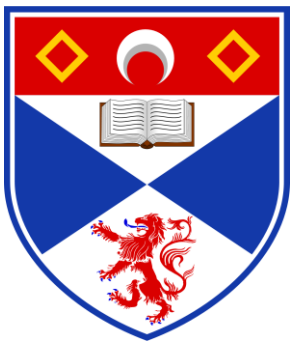
Echinoids from the Early Palaeogene (Danian) of Sangstrup Klint: Preliminary Results



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Abstract

Understanding the end-Cretaceous (K-Pg) mass extinction provides insights into how the Earth responds to deadly external impactors. It provides an extreme case study of the consequences when such impactors are big and hit particularly sensitive areas.

Owing to their excellent fossil record and insights they can provide on palaeoenvironmental conditions, echinoids have long been the focus of studies on ecosystem recovery following the end-Cretaceous mass extinction. Within Denmark, many of these studies have been focused on the chalk formations of the eastern coast of Zealand where the physical K-Pg boundary (66 Ma) is preserved and visible. Whilst incredibly informative on changes immediately following the boundary, the relatively narrow time interval and smaller geographic area do not allow for larger scale changes across the Danish basin to be fully assessed. To address this scientific knowledge gap, this study investigates a site much further north in the Djursland peninsula on the Danish mainland. Sangstrup Klint (Sangstrup cliffs in English) is formed later in the early Danian (between 66–61.66 Ma) and represents a continuation of the stratigraphic sequence seen on the eastern coast of Zealand. A collection was made of specimens from this site which were then compared to other sites in Europe and further afield. Many of these species were found to have wide geographic distributions during this period, even stretching beyond Europe. Temporal distributions pointed towards unequal impacts of the extinction event and corresponding regional loss of the species *Phymosoma Ravni*, whilst also revealing potential migration patterns for *Adelopneustes montainvillensis*. These in turn also reflect later recovery of ecosystems and the mixing of global fauna. These results reveal the widespread turmoil amongst ecosystems following the catastrophe and emphasise the significance of migration as a consequence of it. Identifying such migration patterns are important for understanding the potential impacts these new species may have had on later ecosystem recovery and development.

Introduction

The chalk beds of Denmark are famous for their links to the end-Cretaceous mass extinction event. They have been the subject of innumerable studies, for example playing an integral part in Alvarez's revolutionary paper suggesting a bolide impact as a cause for the extinction (Alvarez *et al.*, 1980). These beds are rich in echinoids and other macro-fauna with many of them deposited directly preceding or following the boundary (most famously Stevns Klint and Møns Klint which show the famous fiskeler layer). This makes them indispensable for understanding the impact of the event on ecosystems and their subsequent recovery. However, the fame of sites displaying the physical boundary layer has meant that even marginally earlier or later localities across Denmark have received comparatively less attention. One such site is Sangstrup Klint which formed in the Danian (between 66–61.66 Ma) and represents a continuation of boundary sections further south. Amongst the rich macro-fauna within this section is a particular abundance of echinoid fragments. Variety in morphology and community composition makes this fauna highly informative on the palaeoenvironment and wider ecosystem conditions during this time period. In Sangstrup, their exceptional preservation makes it an ideal site of study, however, there has to date not been any study dedicated to this site.

Aims and Objectives

This work aims to improve the resolution of Danish echinoid assemblages immediately following the extinction event, both temporally and geographically. It is hoped this will allow for an improved understanding of wider Eurasian trends such as migration patterns and ecosystem recovery.

The major objectives are:

- To describe echinoid and assess the composition of echinoid assemblages from Sangstrup Klint.
- To compare the results from Sangstrup to other Danish and Eurasian sites in order to improve the resolution of larger scale recovery patterns and the position of Danish echinoids in them.
- To determine the role of the K-Pg extinction in dictating Palaeogene echinoid assemblages and identifying their potential origins.

Depositional Environment

Sangstrup Klint is a lower Danian limestone cliff which stretches ~3km north-west to south-east along the coastline of the Djursland peninsula in eastern Jutland. The cliffs extend to 5km if combined with the neighbouring Karlby Klint to the north-west and reach up to 17 metres in height. The site borders the Sorgenfri-Tornquist Zone which lies just offshore to the north. The Klints are comprised of large bryozoan mounds which formed in the European Chalk Sea in cooler waters at moderately northern latitudes. This epeiric sea was present during the relatively high sea levels of the late Cretaceous and into the early Palaeocene, leading to the numerous chalk deposits present across Europe from this time.

The Klints are composed of distinct bryozoan mounds with bank structures. Analysis of these structures was not carried out in this investigation; however, Nielsen, (1973) has created detailed descriptions of those at the neighbouring Karlby Klint which are very similar. These mounds likely formed in an outer shelf environment below the wave-base. The diversity of fauna at Sangstrup suggests that it didn't form at any substantial depth. Ehrhard (1930) posits a maximum depth of 300m for the mounds at Stevns Klint which formed as an earlier part of the same sequence of deep-shelf mounds as in the Danish Basin. Modern counterparts to the branching bryozoan fauna observed at Sangstrup are unable to survive in higher energy environments (Nelson *et al.*, 1988). This suggests that the abundance of branching bryozoans present here are likely to have resided below the storm wave base. Similar fragile specimens were found by Bjerager and Surlyk (2007) to make up a majority of the skeletal material in mounds of roughly the same age in the Rødvig area, leading to their conclusion of a low energy environment in the southern end of the bryozoan mounds. A deeper, lower energy environment is also supported by the heterozoan association of fauna present here which have no photic demands.

Materials and Methods

Fieldwork was carried out from the 6-11 June 2026 at Sangstrup Klint in northeastern Denmark. The studied sections of the cliffs were the western end by the main car park just before they become Karlby Klint and the eastern end near Fornæs camping site (Fig. 1).

