Fig. 5. *Parapropercarina multispinata* gen. et sp. nov. Micrographs of the branchial tooth plate and different scale types, paratype FUM-N-10535. **A:** High-resolution photo image showing the entire paratype, with each frame indicating the magnified sections in this figure. **B:** A partly preserved branchial tooth plate in transverse section. Arrows indicate the most noticeable teeth. **C:** The overlapping scales covering most of the body, of which only the posterior portion is exposed showing the longitudinally oriented circuli. **D:** Ovoid cycloid scales by the posterodorsal body margin are indicated with arrows. **E:** Three elliptic lateral-line scales. The upper (E1) and lower (E2) micrographs were taken of the exact same portion, but on two different micro-setups, highlighting the glasslike appearance of these scales.

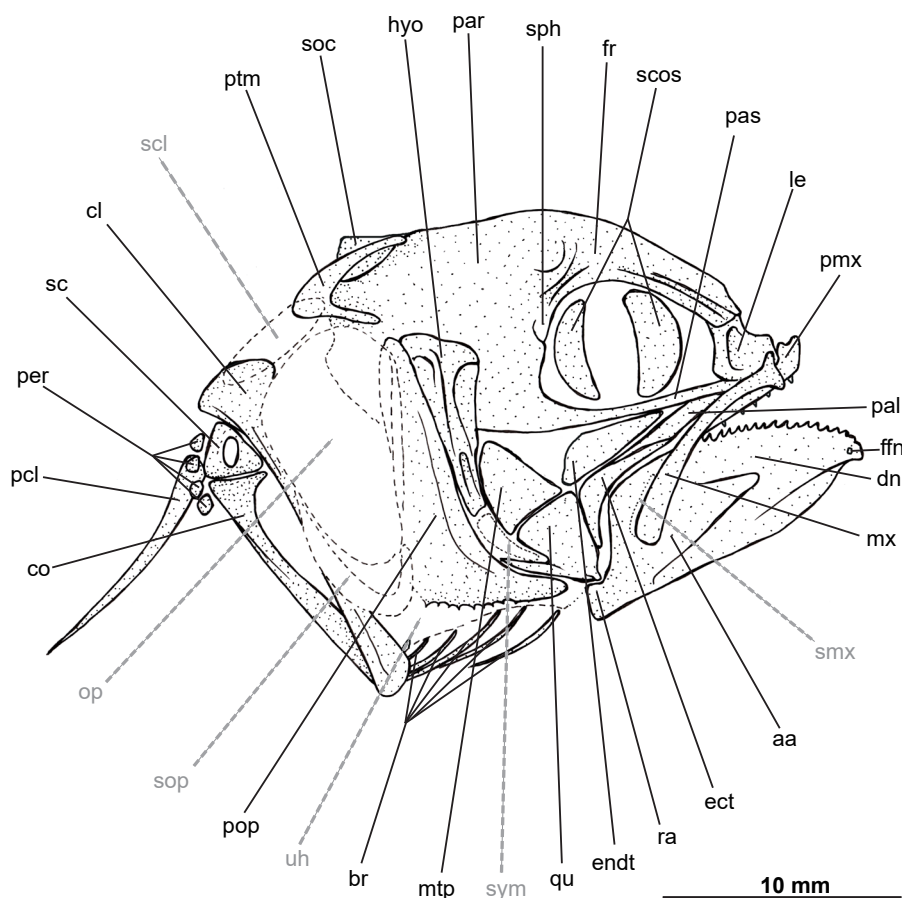


Fig. 6. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the head, based on the holotype NHMD-625079.

of the ectopterygoid (NHMD-625079). There is no evidence of pterygoid teeth. The quadrate is shaped as an isosceles triangle and has a well-developed, rounded articular head for the lower jaw.

Opercular series. The bones of the opercular series are generally poorly preserved in the available material. The preopercle is L-shaped; the vertical limb appears to be more than twice as long as the horizontal one. The ventral margin and posteroventral corner of the bone bear several small, short spines (NHMD-625079, NHMD-1351141). The morphology of the posterior margin is not clearly recognisable. The opercle is very thin and appears to be rhomboid-shaped, and deeper than wide; no ornamentations or spines can be recognised along its posterior border. The dorsal margin of the subopercle has a deeply notched shape, but no other details of the subopercle and of the interopercle are recognisable.

Hyoid apparatus and branchial skeleton. The hyoid bar has a straight dorsal and a slightly concave ventral margin (NHMD-625079, FUM-N-17356, partially visible also in NHMD-1351141). The hypohyals and the articulation between the anterior and posterior ceratohyals cannot be recognised. Six

branchiostegal rays appear to be present. Although some branchial remains are faintly recognisable in NHMD-1351141, including several well-developed gill rakers, the morphology of the branchial arches is not clear. In the paratype FUM-N-10535 (Figs 3E, 5), a small fragment of bone with evident presence of tiny teeth is preserved in the region between the posterior opercular margin and the anterior margin of the cleithrum; these are mostly preserved in transversal section and it is reasonable to assume that this tooth bearing structure represents a partly preserved branchial tooth plate (Fig. 5A–B). None of the available material shows any evidence of the pharyngeal sacs or individual pharyngeal sac rakers (Fig. 6).

Vertebral column and intermuscular bones. The vertebral column comprises 36 vertebrae, including the compound centrum (15 abdominal and 21 caudal). The morphology of the first and second vertebrae is not entirely clear. The dorsal prezygapophyses of the vertebrae from the 3rd through the 33rd exhibit an anterior articular surface for the respective dorsal postzygapophyses of the preceding neural arch. On the lateral side of the neural arches, including those of the second preural vertebra, slightly above the

vertebral centrum, there is a rounded foramen. There are ventral parapophyses developed from the eighth up to fifteen abdominal vertebrae, which gradually increase in size posteriorly. The haemal spines of the caudal vertebrae are slightly longer and more curved backwards than the opposite neural spines, which are shortened posteriorly in the series.

Twelve pairs of ribs occur from the fourth to the fifteen abdominal vertebrae, being strongly developed and posteriorly inclined. From the fourth to the seventh vertebrae, the ribs articulate with the ventral margin of the centra, moving subsequently to the posteroventral surface of the parapophyses. Anteriorly, the ribs are generally more massive and elongate reaching one third of the body depth, while they are thinner and shorter posteriorly. Remains of at least three pairs of epineurals, associated with the dorsal portions of the anterior ribs, are visible in the holotype (Fig. 2).

Caudal skeleton and fin. The caudal skeleton consists of a compound centrum, fused hypurals 1 and 2, partially fused hypurals 3 and 4, autogenous hypural 5, autogenous parhypural (without parhypurapophysis), two uroneurals, and three epurals. The parhypural has a massive proximal portion. The haemal spines of PU2 and PU3 are autogenous. The neural spine of PU3 is fully developed. The neural spine of PU2 is strongly reduced to a low, blade-like crest. The caudal fin is deeply forked. There are 17 (1,8 + 7,1) and eight or nine upper and nine to ten lower procurent rays. There is no evidence of a procurrent spur (Figs 2, 7).

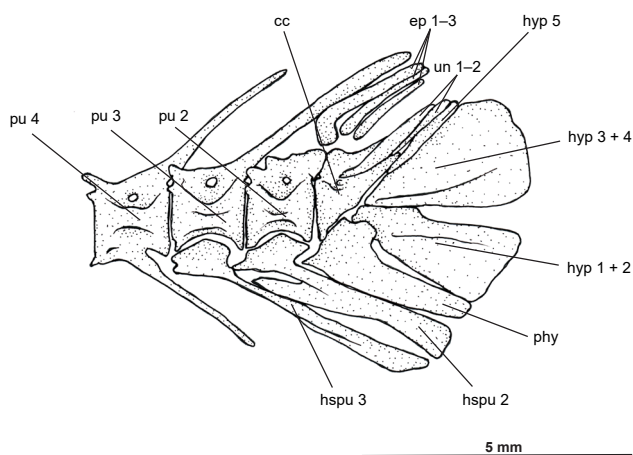


Fig. 7. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the caudal-fin skeleton, based on the holotypic part NHMD-625079A.