Figure 1. *The location of Sangstrup Klint within Denmark and the location of sampling sites at west and east ends of Sangstrup Klint. Generated using Google Earth imagery (Google Earth, 2026).*

Fieldwork consisted of geological observations and fossil echinoid sample collection and identification. The lithostratigraphy was recorded at the study site in the eastern end and is shown by the stratigraphic log below (Fig. 2). Convenience sampling was conducted on fallen or loose rock fragments from the cliff face as the age of the cliffs is already known and a precise position within the stratigraphic sequence is not necessary for this study. Moreover, this is a much less destructive method and meant a greater volume of material could be searched for fragments. Any fragments were given a rough initial description and separated into sampling bags recording time and location. They were later described in detail and grouped according to species. Many specimens taken from the field were not sufficiently well preserved for an accurate description to be made.

Exceptionally, in situ sampling was used for the index genus *Tylocidaris* whose abundance meant that observed spine fragments could be identified and recorded in the cliff face. Access was also granted to the private collection of Michael Lykke Bertelsen of Grenaa Geocenter, which contains a vast quantity of echinoid and other fossils collected at this location over the past several years and hence provides a highly valuable complementary archive. Due to time restrictions, specimens here were only given a preliminary description in-person and then photographed extensively using a regular phone camera to allow for more

detailed description later. These specimens had also been previously cleaned using an abrasive unit, making their identification and analysis much easier. As a result, they make up a large proportion of the overall dataset. Many images included within this report are of these specimens (Figs. 3 – 7).

Collected specimens were systematically described and identified if possible. Comparisons were also made with three other sites – Stevns Klint, the Maastricht type area and the Mangyshlak peninsula – based on a literature review of published results from these sites. Reasons for the selection of these sites are given in the section “Comparisons with other Eurasian sites”.

Results and Discussion

Stratigraphy

There is a general shallowing trend across the section. The numbers refer to the stratigraphic log below (Fig. 2).

1. Hard bryozoan mounds: ~280cm; packestone; fossiliferous biomicrite; uneven and undulating upper contact dipping to the west, lower contact is not visible; bed is homogenous; scattered flint nodules; relatively hard but can be broken apart by hand; beige/creamy white; predominantly bryozoan fragments, additionally with crinoid stems, bivalves, gastropods and echinoids.

2. Clay layer: ~5cm; wackestone; sparse biomicrite; sharp bounding contacts; internal banding of darker and lighter greys; soft and crumbly, friable; notable reduction in macroscale fossil abundance, primarily bryozoan fragments visible.

3. Soft bryozoan chalk: ~300cm; wackestone; biomicrite; sharp lower and gradational upper contacts; alternates in layers of banded flint and blocky chalk; flint bands are more sheet-like, apparently following bands of thalassinoid burrows; chalk is soft and crumbly, friable, similar texture to (2); very light grey/dirty white; still predominantly bryozoan fragments in a similar fossil assemblage but reduction in overall numbers.

4. Scree: ~250cm; obscured by scree which contains abundance of bryozoan fragments.

5. Jutting-out bed: ~50cm; wackestone; sparse biomicrite; gradual contact above and below; harder than below and difficult to break apart by hand; creamy white colour; similar fossil comp although significantly reduced (almost a mudstone).

6. Soil: ~50cm; limestone from 5 makes up the regolith; very dark brown/black colour of soil; short root network; clasts in soil are largely flint.

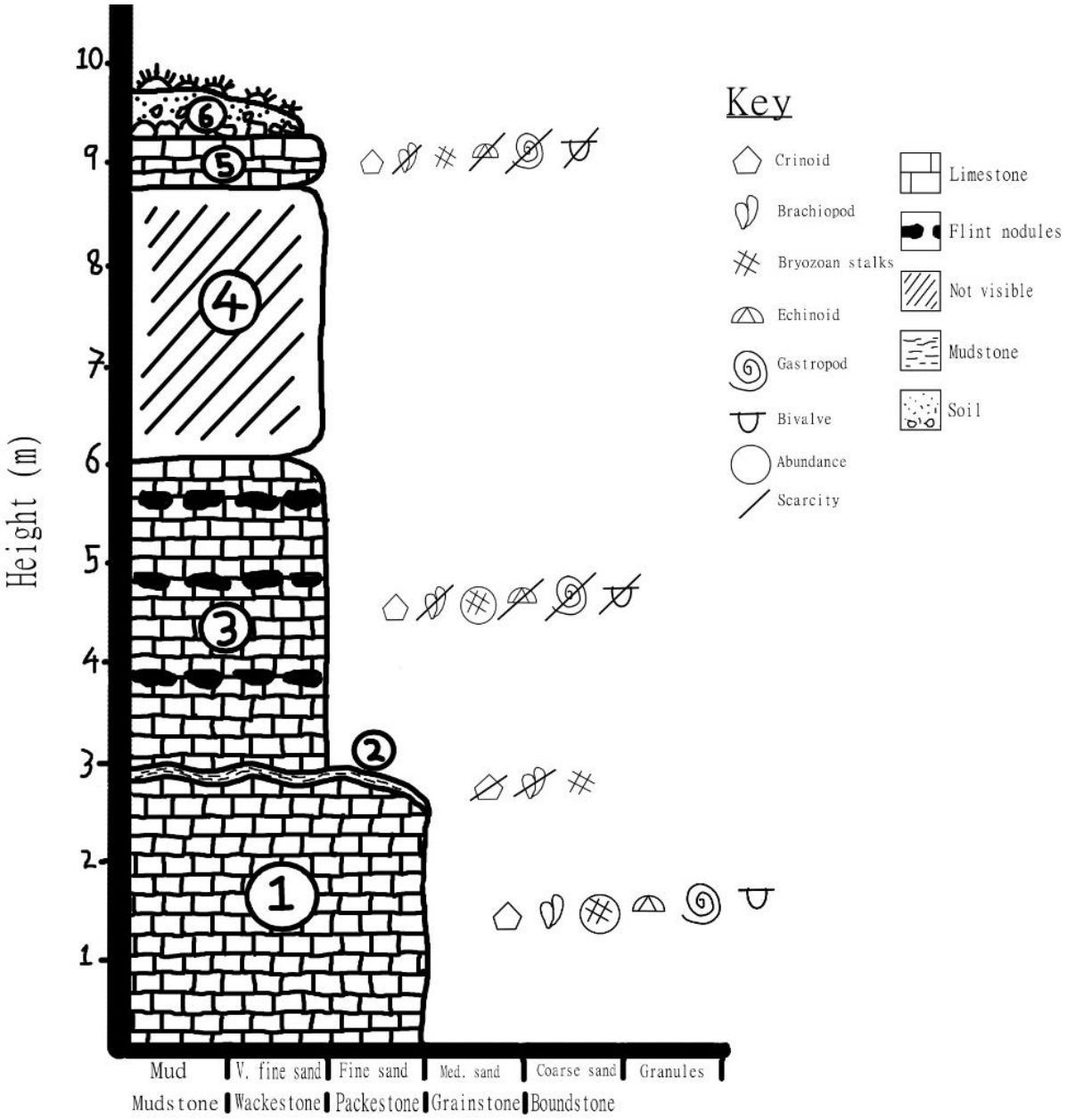

Figure 2. *Stratigraphic log of eastern sampling site.*

Sangstrup Klint is of lower Danian age. The mounds lie just above the Cretaceous-Palaeogene (K/Pg) boundary which is interpreted here to surface just offshore (see Galerites remarks). They are assigned to the D2 nannofossil zone (Håkansson and Thomsen, 1999), the P1b planktonic foraminiferid zone (Rasmussen, Heinberg and Håkansson 2005) and the *Tylocidaris oedumi* echinoid zone (Rosenkrantz, 1937). As accessibility to the uppermost sections of the cliff face was difficult, it is unknown whether this passes into the *T. abildgaardi* zone.

The primary variation within the chalk of these cliffs is its clay content which increases as the section progresses upwards. This could be due to a reduction in the input of terrigenous material, potentially from changing hydrodynamics which altered transport paths to this site as the Danish basin shrank throughout this time period (Bjerager and Surlyk, 2007). If so, regression layers have been eroded. Alternatively, a transgression pulse may have favoured pelagic organisms over epibenthic/infaunal species due to increased water depth causing the rock to have a greater matric component as opposed to fossiliferous material. Of note is the change in flint layout across this section, from irregularly dispersed nodules in the hard bryozoan chalk to regular, almost continuous thalassinoid galleries in the softer material. Such banding likely indicates externally forced periodic cessation of sediment deposition, potentially caused by Milankovitch cycles (Huygh *et al.*, 2025).

Diagenetic Alteration

Samples collected at Sangstrup are more altered than those observed in collections from other Danish sites, namely Stevns Klint for which there exists a substantial body of work. A significant number of specimens were found as flint steinkerns which appeared to occur with much greater frequency. This was particularly visible in the case of *Galerite* specimens which were exclusively collected as steinkerns, contrasting with Stevns Klint where they are more commonly found as calcite tests (Rasmussen, 1971). Further diagenetic alteration was seen in the form of a pinkish discolouration in many preserved calcite tests (Fig. 3). The colour is not a coating but rather continuous throughout the calcite crystals. It is likely caused by the full recrystallisation of calcite tests, incorporating manganese from the movement of porewater through the sediment into the structure. This alteration warrants further examination. Diagenetic differences are interpreted here as being caused by a higher redox boundary in Sangstrup, likely due to its position further offshore on the shelf. Reducing conditions can indirectly promote the dissolution of biogenic silica, allowing it to more easily fill tests and form abundant steinkerns (Zijlstra, 1987).

Moreover, manganese is an ion which is significantly controlled by redox conditions, with its solubility increasing substantially in more reducing conditions (Burdige, 1993; Miao, DeLaune and Jugsujinda, 2006). Therefore, for it to be as abundantly present as it is, high solubility would be required to allow manganese ions to be carried and accumulated into calcite tests in the abundance seen at this site.

Systematic Descriptions

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Holectypoida* (Duncan, 1889)

Family: *Conulidae* (Lambert, 1911)

Genus: *Adelopneustes* (Gauthier, 1889)

Adelopneustes montainvillensis (Sorignet, 1850)

Figure 3. One complete test and test fragments, tests uncommon; complete test is 30 mm width at ambitus; test outline is oblong and subcircular (slightly pentagonal); small apical disc (diameter <5% that of test), centrally located on aboral surface, poorly preserved; ambulacra are straight sided and taper both adorally and adapically, plating changes from simple on adapical side to pyramid plating on aboral side, contain simple pore pairs; peristome centrally located; interambulacra have a scattered cover of primary tubercles with numerous granules; oral side of the test curves up inwards towards peristome; tear drop shaped periproct along III-5 plane.

Dimensions - Width/Length (mm):

28/30

25/27

Remarks:

Occurs abundantly and across a large geographic range, especially in the Danian.

Occurrences include: the lower Guelhelm member (early Danian) of the Maastrichtian type area in the Netherlands and Belgium (Jagt, 2000); the uppermost Senonian and lower Danian of the Guelaat es snam district in Tunisia (Gauthier, 1889); Danian of the Montainville Pisolitic Limestone type locality in the Paris Basin, France (Roman, 1989); early to late Danian of the Mangyshlak peninsula (Kazakhstan), Crimea and the Caucasus (Endelman, 1980); the Bruderndorf formation (late Danian) at Haidhof, Austria (Kroh, 2001); the late Danian of Aggersborggaard in Denmark (Ravn, 1927); the Danian of Stevns Klint (Ravn, 1927).