Median fins and supports. There are three tiny supraneurals, about one mm in length each (FUM-N-16161 and MM-9628, Figs 3–4, 8); in some specimens, including the holotype NHMD-625079 and paratype FUM-N-17536, only two supraneurals can be recognised, most likely the missing one being hidden under other skeletal elements or not preserved at all (note this region in particular in FUM-N-17536). The first supraneural is nearly T-shaped, with a larger anteriorly projecting process. The second supraneural is faintly enlarged anteriorly, and the third supraneural is rod-like. The predorsal formula is 0/0+0/2/1. The dorsal fin is continuous and contains 15 spines plus 18 rays supported by 33 pterygiophores (Fig. 9). The first spine is in supernumerary association on the first dorsal-fin pterygiophore. The second to fifth dorsal-fin spines are much longer than the others. The 9th to 13th spines are nearly equal in length, much shorter than the preceding ones. This condition is also supported by the preserved impression of this part of the dorsal fin in the paratype FUM-N-10535 in which an indented outer profile of the dorsal fin is recognisable. The 14th spine is very short, and the 15th is significantly longer and thinner. The rest of the dorsal fin comprises 18 distally branched and segmented rays, the longest being the 16th and the following ones decrease in length posteriorly. The dorsal-fin formula cannot be determined in the holotype, due to taphonomic modification of the anterior postcranial portion of the body.

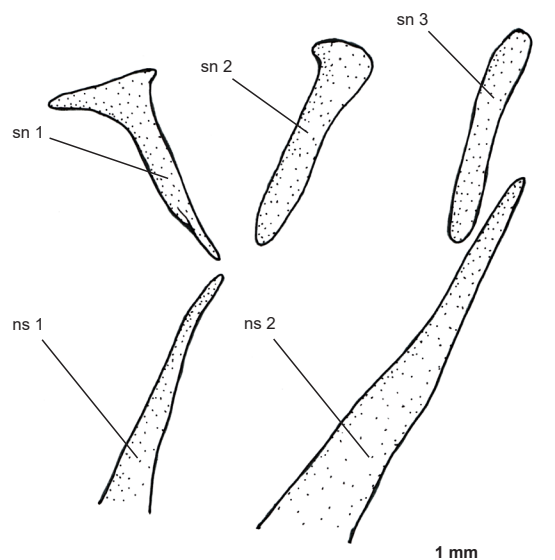


Fig. 8. *Parapropercarina multispinata* gen. et sp. nov. Interpretative reconstruction of the three supraneurals with the first being nearly T-shaped and the two following rod-like. Based on the paratypic counterpart FUM-N-16161B.

The anal fin consists of two (FUM-N-17536, NHMD-1351141, Figs 3–4) or three (holotype NHMD-625079, FUM-N-10535, FUM-N16161, Figs 2–3) spines plus 24 rays that decrease in length posteriorly. The posterior anal-fin spine is considerably longer than the preceding ones.

Paired fins and girdles. The posttemporal has two limbs, the dorsal one being massive, slightly arched and more than twice as long as the ventral limb. The limbs form an angle of about 50°. The supracleithrum articulates with the dorsal extremity of the cleithrum and the posteroventral margin of the posttemporal. The cleithrum is crescent-shaped and bears an expanded bony lamina along its posterodorsal margin. The scapula is rounded and centrally pierced by the scapular foramen. The ventral margin of the scapula and surface of the cleithrum just below it articulate with the coracoid, which has an expanded and curved ventral limb. The postcleithrum is rod-like and reaches almost the ventral margin of the body. The pectoral fin inserts at midheight of the body and contains about 18 rays supported by four radials, two of which articulate with the scapula and two with the coracoid. The distal portions of the pectoral-fin rays reach the level of the 10th abdominal vertebra (see MM-9628).

The basipterygium is elongate and triangular, with a well-developed postpelvic process. The pelvic fin comprises a single spine plus five rays, extending back up to the 10th or 11th vertebra.

Squamation. The body, including the proximal portion of the median fins, is densely covered by overlapped scales, of which only the posterior field is exposed showing longitudinally oriented circuli (Fig. 5C). Along the dorsal and ventral margins of the body, three or four rows of small ovoid cycloid scales form a very dense sheath (Fig. 5D). The same type of scales is also recognisable in the proximal part of the caudal fin, extending to the level of first bifurcation of the caudal-fin rays, as well as along the basal portion of the dorsal and anal fins. Cycloid scales of larger size cover most of the head, including the cheek, opercular series, and nape, being absent on the frontals, orbital area and the snout. Furthermore, the lateral-line series can be recognised in the paratype FUM-N-10535 between the dorsal body profile and the vertebral column. The lateral-line scales are recognisable based on the impression on their internal canal; there are approximately three lateral-line scales per interneural space (Fig. 5E), at least in the anterior half of the body.

The nomenclatural acts of this paper are registered on ZooBank. LSID of the new genus *Parapropercarina*: <https://zoobank.org/urn:lsid:zoobank.org:act:85FF6F95-495B-460D-95C0-7494083DEDAA> and the LSID of the new species *Parapropercarina multispinata*: <https://zoobank.org/urn:lsid:zoobank.org:act:440E329F-9BF2-4303-AE61-1027AFFD0A02>

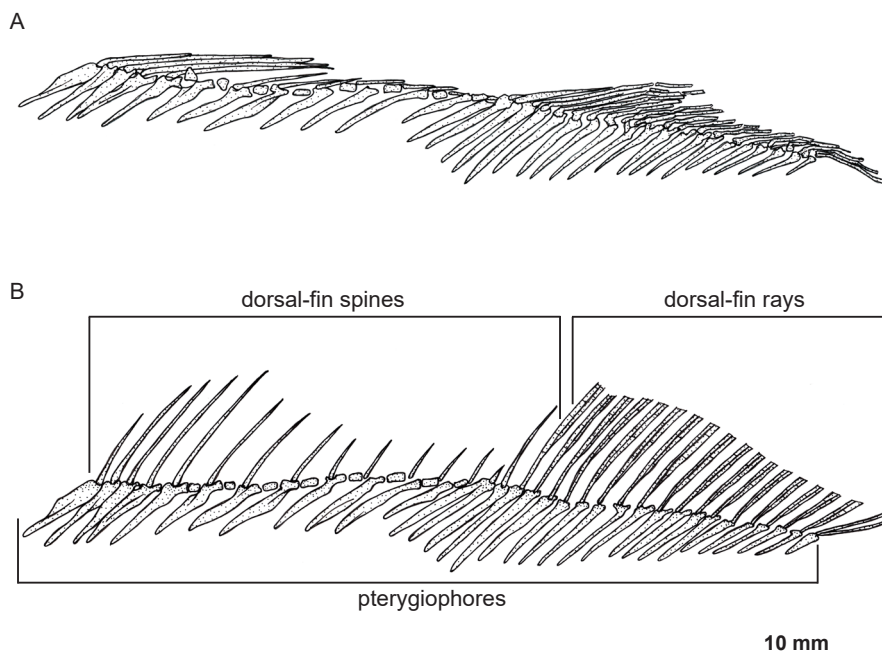


Fig. 9. *Parapropercarina multispinata* gen. et sp. nov. **A:** Interpretative drawing of the dorsal fin, based on the holotypic part, NHMD-625079A. **B:** Reconstruction of the dorsal fin, with dorsal-fin spine section, dorsal-fin rays and pterygiophores indicated.

Comparative discussion

The new taxon described herein, *Parapropercarina multispinata* gen. et sp. nov., possesses a number of characters that unequivocally place it within the Percomorphacea, including the absence of a separate second ural centrum, presence of five hypurals, pelvic fins with less than six rays, and the caudal fin composed by 17 (1,8+7,1) principal rays (see Wiley & Johnson 2010).