The entire Guelaat es snam (Tunisia) section shows a continuous Maastrichtian to Palaeocene succession with both a K-Pg and Danian/Selandian boundary identified across the wider region. Despite explicitly stating an occurrence in the Upper Cretaceous, Gauthier (1889) does not record the exact position of the material. With later works disputing earlier accounts of the region's succession, it is possible that the material collected by Gauthier (1889) was incorrectly assigned to the Late Cretaceous (Pervinquière, 1903; Steurbaut *et al.*, 2000). However, as the most recent reference to this material describes it as occurring in the Uppermost Senonian and there is currently no work directly addressing any potential issues at present, it will continue to be assumed that material is derived from the Upper Cretaceous in this paper (Kroh, 2001).

Its absence in Maastrichtian beds of Europe but potential presence in north Africa possibly indicates that there was some environmental or facies change which caused *A. montainvillensis* to spread into more northerly habitats following the extinction event. Jagt, (2000) suggests that *A. montainvillensis* was an infaunal grazer or detritivore which lived at shallow depths. This suggests that sea levels had dropped from the time of extinction event, providing a suitable habitat for *A. montainvillensis* to move into, and supports the common view of a regression between the Cerithium Kalk and bryozoan mounds of Danish beds during the mid-lower Danian (Schmitz, Keller and Stenvall, 1992).

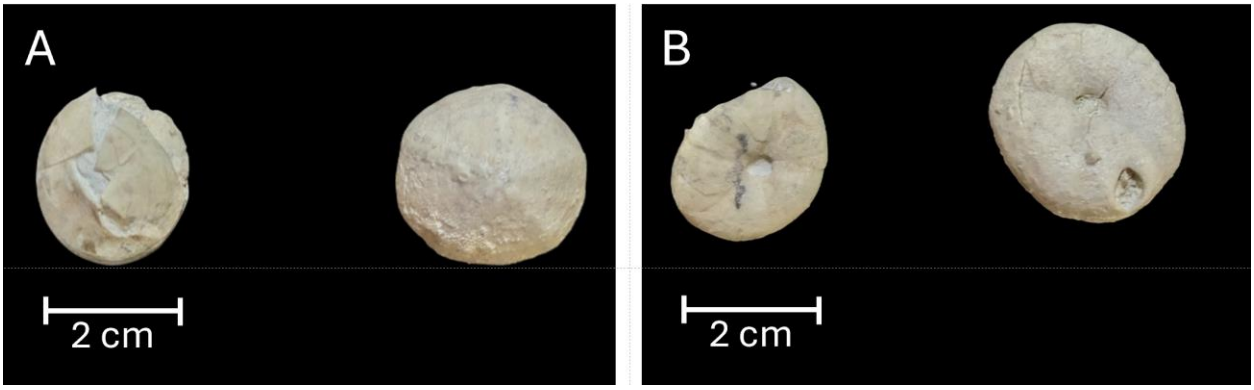

Figure 3. *Two Adelopneustes montainvillensis specimens (A) adapical surfaces and (B) adoral surfaces. Photographed with permission from the private collection of Michael Lykke Bertelsen. Units in centimetres.*

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Phymosomatoida* (Mortensen, 1904)

Family: *Phymosomatidae* (Pomel, 1883)

Genus: *Phymosoma* (Haime, 1853)

Phymosoma ravni (Schluter, 2012)

Figure 4. One complete test and test fragments; tests uncommon; complete test is 21mm width at ambitus; test outline is circular; apical disc always absent but diameter no more than 40% of test; ambulacra are straight sided and taper both adorally and adapically; peristome centrally located; ambulacral plates each have a large primary tubercle taking up almost the entire plate with few granules; interambulacral plates oblong, up to 5mm long, contain a large primary tubercle taking up ~50% of the plate, few granules and secondary tubercles, one or two secondary tubercles as opposed to a scrobicular ring; primary tubercles are crenulate; aboral side not visible in specimens.

Dimensions - Width/Length (mm):

18/21

Remarks:

Occurrences have a long range throughout Europe including the Lower to Upper Maastrichtian of the Don Basin (Bulgaria), the Isle of Rügen (Germany), and the Mangyshlak peninsula (Kazakhstan) (Jeffery, 1997); the Maastrichtian type area in the Netherlands and Belgium (Jagt, 2000); the Maastrichtian and Danian of Stevns Klint, Denmark (Schlüter *et al.*, 2012).

Specimens from these sites have all received later reclassifications by Schlüter et al. (2012) from *Phymosoma granulosum* to *P. ravni* after they found morphological distinctions across different identifications of *P. granulosum*. The exact range and location of specimens of *P. ravni* may therefore be complicated by this historical generalisation with difficulties in precisely distinguishing these two species in past works.