The overall morphology of *Parapropercarina multispinata* gen. et sp. nov. is strongly reminiscent of that of stromateiform fishes. The monophyly of the order Stromateiformes is supported by eight synapomorphies (Pastana *et al.* 2022), including: 1) at least 24 distally branched anal-fin rays; 2) number of ventral procurrent caudal fin rays 10–12; 3) premaxillary teeth uniserial; 4) palatine teeth absent; 5) medial bony suture between the dorsal and ventral hypohyals absent; 6) adductor mandibulae pars malaris subdivided into retromalaris and promalaris subsections; 7) anteroventral section of epaxialis present; and 8) interdermal canal plexus present, with the first three being clearly recognisable in the studied material of *Parapropercarina* gen. nov., thereby supporting its attribution to the Stromateiformes. The majority of the other features refer to soft structures that can be preserved in fossils only in exceptional cases. The order Stromateiformes comprises six extant families, the Amarsipidae, Ariommatidae, Centrolophidae, Tetragonuridae, Stromateidae, and Nomeidae (see Haedrich 1967, 1969; Pastana *et al.* 2022), one extinct family, the Propercarinidae (see Bannikov 1995, Přikryl *et al.* 2014, Micklich & Přikryl 2025), plus several fossil taxa of uncertain familial affinities [see Bannikov (2018) for review and critical comments]. The oldest skeletal record of this lineage is represented by *Butyrumichthys henricii* (see Schröder *et al.* 2023a), which also originates from the Eocene deposits of the Fur Formation. The recognisable characters of *Parapropercarina* gen. nov. listed above, support its

attribution within the suborder Stromateoidei (=non-Amarsipidae Stromateiformes *sensu* Pastana *et al.* 2022).

The attribution of *Parapropercarina* gen. nov. to Ariommatidae, Tetragonuridae, and Stromateidae can be ruled out based on the higher number of dorsal-fin spines (15 vs. 11), which Pastana *et al.* (2022) considered an unambiguous synapomorphy of these families. The Centrolophidae can be ruled out as well, including *Butyrumichthys*, based on the general morphological features, such as an elongated body (vs. deep), low supraoccipital crest (vs. high supraoccipital crest), a single dorsal fin exhibiting a deep notch, containing 15 spines and 18 rays (vs. notch absent and 3–7 spines plus 23–50 rays).

The overall morphology of *Parapropercarina* gen. nov. most closely resembles that of the Nomeidae and the extinct family Propercarinidae (Table 3).

The Nomeidae has traditionally been considered as a stromateoid group, characterised by two dorsal fins, teeth on the vomer and palatines, six branchiostegal rays, four hypurals and three epurals in the caudal-fin skeleton, and papillae in the pharyngeal sacs with stellate bases, arranged in about five broad longitudinal bands (Haedrich 1967; see also interpretative comments by Pastana *et al.* 2022: 947). The definition of this family based on unambiguous synapomorphies was detailed by Pastana *et al.* (2022) and includes the ventral limb of the coracoid being curved, dorsal surface of the head with scales, interrarial membrane of the pectoral fin covered by scales, and modified pectoral girdle, which reflects the specialisation of the pectoral fin (Pastana *et al.* 2022). Conversely, six branchiostegal rays, palatine teeth, presence of some cycloid scales on the dorsal surface of the head, partial fusion of some of the hypurals, and a single dorsal fin with a deep notch, are present in both *Parapropercarina* gen. nov. and in nomeids. The other characters appear not to be present in the examined material of *Parapropercarina* gen. nov. However, it cannot be ruled out that some of

Table 3. Comparative overview of *Parapropercarina*, Propercarinidae and Nomeidae

Characters	<i>Parapropercarina</i>	Propercarinidae	Nomeidae
Elongated body	+	+	+/-
Low supraoccipital crest	+	+	—
Vomerine and palatine teeth	+	+	+
Single dorsal fin with deep notch	+	—	+/-
Rayless pterygiophores	—	+	?
Six branchiostegal rays	+	+	+
Vertebral column 35–37	+ (36)	+ (35–37)	+ (30–42)
Modified pectoral girdle	—	—	+
Slightly curved ventral limb of coracoid	+	+	+

these may have been present in origin and lost due to the fossilisation processes.

As mentioned above, *Parapropercarina* gen. et sp. nov. also exhibit considerable morphological similarities to the monotypic family Propercarinidae, which was recently emended by Micklich and Přikryl (2025) as a lineage of stromateoid fishes with elongated body, pelvic fin present in adults, number of anal fin-rays that exceeds the number of rays in the second dorsal fin, presence of about 36 vertebrae, posterior abdominal ones with well-developed parapophyses, caudal-fin skeleton non-oligomerized, teeth rather strong, scales thin, cycloid or ctenoid, and the lateral line high, running parallel to the dorsal margin of the body. The most striking differences between *Parapropercarina* gen. nov. and *Propercarina* are represented by the possession of a single vs. two deeply separated dorsal fins; no free rayless pterygiophores vs. five free rayless pterygiophores in between the first and second dorsal fins; and relatively long pectoral fins vs short.

Concluding remarks

Parapropercarina multispinata gen. et sp. nov. clearly exhibits morphological characters shared with representatives of both families, Propercarinidae and Nomeidae. This confirms the hypothesis by Micklich & Přikryl (2025) that the propercarinids are likely much closer to the nomeids, than to the amarsipids, as suggested earlier (compare Bannikov 1995 and Přikryl *et al.* 2014). Up to date propercarinid-like stromateiforms are known from Oligocene Paratethyan deposits (Bannikov 1995; Přikryl *et al.* 2014; Micklich & Přikryl 2025). The new taxon described herein suggests that a body plan similar to that of propercarinids was in existence at much higher northern latitudes in the immediate aftermath of the PETM, thereby expanding both the temporal and latitudinal distribution. Due to the preservation of all current available material kept in the museum collections in Denmark, it is not possible to conclusively resolve the attribution at the family level of *Parapropercarina multispinata* gen. et sp. nov.

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The Cambro–Ordovician stratigraphic successions encountered in the Vasegård-1, Hjulmagergård-1 and Gravgærde-1 shallow boreholes on Bornholm, Denmark

ARNE THORSHØJ NIELSEN & NIELS HEMMINGSEN SCHOVSBO



Geological Society of Denmark
<https://2dgm.dk>

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The Cambro–Ordovician successions penetrated by the fully cored shallow boreholes Gravgærde-1, Hjulmagergård-1 and Vasegård-1 are summarised; none has been described previously. All three boreholes are located south-west of Åkirkeby on Bornholm, Denmark. Gravgærde-1 drilled 4.1 m of the Alum Shale Formation and the upper 2.2 m of the Rispebjerg Member (Læså Formation). Hjulmagergård-1 drilled 7.65 m of the Dicellograptus Shale, 1.55 m of the Sularp Formation and 4.6 m of the Komstad Limestone before being terminated 3.7 m into the Alum Shale. The basal part of the Komstad Limestone is faulted and shows slight repetition, suggestive of reverse reactivation of the fault. The underlying Alum Shale is completely brecciated and clearly represents a fault zone. Vasegård-1 drilled the basal 2.0 m of the Dicellograptus Shale, the Sularp (1.65 m) and the Komstad Limestone (4.8 m) formations in their entirety, before being terminated 9.65 m into the Alum Shale.

The Alum Shale succession in Vasegård-1 was analysed using a handheld XRF analyser, allowing construction of a core gamma-ray curve that can be correlated with wireline-logged boreholes as well as with the Alum Shale exposed at Limensgade, where a detailed tie between the gamma-ray log pattern and the Tremadocian graptolite zonation has been established using a handheld gamma-ray logger. The correlation indicates that the upper part of the Alum Shale Formation in the Vasegård-1 core represents the Tremadocian (4.9 m) and the Furongian *Acerocarina* (1.5 m) plus the uppermost *Peltura* (3.2 m) superzones.

Gravgærde-1 confirms that the Alum Shale constitutes the bedrock in a belt extending from Soldatergård to north of Gravgærde. This belt is separated from the Ordovician strata to the east by a NW–SE striking fault with a vertical offset of around 40–50 m, which was intersected by the Hjulmagergård-1 borehole. A combination of data from Vasegård-1, Limensgade quarry and the nearby St. Bukkegård-1 borehole indicates that the Alum Shale Formation is at least 35.6 m thick in the Læså area but may reach 38 m. The maximum documented thicknesses on Bornholm of the Komstad Limestone (4.8 m) and the Ordovician Alum Shale (4.9 m) are recorded in the Vasegård-1 borehole.

Keywords: Bornholm, Cambrian, Ordovician, lithostratigraphy, Alum Shale Formation, Komstad Limestone, wireline log correlation.