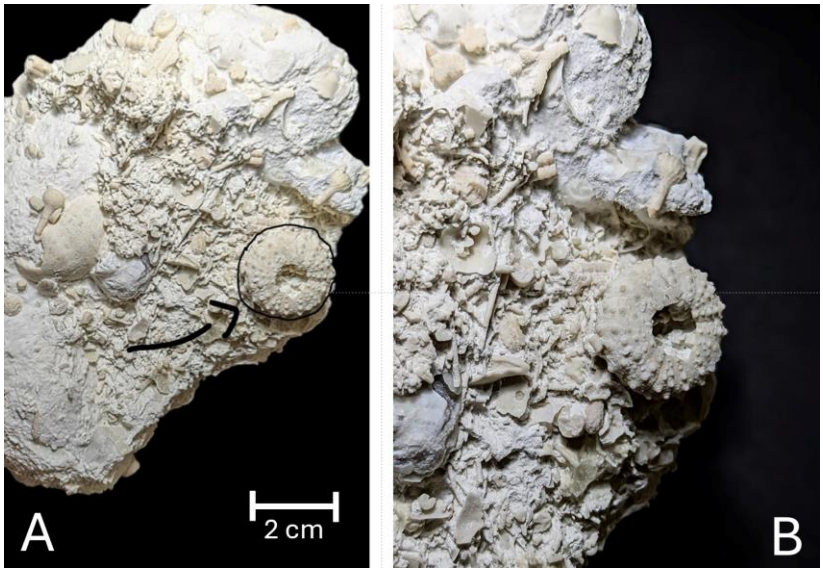

Figure 4. *Phymosoma ravni specimen (A + B) adapical surface. Photographed with permission from the private collection of Michael Lykke Bertelsen. Units in centimetres.*

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Spatangoida* (Agassiz, 1840)

Family: *Micrasteridae* (Lambert, 1920)

Genus: *Cyclaster* (Cotteau, 1856)

Cyclaster danicus (Schlüter, 1897)

Figure 5. Several complete tests; tests relatively uncommon; largest complete test 25mm width at ambitus; sub-ovular, heart-shaped test outline; off-centre, depressed apical disc on aboral surface with a shorter ambulacrum III and longer I and V; apical disk is also very small (diameter <5% that of test), 3 visible gonopores in triangular arrangement; possess a peripetalous fasciole; ambulacra taper adapically; curved and undulating rows of simple pore pairs that are slightly depressed with ridges between pores, there is also notable distance between each pore of a pair; peristomes slightly larger than apical disc and located along III-5 plane near the margin of ambulacrum III; individual interambulacral plates not clearly distinguishable; relative density of primary tubercles with up to two secondary tubercles in proximity and few granules; oral side of the test is not flat with a slightly undulating surface; circular periproct located on the rim at interambulacra 3, with broad shallow groove connecting to the apical disc across its aboral side.

Dimensions - Width/Length (mm):

20/25

21/26

Remarks:

Despite longer range occurrences elsewhere in Europe across the K/Pg boundary, no occurrences have been found in the Maastrichtian in Denmark.

Occurrences include: the Greensand Formation (upper Maastrichtian and lower Danian), Kazimierz Dolny, Poland; Korsnæb member (lower Danian) Stevns Klint, Denmark (Rasmussen, 1971; Rasmussen, Rasmussen and Hansen, 2011)). Smith and Jeffery (2000) included *C. integer* as a senior synonym to *C. danicus* and therefore have also noted occurrences in Azerbaijan, the northern Caucasus, the French Pyrenees Georgia, Kazakhstan (Mangyshlak), Madagascar and the Transcaspian region.

Cyclaster danicus is abundant across all lower Danian outcroppings in Denmark, particularly the bryozoan mounds which are indicative of this period. Unlike other Danish specimens which are obscured by the overgrowth of calcite cement, specimens studied at Sangstrup retain many of their finer details (Bjerager and Surlyk, 2007). Abnormal specimens with an apical depression have been described by (Asgaard, 1976). These are found situated on the surface of the hardground overlying the Cerithium Kalk of Stevns Klint (lowermost Danian) and in burrows penetrating down into the uppermost Maastrichtian chalk (Rasmussen, 1971). At the time of writing, no such specimens are known of at Sangstrup Klint suggesting

they are temporally confined to the lowermost Danian which lies just below the visible section at Sangstrup. This supports Asgaard's conclusions that growth had been retarded by environmental factors including their inability to burrow into the hardgrounds on which they are found. The peripetalous fasciole of *C. danicus* represents the first appearance of this structure in Denmark and represents an initial burrowing form that will develop into deeply burrowing forms later in the upper Danian (Asgaard, 1979).

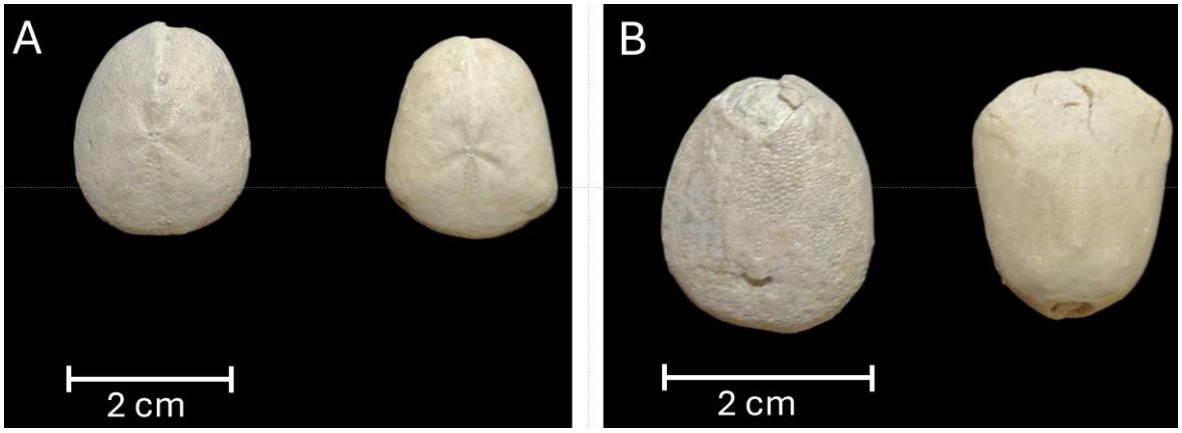

Figure 5. *Cyclaster danicus specimen (A) adapical surface and (B) adoral surface. Photographed with permission from the private collection of Michael Lykke Bertelsen. Units in centimetres.*