Arne Thorshøj Nielsen [arnet@ign.ku.dk], Department of Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark. Niels Hemmingsen Schovsbo [nsc@geus.dk], Department of Geoenery and Storage, Geological Survey of Denmark and Greenland. Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

The Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland (GEUS), developed a lightweight mobile drilling rig in the early 1980s for use in Greenland. To test the rig, two short boreholes (10.4 m and 19.6 m) were drilled on Bornholm in 1982: one in the garden at

Gravgærde (then a field station of the Geological Institute, University of Copenhagen) and one in the meadow north-west of Vasegård in the Læså area, both south-west of Åkirkeby (Fig. 1). These boreholes are hereafter referred to as Gravgærde-1 and Vasegård-1. Both were fully cored; the core is 1 inch

(25 mm) in diameter. They have not previously been described, apart from a sketch log of the Sularp Formation in Vasegård-1 (Pedersen 1989, fig. 8). Given their usefulness for mapping, they are briefly documented here. Neither borehole was wireline logged, but the Vasegård-1 core has subsequently been analysed using a handheld XRF analyser, allowing construction of a gamma-ray log. All depths mentioned are drilled (isochore) depths below ground level.

The Hjulmagergård-1 borehole was drilled in 2012 using a larger rig operated by Faxe Kalk (see Schovsbo *et al.* 2015); the core diameter is 2 inches (55 mm). The borehole was planned to penetrate the Komstad Limestone Formation and the Alum Shale Formation in their entirety, and was therefore located a little WSW of the water-filled former Komstad Limestone Quarry in the field to the south-east of Hjulmagergård (c. 250 m ESE of Gravgård-1; see Fig. 1). However,

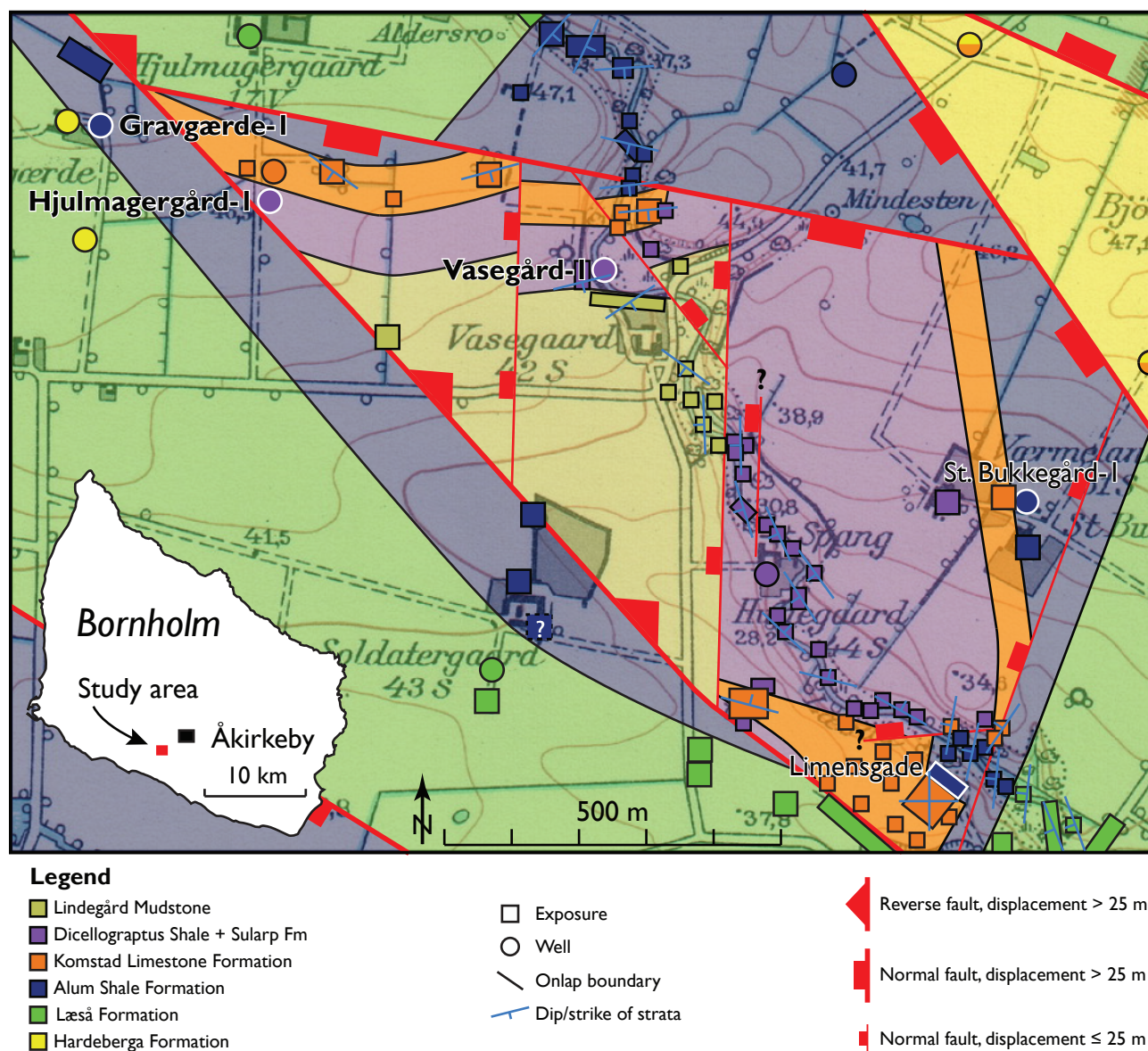


Fig. 1. Location of the discussed boreholes Gravgård-1, Hjulmagergård-1, Vasegård-1 and St. Bukkegård-1 on southern Bornholm, plotted on a revised geological map of the area (ATN, unpublished). The abandoned shale–limestone quarry at Limensgade is also shown. The inset map of Bornholm in the lower left corner indicates the location of the mapped area (red square). The Rispebjerg sandstone (marked in yellow in wells) is mapped together with the Norretorp Member as the Læså Formation. Two wells within the north-eastern area mapped as the Hardeberga Formation are shown in two colours, indicating that it is not possible to determine whether these wells penetrate the Hardeberga or Langeskanse sandstone. The revised map will be discussed in greater detail in a forthcoming paper.

an unexpected major fault was encountered at the drill site, and drilling was abandoned at 20.5 m after penetrating only a short distance into the Alum Shale. The borehole collapsed after retrieving the drill string and no wireline logs were recorded.

All described cores are archived at GEUS. Synoptic logs of the three boreholes are presented in Fig. 2, and the lithostratigraphy is summarised in Table 1.

The Alum Shale on Bornholm straddles the Miaolingian ('Middle' Cambrian), Furongian ('Upper' Cambrian) and lower part of the Tremadocian (Lower Ordovician); the modern global series names are used hereafter.

The Gravgærde-1 borehole (DGU 246.912)

The core obtained is somewhat incomplete; the relatively low recovery for the Alum Shale as a whole (average 61%) reflects that this was the first borehole drilled with the then new equipment, and the operation – notably core take-up – was complicated by technical start-up issues. The approximate coordinates of the well site are N 55° 3' 26.52", E 14° 52' 27.11" (garden east of the Gravgærde farmhouse, north of the small pond).

The core from the Quaternary till (0–4.05 m) was not preserved, except for a 0.2 m section from the interval 3.00–3.75 m. Alum Shale was encountered between 4.05 and 6.95 m, the basal 0.02 m of which consists of anthraconite (bituminous limestone). The recovered core totals 1.95 m and almost certainly represents the Miaolingian (cf. Nielsen *et al.* 2018, table 4).

Below follows grey, bedded limestone, presumably the Andrarum Limestone Bed, between 6.95 and 7.40 m; however, only 0.21 m of core was recovered from this section, so the true thickness is uncertain. The core from the interval 7.40–8.15 m consists predominantly of anthraconite with minor crumbling Alum Shale between 8.0–8.1 m. The recovered core from this 0.75 m thick interval is only 0.35 m. There is no Exsulans Limestone Bed in the core; whether this interval was lost during core recovery or whether

the bed is genuinely absent at the drill site remains unknown. The total thickness of the Alum Shale in Gravgærde-1 is thus 4.1 m. Below follows the Rispebjerg Member of the Læså Formation (8.15–10.35 [TD] m). It consists mostly of grey, medium-grained, well-cemented sandstone. Between 8.98 and 9.11 m, common black nodules, up to 15 mm in diameter are present, presumably phosphorite. The basal interval (10.21–10.35 m) consists of fine-grained sandstone to siltstone containing some glauconite. A total of 2.03 m of core was recovered from the Rispebjerg Member, corresponding to a recovery of 92%.