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Holasteroida* (Durham and Melville, 1957)

Family: *Holasteridae* (Pictet, 1857)

Genus: *Echinocorys* (Leske, 1778)

Echinocorys sulcatus (Goldfuss, 1826-33)

Figure 6. Numerous complete tests and fragments; tests common; complete tests are much larger than other specimens, with sizes between 55-80mm; convex apical disc with oval outline and diameter 15-20% that of tests, centrally located on aboral side, 4 gonopores in trapezoid arrangement in disc; majority of

tests have borings condensed on the top of the aboral side; ambulacra relatively narrow and straight sided, taper adapically with simple pore pairs; peristome located along III-5 plane slightly further from the margin of ambulacrum III than *Cyclaster danicus*; 7 interambulacra plates in a series, oblong and subhexagonal; tubercles not well preserved, up to 5 primary tubercles on a plate; ambulacral plates are much shorter in height, up to 16 in a row; oral side of the test slightly indented around peristome; periproct located along the edge of interabulacrum 5.

Dimensions - Width/Length (mm):

57/69

63/70

Remarks:

Occurrences across Europe exclusively in the Danian.

Occurrences include: the Bruderndorf formation (late Danian) at Haidhof, Klement and Bruderndorf, Austria (Kroh, 2001); lower Maastrichtian to upper Danian of the Navarra district, Spain (Smith *et al.*, 1999); upper Maastrichtian of the Mangyshlak peninsula, Kazakhstan (Jeffery, 1997).

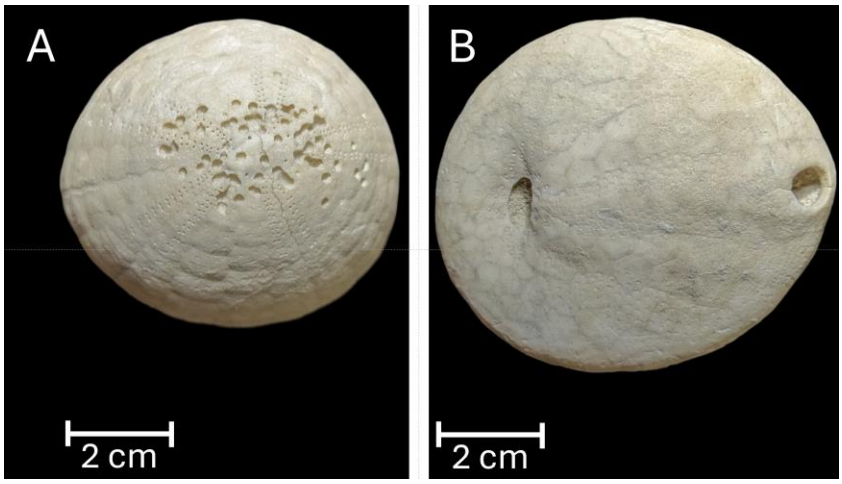

Figure 6. *Echinocorys sulcatus specimen (A) adapical surface and (B) adoral surface. Photographed with permission from the private collection of Michael Lykke Bertelsen. Units in centimetres.*

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Holectypoida* (Duncan, 1889)

Family: *Galeritidae* (Gray, 1825)

Genus: *Galerites* (Lamarck, 1801)

Galerites stadensis (Lambert, 1911)

Figure 7. Found exclusively as steinkerns washed up along shoreline; very common; sizes amongst specimens hover around 20mm; profile is gently rounded and not pointed; apical discs have a diameter ~10% that of tests, centrally located on aboral side; ambulacra are straight sided and taper both adorally and adapically; peristome circular and centrally located on flat oral side; periproct located along III-5 plane towards the margin of interambulacrum 5.

Dimensions (Width/Length):

19/20

20/21

21/23

Remarks:

Occurrences across Europe are found in the Senonian to Maastrichtian and do not appear to cross the boundary into the Danian.

Occurrences include: the upper Maastrichtian of Stevns Klint, Denmark (Estrup and Kjær, 2024); Koshak (uppermost Maastrichtian) of the Mangyshlak peninsula, Kazakhstan; the lower Maastrichtian of the Isle of Rügen, Germany; the lower to upper Maastrichtian of the Maastricht type area, the Netherlands and Belgium (Jeffery, 1997).

Steinkerns at Sangstrup are solely found washed upon the shoreline, indicating they come from a chalk bed offshore. The abundance of them and high quality of preservation indicates they have not travelled too far. As they do not appear to cross the K/Pg boundary across other Danish sites, it can therefore be

assumed that the boundary is present some way not too far off the coastline at Sangstrup. This similarly supports an age of lower Danian for the cliffs at Sangstrup.