The Hjulmagergård-1 borehole (DGU 246.838)

This borehole was drilled to a depth of 20.5 m in December 2012. The coordinates of the well site are N 55° 3' 23.90", E 14° 52' 40.98". Below 3.0 m of till, a strongly fractured section of the Dicellograptus Shale was encountered down to 10.65 m. For this reason, the stated depths are approximate, as the recovered core expanded in the boxes upon retrieval. Between 9.5 and 9.7 m, the core is finely crushed, and the interval presumably represents a minor fault. Thin bentonites were observed at 9.6 m (6–7 mm thick), 9.65 m (5 mm thick), 9.95 m (*c.* 5 mm thick), *c.* 10.5 m (a few mm thick) and possibly also at 9.9 m (a few mm thick), though the latter is uncertain owing to the fractured state of the core. Indistinct bioturbation (probably *Chondrites*) is seen from 9.65 m and continues down to *c.* 10.55 m. In this part the shale is dark grey and unlaminated. The bioturbation is recognised as a faint mottling and lack of lamination.

At 10.55 m, the colour of the shale changes to light grey. This shale contains dark burrows (probably *Chondrites*). At *c.* 10.72 m, a dark angular clast, 50 x 35 mm, is present together with several smaller black clasts in the light grey shale; this level evidently represents a sedimentary breccia. The bentonite-rich strata below this horizon are assigned to the Sularp Formation, traditionally regarded as the lower part of the Dicellograptus Shale on Bornholm.

Table 1. Thicknesses of the Cambro–Ordovician formations in the Gravgærde-1, Hjulmagergård-1 and Vasegård-1 boreholes

		Gravgærde-1	Hjulmagergård-1	Vasegård-1
Ordovician	Dicellograptus Shale		3.0–10.72 m (>7.72 m)	1.58–3.56 m (>1.98 m)
	Sularp Formation		10.72–12.20 m (1.48 m)	3.56–5.23 m (1.67 m)
	Komstad Limestone		12.20–16.80 m (~4.6 m)	5.23–10.01 m (4.78 m)
Cambrian	Alum Shale Formation	4.05–6.95 m (>2.9 m)	16.80–20.50 m (>3.7 m)	10.01–19.64 m (>9.63 m)
	Rispebjerg Member	6.95–10.35 m (>3.4 m)		

The Sularp Formation (proposed by Lindström 1953) has traditionally been regarded as the lower part of the Dicellograptus Shale on Bornholm. The Rispebjerg Member forms the upper part of the Læså Formation (Nielsen & Schovsbo 2007).

Below 10.85 m the core was intact when recovered but has since disintegrated. The main part consists of a slightly more than 1-m-thick bentonite with a few thin shale interbeds (not logged in detail). A 0.1 m-thick conglomerate follows between 12.10 and 12.20

m, underlain by the Komstad Limestone Formation. The core of this grey, compact limestone is in good condition. Between 15.45 and 15.7 m, the limestone is crushed (later cemented, presumably with calcite), forming a fault breccia (Fig. 5A). Below this level,

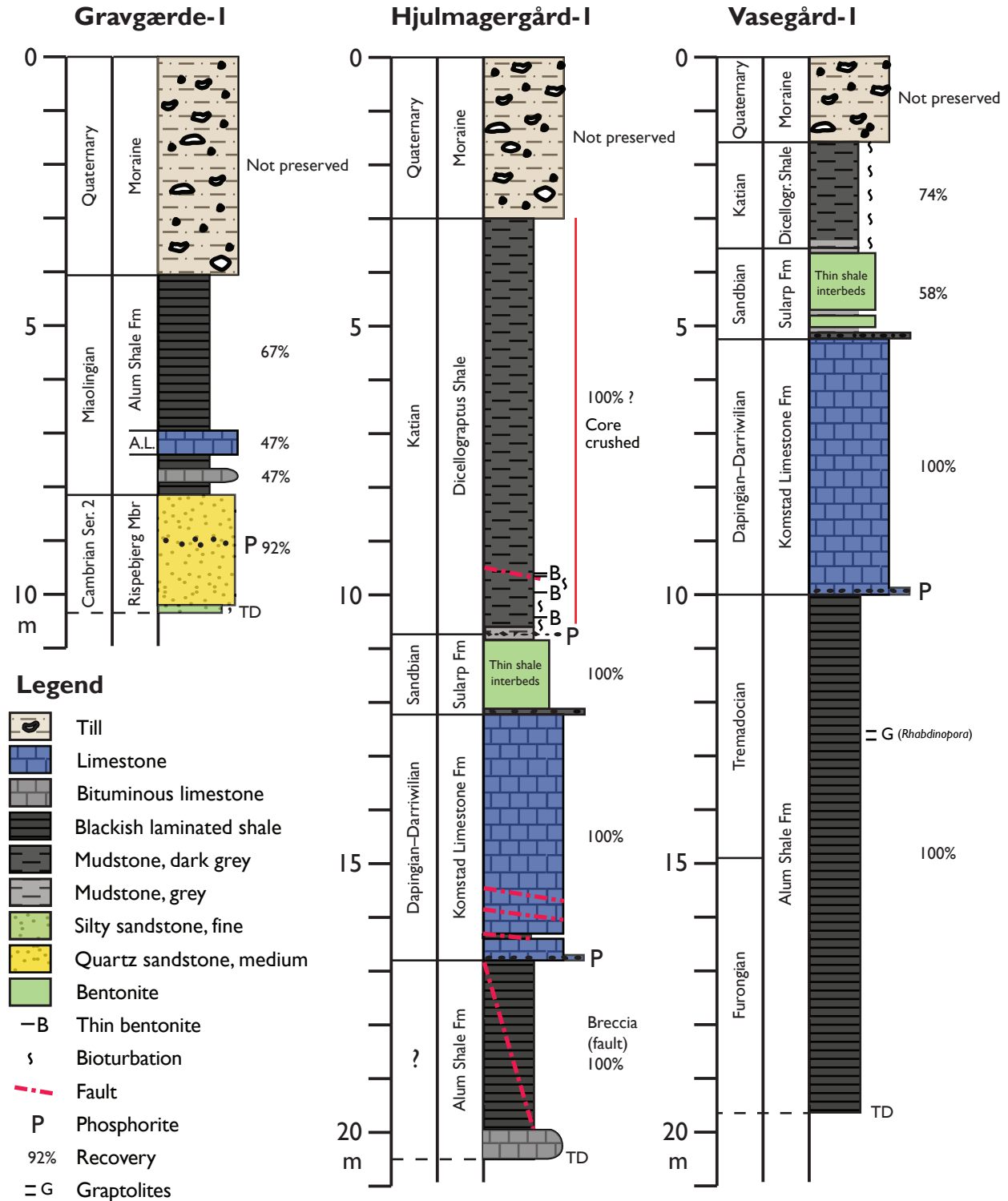


Fig. 2. Synoptic logs of the three boreholes described in this paper. For location of the boreholes, see Fig. 1.

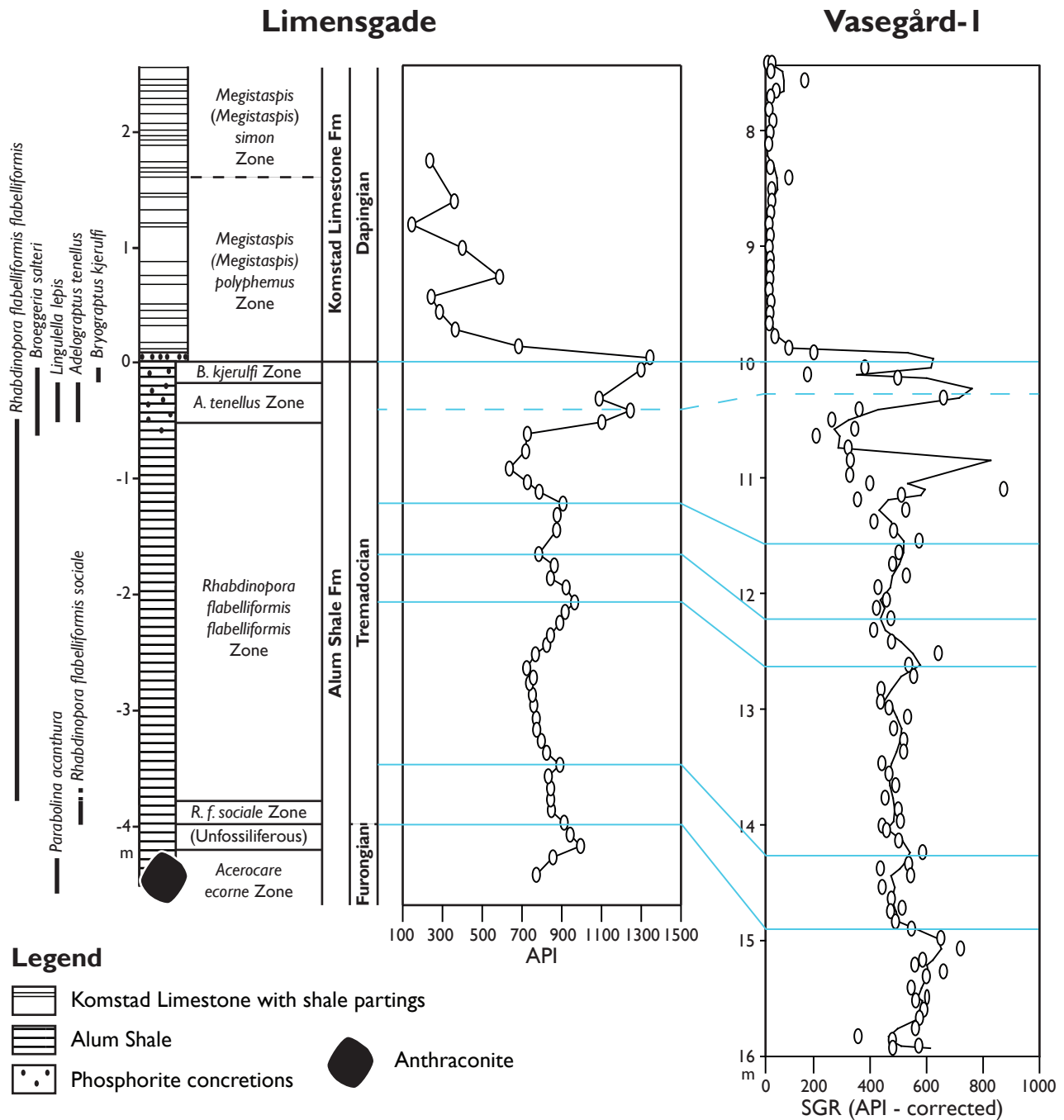


Fig. 3. Log of the Alum Shale and Komstad Limestone exposed in the abandoned limestone/shale quarry at Limensgade (for location, see Fig. 1). The Komstad Limestone log is adopted from Nielsen (1985), while the graptolite stratigraphy is taken from an unpublished study by von Jansson (1979). *Rhabdinopora flabelliformis sociale* is synonymised in modern literature with *R. canadensis* (see Maletz *et al.* 2023), which has its first appearance in the upper half of the *Rhabdinopora campanulatum* Zone. However, since the fossil material from Limensgade has not been re-examined by a graptolite expert, the original naming is retained. This also applies to the *R. flabelliformis* Zone, now included within the *Anisograptus matanensis* Zone (see Nielsen *et al.* 2023 for a brief review of the current graptolite zonation). Rare specimens of the trilobite *Parabolina acanthura* were reported from the site by Poulsen (1923); see also Nielsen & Andersen (2021). No anthraconite is currently exposed at this level in the abandoned quarry, not even after the site was extensively cleared in 2017. Accordingly, no limestone nodules were present where the gamma-ray profile was logged. The conodont zonation of the Komstad Limestone was investigated by Stouge (1974), and based on this, a correlation with the detailed trilobite zonation developed in the Skelbro Quarry by Nielsen (1995) has been established, as shown.

the strata dip more steeply, around 30–40°, increasing downwards. There is also a minor internal disturbance in the Komstad Limestone between 15.85 and 16.05 m, where the core is cut by small, oblique faults with slight crushing and smearing of Alum Shale along the fault planes. A larger fault, dipping c. 30°, truncates the Komstad Limestone at 16.3 m and is underlain by a breccia of crushed Alum Shale between 16.3 and 16.4 m. A lower slice of the Komstad Limestone then extends down to 16.78 m; this interval includes the characteristic basal conglomerate, 0.10–0.12 m thick. In this part of the core, the strata are obliquely oriented, dipping at c. 40°. Excluding the intervening brecciated Alum Shale, the total thickness of the Komstad Limestone is therefore c. 4.6 m; however, given the tectonic complications (and the strong dip of the lower part), this figure should be treated with caution.

Below 16.78 m, the core consists of brecciated Alum Shale with angular fragments generally < 2 cm (Fig. 5B). A few larger core pieces consist of anthraconite, also crushed and cut by mm-thick calcite-cemented veins. However, even so, the core quality on recovery was surprisingly good, although it has since disintegrated to the extent that it can no longer be removed

from the boxes in a coherent state. The breccia also appears to dip at around 40°; this is obviously a fault zone. The breccia continues to 20.0 m, and the shale between 19.4 and 20.0 m is completely crushed and much more finely fragmented than the rest of the brecciated shale, presumably representing a discrete fault plane. The interval 20–20.5 m (TD) consists of an uncrushed anthraconite concretion. Drilling was terminated at 20.5 m, and it is therefore unknown whether the crushed fault zone continues below the anthraconite having a more resistant lithology.

The slight repetition of the lower part of the Komstad Limestone, together with the presence of smeared Alum Shale along minor fault planes, indicates modification of the fault by later reverse movements.

The Vasegård-1 borehole (DGU 246.913)

This borehole was drilled in the meadow adjacent to the Læså, north-west of Vasegård (Fig. 1). The approximate coordinates of the well site are N 55° 3'19.86", E 14°53'9.34". Vasegård is well known for the instructive exposures of Dicollograptus Shale