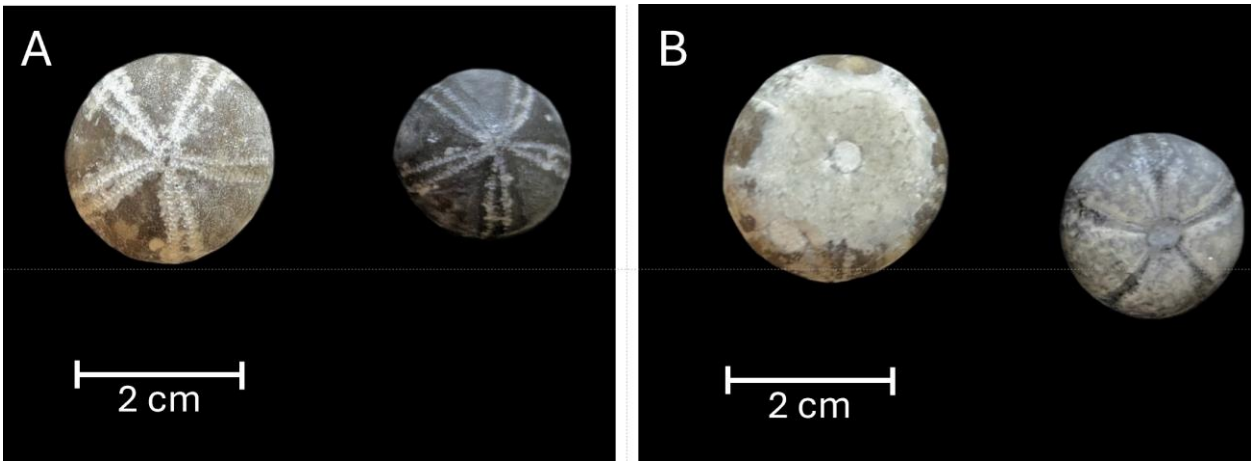

Figure 1. *Galerite stadensis specimen (A) adapical surface and (B) adoral surface. Photographed with permission from the private collection of Michael Lykke Bertelsen. Units in centimetres.*

Class: *Echinoidea* (Leske, 1778)

Subclass: *Euechinoidea* (Bronn 1860)

Order: *Cidaroida* (Claus, 1880)

Family: *Cidaridae* (Gray, 1825)

Genus: *Tylocidaris* (Pomel, 1883)

Tylocidaris oedumi

Only spines found; spines are common, especially in packestone bryozoan mounds; spine bodies are commonly found without the neck; two distinct forms are found, one slimmer and more cylindrical, the other more club-shaped; the head of the cylindrical form tapers with a very shallow gradient to the neck while the club-shaped form has a sharper gradient to a more bulbous head (although much more gradual

than the transition from head to neck on *T. abildgaardi*); the head of the cylindrical form has a diameter 33-50% of its length whilst the other has a diameter 75-100% of length; both have spiny, denticulated ridges composed of thorns running lengthwise of the head; apex of the cylindrical form is obtuse whilst the club-shaped form is acute and more pointed.

Remarks:

Despite occurrences across Europe, *Tylocidaris oedumi* is best known from sites in southern Sweden and eastern Denmark (Brotzen, 1960; Gravesen, 1993; Jagt, 2000). It represents an important, although outdated, stratigraphic marker which has historically been used across European localities to identify lower Danian material (Gravesen, 1993). The intermediately sized spines of *T. oedumi*, which are neither too broad and bulbous nor particularly long and slender, reflect on the more stable substrate these echinoids would have lived on in the bryozoan mounds (Bjerager and Surlyk, 2007). Too broad and they would have been unable to get a 'footing' amongst the assortment of bryozoan fragments making up the seabed. Too long and they would have likely had difficulty navigating the scattered fragments to move with any real pace.

Figure 2. *Tylocidaris oedumi spine in situ in layer (1) at eastern sampling site*

Comparisons with other Eurasian Sites

Table 1 summarises the distribution of echinoid species found at Sangstrup across 3 other key sites. These sites were selected as points of comparison for a number of reasons. The 3 sites all cross the K/Pg boundary, meaning that assemblages can be collected right up to and following the extinction event, creating an improved image of where Sangstrup fits into the recovery. These sites have been extensively studied increasing the likelihood of good resolution assemblages to be constructed for them. They are also all formed in mostly similar environments. Moreover, they each represent a point of varying geographical distance from Sangstrup. Stevns Klint is a part of the same sequence of bryozoan mounds as Sangstrup Klint but located on their southern end. Variations between these two sites will show differences in local conditions and likely reflect small scale controls on distribution. The Maastricht type area is formed further away within the same European Chalk Sea which includes the Danish Basin, but at a shallower depth (Smit and Brinkhuis, 1996). Differences here may inform on regional influences over both a longer period and at a more general level. The Mangyshlak peninsula is formed the furthest away in the Turgai Strait which bordered Europe to the East. It is formed under similar conditions in an epeiric chalk sea at a similar palaeolatitude (Kopaevich *et al.*, 1999). Comparisons to this area could give insight into migration patterns and the endemicity of fauna at a broader scale.

Species	Stevns	Maastricht	Mangyshlak
A. montainvillensis	+	+	+
C. danicus	+	-	+
E. sulcatus	+	-	-
P. ravni	+	+	+
G. stadensis	+	+	+
T. oedumi	+	-	-

Table 1. *Presence (+) or absence (-) of species at select Eurasian sites.*

Stevns Klint

Stevns Klint was found to have the greatest overlap with the assemblage found at Sangstrup Klint, with all 6 species confirmed to be present here (Ravn, 1927; Rosenkrantz, 1939; Brotzen, 1960; Rasmussen, 1971;

Bjerager and Surlyk, 2007). This is unsurprising given that they are both part of the same bryozoan mound sequence.

30% of confirmed Maastrichtian species found at Stevns Klint are regular (Rosenkrantz, 1939; Brotzen, 1960; Rasmussen, 1971). This rises to 75% in Danian sections, showing an increase across the boundary (Ravn, 1927; Bjerager and Surlyk, 2007). Despite Maastrichtian beds not being visible at Sangstrup, comparison can still be made with the exposed Danian section. This shows that regular species comprised a notably smaller proportion of the echinoid fauna at Sangstrup (40%). One potential explanation for this may be the hydrodynamic regime present across the mounds at Sangstrup. Movement of regular tests laying epifaunally may have congregated them away from the sampling site whilst a comparatively lesser effect was had on irregular material, protected by the substrate into which they burrow. However, as no measurement was made of the mound structures at the sampling site in this study, this cannot be confirmed. Abundance sampling would also be required to gauge the distribution of similar fauna across the mounds. Moreover, this may also just be a consequence of sampling bias as 12 species were identified from other works as having been confirmed in the lower Danian of Stevns Klint, whilst a relatively small pool of only 6 were identified at Sangstrup in this paper.