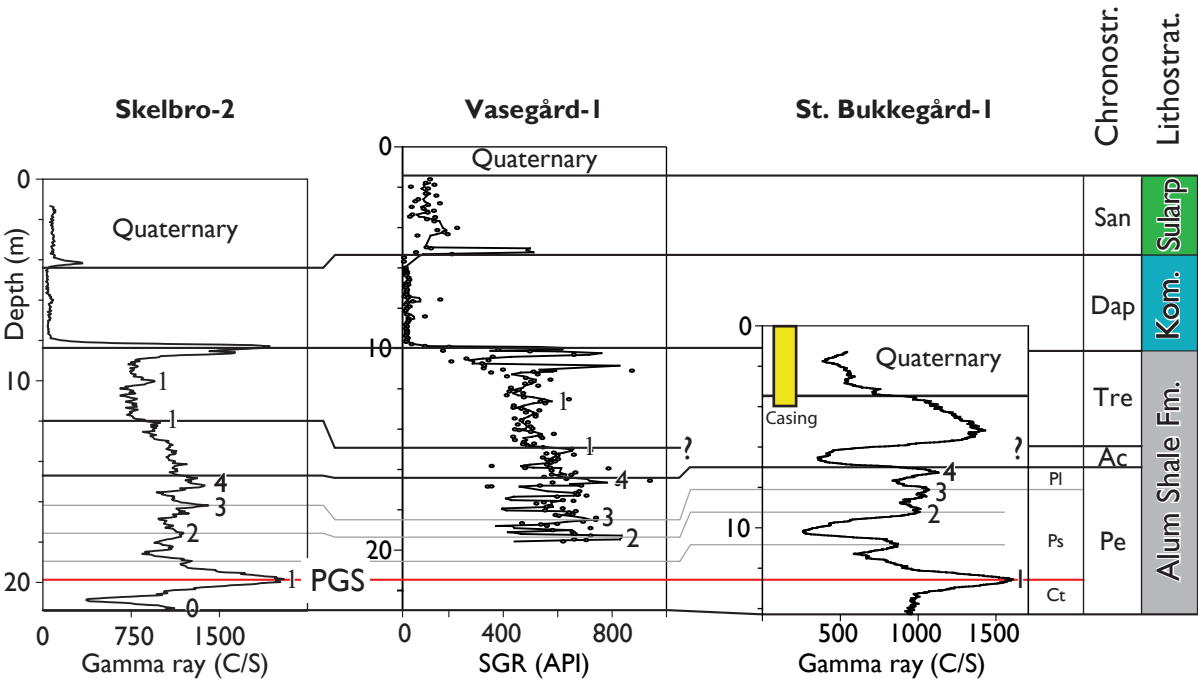


Fig. 4. Correlation of the Alum Shale in the Vasegård-1 borehole with the Skelbro-2 and St. Bukkegård-1 wells, based on gamma-ray logs. The small numbers adjacent to the curves identify correlatable gamma-ray maxima (see Nielsen *et al.* 2018 for details; location of the Skelbro-2 borehole is also shown in that paper). The Vasegård-1 gamma-ray log is constructed based on core hand-held XRF measurements (see text for details). Abbreviations: PGS: *Peltura* gamma-ray spike; C/S: Counts per second; SGR: Sum gamma-ray; Ct: *Ctenopyge tumida* Zone; Ps: *Peltura scarabaeoides* Zone; Pl: *Parabolina lobata* Zone; Pe: *Peltura* Superzone; Ac: *Acerocarina* Superzone; Tre: Tremadocian; Dap: Dapingian; San: Sandbian.

and Lindegård Mudstone in the southwestern bank of the Læså stream (Hadding 1915a,b; Poulsen 1936; Gry 1948; Bergström & Nilsson 1974; Vandenbroucke *et al.* 2013; for a review of the current lithostratigraphic nomenclature, see Nielsen *et al.* 2023). The underlying Sularp Formation was excavated and described by Funkquist (1919) (see also Nørregård 1925), and the upper part of the Komstad Limestone Formation is exposed across the meadow in a water-logged abandoned quarry situated just east of the Læså, about 100 m NNE of the well site, as well as in the riverbed adjacent to the quarry (Fig. 1).

The Vasegård-1 borehole penetrated the basal part of the Dicellograptus Shale, the entire Sularp and Komstad Limestone formations, and was terminated at 19.64 m within the Alum Shale Formation. The core from the overlying till (0–1.58 m) was not preserved. The core recovery was low in the upper part of the borehole above the Komstad Limestone; this interval is illustrated by Pedersen (1989, fig. 8). It comprises the basal part of the Dicellograptus Shale (1.58–3.56 m), consisting of dark grey shale that is partly non-laminated (likely bioturbated, although the burrows are generally indistinct). Core recovery in this interval was 74%. This unit is underlain by the bentonite-rich Sularp Formation (3.56–5.23 m). The boundary is marked by a shift in colour to bioturbated light grey mudstone with a greenish tint and, shortly below, thick bentonites appear. No conglomerate was observed at the boundary, although Pedersen (1989, fig. 8) indicated such a layer. The core has rotated during drilling at this level, presumably resulting in some core loss. A conglomerate is present at the boundary in the nearby section excavated and described by Funkquist (1919), and the thickness of the Sularp Formation in the borehole closely matches that recorded in the excavated section. The core recovery within this unit was low (58%), owing to the numerous bentonite beds. The top of the basal conglomerate of the Sularp Formation is located at 5.11 m. The upper 50 mm contains black, rounded clasts (probably phosphorite) up to 25 mm in diameter. Below follows 30 mm of light grey shale with common black burrows, probably *Chondrites*, underlain by 40 mm of grey shale rich in small pyrite nodules. There are thus no black clasts in the 70 mm of shale between the conglomerate *sensu stricto* and the top of the Komstad Limestone, which is marked by a sharp, smooth surface. It remains an open question whether these 70 mm of grey shale represent a thin veneer of the Almelund Shale known from Skåne (see Nielsen

et al. 2023 and references therein) or simply an atypical development of the conglomerate, which is up to 20 cm thick elsewhere on southern Bornholm (Grönwall 1916, p. 74). For the time being, the interval is assigned to the Sularp Formation.

The underlying Komstad Limestone Formation is 4.78 m thick (5.23–10.01 m) and represents the thickest development of this unit recorded on Bornholm (cf. Nielsen 1995; Nielsen *et al.* 2018, fig. 16). Core recovery from the Komstad Limestone and the underlying Alum Shale was essentially 100%. The upper part of the underlying Alum Shale was drilled between 10.01 and 19.64 m, including the entire Tremadocian part of the formation. Stipes of the graptolite *Rhabdinopora* were observed on surfaces at 12.53 m and 12.70 m. Drilling was terminated in the Furongian part of the formation (see below).



Fig. 5. Breccias in the 55 mm wide Hjulmagergård-1 core. **A.** Crushed and re-cemented Komstad Limestone, 15.45–15.65 m. **B.** Crushed Alum Shale, 17.9–18.1 m, photographed in a dry state so that the blackish shale appears grey.

Correlation of the Alum Shale in Vasegård-1

The Vasegård-1 core was analysed in 2018 using a handheld Niton™ XL3t GOLDD+ XRF device at the Subsurface Laboratory, GEUS. Element concentrations were measured at 214 levels in the core, corresponding to approximately every 80 mm in the interval 1.61–19.57 m. Details of the analytical procedure and applied corrections are provided by Schovsbo *et al.* (2018). The corrected U, K and Th concentrations were converted to American Petroleum Institute (API) units using the algorithm by Ellis & Singer (2007):

Sum gamma-ray (API units) = $4 \times \text{Th (ppm)} + 8 \times \text{U (ppm)} + 16 \times \text{K (wt\%)}$.

Three outliers with anomalous U concentrations were removed from the data before a running average of three data points was used to construct the gamma-ray curve shown in Fig. 3. The gamma-ray log is an excellent tool for correlating the Alum Shale due to its high and strongly variable uranium content (cf. Schovsbo *et al.* 2018; Nielsen *et al.* 2018).

Correlation with the Limensgade section

The abandoned shale/limestone quarry at Limensgade was cleared in the spring of 2017, resulting in excellent exposure of the Alum Shale and the overlying Komstad Limestone. Shortly afterwards, a survey of the section (with primary focus on the Alum Shale) was carried out in May 2017 using a Georadis GT-32 portable gamma-ray logger provided by the Department of Geosciences, University of Copenhagen. Measurements were acquired at approximately 10 cm intervals, with each data point representing a two-minute recording period. On this basis, the gamma-ray log shown in Fig. 3 was produced. Figure 3 also shows a detailed correlation of the log pattern with the unpublished graptolite zonation established by von Jansson (1979); for remarks on correlation with the current zonation, see the caption to Fig. 3. Von Jansson found that the Tremadocian Alum Shale at this locality is 4.0 m thick, not 2.6 m thick as originally reported by Poulsen (1922). The gamma-ray log obtained, which can be correlated with the Gislövshammar-2 borehole in Skåne and several wireline-logged wells on southern Bornholm (Nielsen *et al.* 2018), corroborates this conclusion (see further remarks below).

The basal conglomerate of the Komstad Limestone contains phosphorite and glauconite and is marked by a prominent spike on the gamma-ray log, which can also be clearly identified on the gamma-ray log of Alum Shale constructed for the Vasegård-1 core (Fig. 3). At Limensgade, this bed is underlain by 0.6 m of Alum Shale containing small phosphorite nodules (Fig. 3), as already noted by Poulsen (1922); these account for the high gamma-ray intensity in this interval. This upper interval of the Alum Shale with elevated gamma-ray readings is consistently double-peaked in all investigated sections on Bornholm, except in the Billegrav-2 borehole (cf. Nielsen *et al.* 2018, fig. 16), suggesting that two levels with more common phosphorite are present. This is unsurprising, given the very strong condensation of this interval (compare with the Gislövshammar-2 borehole in Skåne, see Nielsen *et al.* 2018, fig. 14). The lower 3.4 m of the Tremadocian Alum Shale include four moderate maxima that can be correlated between Vasegård-1 and Limensgade (Fig. 3). There are no obvious lithological differences between the shale at these levels and the remaining Alum Shale.

The basal part of the Tremadocian Alum Shale is incomplete on Bornholm, with most of the *Rhabdinopora campanulatum* Zone absent, representing a hiatus of approximately 2–2.5 million years (see Nielsen *et al.* 2023 for a brief review of the current graptolite zonation). Given this strong condensation, it is possible that the unfossiliferous interval separating the graptolite-bearing shale from the Furongian strata at the base of the section is, in fact, of Ordovician age (see Fig. 3). If this interpretation is correct, the Cambro–Ordovician boundary is marked by a small peak in gamma-ray values followed by a decline in gamma-ray intensity. However, in Scandinavia it is customary to place the boundary at the first occurrence of planktonic graptolites, a convention that is also followed here, as in Nielsen *et al.* (2018). Accordingly, the boundary is placed on the descending limb of the gamma-ray log curve above the minor maximum that marks the top of the Furongian *Acerocarina ecorne* Zone. In Skåne, an unfossiliferous interval included within the *Acerocarina* Superzone also separates the trilobitic uppermost Cambrian from the graptolite-bearing Ordovician shales (see Nielsen *et al.* 2018 and references therein). If the Cambro–Ordovician boundary is located at c. 14.9 m in Vasegård-1 as indicated, the Ordovician section of the Alum Shale is c. 4.9 m thick, which represents the thickest development recorded on Bornholm.

Comparison with Skelbro-2 and St. Bukkegård-1

The double gamma-ray peak marking the boundary between the Alum Shale and the Komstad Limestone in Vasegård-1 is also well developed in the Skelbro-2 gamma-ray log (Fig. 4). Below that, the moderate gamma-ray peak labelled 1 is likewise correlatable, whereas correlation of the smaller maxima at lower levels is less convincing. The gamma-ray log response across the Cambro–Ordovician boundary, marked by a minor peak followed by a slight decrease in intensity (as discussed above), is similar to that observed in the Skelbro-2 gamma-ray log. The upper part of the Furongian exhibits three gamma-ray peaks (Pe-2, Pe-3 and Pe-4) above the prominent PGS spike, which can also be correlated between Skelbro-2 and Vasegård-1 (see Nielsen *et al.* 2018 for details of the Alum Shale gamma-ray log stratigraphy). The Vasegård-1 borehole appears to terminate c. 2 m above the level of the PGS spike, while the overlying three peaks are well expressed.

In the Vasegård-1 gamma-ray log, there is a conspicuous peak at 11 m, overlain by a pronounced low (Fig. 4). This log pattern is not observed in the Skelbro-2 borehole or in any other boreholes on southern Bornholm (cf. Nielsen *et al.* 2018, fig. 16). Phosphorite nodules appear to be present in the interval with high gamma-ray readings just below 11 m. At 11.0 m, there is a thin limestone bed (c. 10 mm) with an erosive top overlain by small clasts (up to 5 × 15 mm), suggestive of a minor hiatus. Immediately above, small nodules of limestone occur between 10.86–11.0 m, which may account for the low gamma-ray intensity in that interval.

The gamma-ray log motif of the Ordovician and uppermost Furongian succession is atypical in the St. Bukkegård-1 well (Nielsen *et al.* 2018, fig. 12), complicating assessment of the total thickness of the Alum Shale Formation in the Læså area. The St. Bukkegård-1 well penetrated Alum Shale from c. 3.1 m directly below the Quaternary section to a depth of 37.8 m; hence, the Alum Shale Formation is at least 34.7 m thick at the drill site. The Tremadocian section of the Alum Shale in this borehole is probably at least 4 m thick, as at Limensgade, located c. 400 m south of St. Bukkegård. If the thickness of the Furongian *Acerocarina* Superzone – overlying the recognisable Pe-2 to Pe-4 peaks – is comparable to that in the Vasegård-1 borehole, located c. 750 m WNW of St. Bukkegård, where it measures c. 1.5 m (Fig. 4), the total thickness of the Alum Shale Formation in the Læså area may be estimated at ≥ 35.6 m.

Discussion

On unpublished draft maps made by the late Helge Gry (probably in the 1950s), occurrences of Alum Shale are indicated due north of Gravgærde as well as in the garden of Soldatergård (Fig. 1). Strangely, these observations were ignored when Gry (1960, 1969) compiled his geological map of Bornholm. The presence of Alum Shale in Gravgærde-1 is thus consistent with these earlier, unpublished observations. This implies that a belt of Alum Shale extends from Soldatergård to Gravgærde, which must be separated by a major fault from the Ordovician strata exposed farther north-east along the Læså stream, near Vasegård, and in the former Hjulmagergård and Vasegård limestone quarries. Parts of this succession are also encountered in the Hjulmagergård-1 and Vasegård-1 boreholes as described in this paper. Hjulmagergård-1 intersected the separating fault, which has a vertical displacement estimated at around 40–50 m and presumably strikes NW–SE (Fig. 1). The minor repetition of the Komstad Limestone in this well, separated by brecciated Alum Shale, indicates reverse reactivation of the fault. This interpretation accords with the orientation of the Komstad Limestone in the nearby Hjulmagergård quarry, which dips towards the fault, also indicating reverse drag (Fig. 1).

The upper part of the gamma-ray log is atypical in the St. Bukkegård-1 well (Nielsen *et al.* 2018, figs 12, 16; see also Fig. 4). The Alum Shale section cored in Vasegård-1 represents this interval, with the characteristic Pe-2, Pe-3 and Pe-4 gamma-ray log markers identifiable in both wells, providing robust tie-points for comparison. Correlation based on the gamma-ray logs shows that the Tremadocian succession is c. 4.9 m thick in the Vasegård-1 borehole, which – like the 4.8 m thick overlying Komstad Limestone – represents the thickest development of these units known from Bornholm. Somewhat surprisingly, the underlying *Acerocarina* Superzone is thinner (1.5 m) than in the Skelbro-2 core (2.7 m, see Nielsen *et al.* 2018). Adding the thickness of the *Acerocarina* Superzone, as recorded in the Vasegård-1 borehole, and the Tremadocian part of the Alum Shale, as observed in the old quarry at Limensgade, to the confidently correlated lower main part of the Alum Shale in the St. Bukkegård-1 well, suggests that the Alum Shale is at least 35.6 m thick in the Læså area. The maximum thickness may approach 38 m if the Tremadocian at St. Bukkegård is as thick as in the Vasegård-1 borehole and the *Aceroca-*

rina Superzone is as thick as in the Skelbro-2 borehole.

The Alum Shale section exposed at Limensgade provides a detailed tie between the gamma-ray log pattern and the graptolite zonation (Fig. 3). The gamma-ray log pattern, which can also be correlated with the Gislövshammar-2 borehole in Skåne, Sweden, and several wells on southern Bornholm (see Nielsen *et al.* 2018, fig. 14), corroborates the greater thickness of the Ordovician part of the Alum Shale, as identified by von Jansson (1979). The Cambro–Ordovician boundary on Bornholm is marked by a relatively inconspicuous gamma-ray peak followed by a slight decline in gamma-ray intensity. Reliable recognition of this subtle log pattern requires that the interval be viewed in context with the more prominent gamma-ray spikes in the upper Cambrian and at the base of the Komstad Limestone.

Conclusions

- The Cambro–Ordovician successions penetrated by the fully cored shallow boreholes Gravgårde-1, Hjulumagergård-1 and Vasegård-1, hitherto undescribed, are summarised.
- Alum Shale forms the bedrock in a belt from Sol-datergård to north of Gravgårde, which is not shown on the existing geological map of the area.
- This belt is separated from Ordovician strata to the east by a NW–SE striking fault with an estimated vertical offset of around 40–50 m that appears to have undergone minor reverse reactivation.
- A gamma-ray log was constructed for the Vasegård-1 core, based on handheld XRF measurements, allowing correlation with wireline logged boreholes on southern Bornholm.
- The Alum Shale Formation is at least 35.6 m in the Læså area but may reach 38 m. These estimates are based on the succession encountered in the St. Bukkegård-1 well, supplemented by the new stratigraphic data from the Vasegård-1 borehole and the thicknesses known from Skelbro-2, correlated using gamma-ray logs.
- Maximum thicknesses on Bornholm of the Komstad Limestone Formation (4.8 m) and the Ordovician part of the Alum Shale (c. 4.9 m) are recorded in the Vasegård-1 borehole.
- A detailed tie between the gamma-ray log pattern and the graptolite zonation for the Ordovician part of the Alum Shale is established in the section exposed at Limensgade.

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