Maastricht Type Area

The Maastricht type area of Belgium and the Netherlands only had a confirmed crossover with 3 of the same species as in Sangstrup, showing the least similarity of the 3 sites (Jeffery, 1997; Jagt, 2000; Jagt, Deckers and Jagt-Yazykova, 2024). Specimens of *Tylocidaris hardouini* have also been identified here which Jagt (1996) suggests represents a close relative of *T. oedumi*.

A notable absence from this area is *Cyclaster danicus*. From other occurrences, this species appears to radiate widely following the extinction event, even going beyond European basins. However, there is no record of its presence at Maastricht. Such an absence matches the general trend noted at this site of a low species crossover with fauna collected at Sangstrup, even though environmental conditions are similar. The region does however appear to show 100% crossover at a generic level with Sangstrup. This shows that similar living conditions did indeed exist at both sites. Therefore, the discrepancy in species as exemplified by the example of *Cyclaster danicus* may be explained as a case of partial geographical isolation in the Maastricht type area, potentially caused by some biogeographic barrier at the time of the extinction event.

Both regions share the upper Cretaceous species *Echinocorys scutata* and its disappearance occurs simultaneously across the boundary. However, the two sites react differently to its loss. In Danish beds it is soon replaced by *E. sulcatus* which never appears in the Maastricht type area. It is still debated whether *E. sulcatus* is an evolved form of *E. scutata*, but its absence nevertheless suggests that the environmental conditions in Maastricht following the extinction event were not conducive to its development.

The Maastricht type area also appears to display an increase in proportion of regular fauna to the highest across all 4 localities at 75% (van der Ham, 1988). This matches the trend seen across European sites of an increased proportion of regular echinoids after the event.

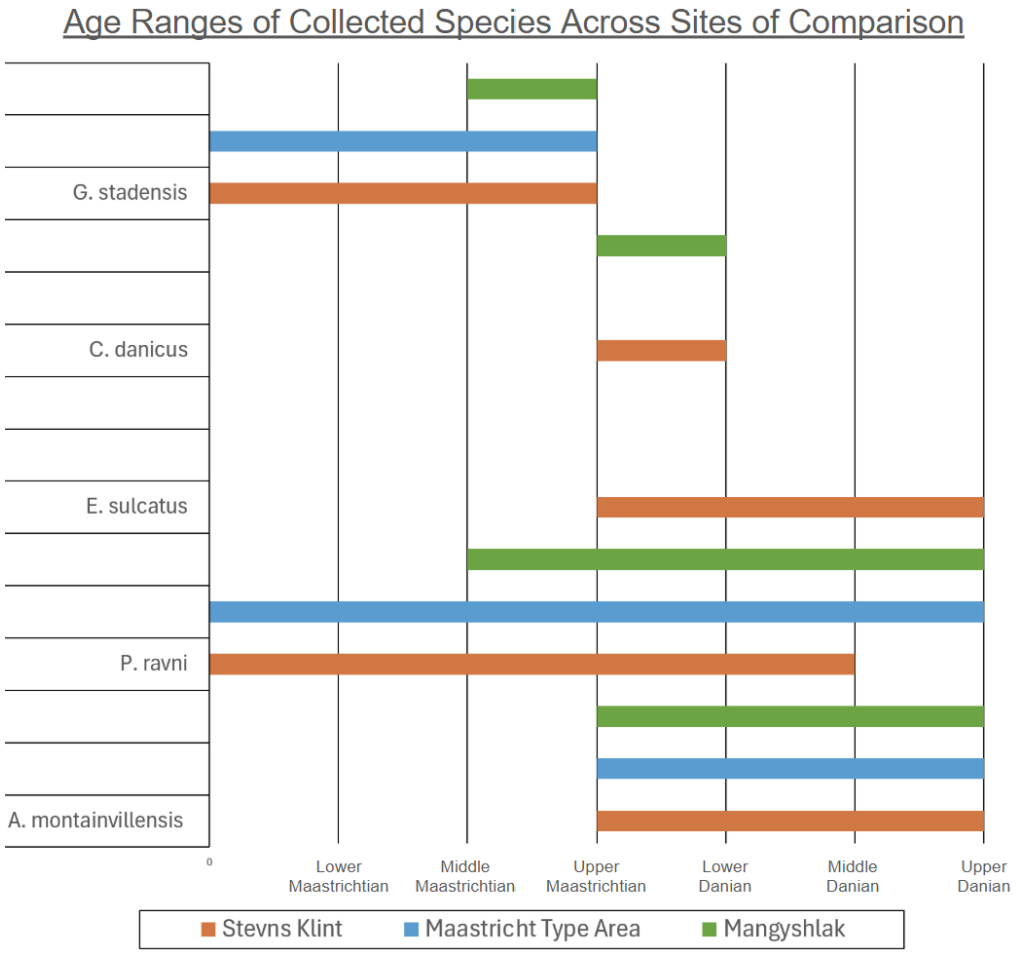

Figure 9. *Age range graph of species collected at Sangstrup across sites of comparison.*

Mangyshlak

Two of the three of the species found at Sangstrup are also found at the Mangyshlak peninsula. These all appear in the same time period as at Sangstrup, with the exception of *Phymosoma ravni* which is restricted to the uppermost Maastrichtian in Mangyshlak (Jeffery, 1997). The upper Maastrichtian and lower Danian chalk of the Mangyshlak peninsula were deposited in the epeiric Turgai Strait which borders the European Chalk Sea. Both Sangstrup Klint and the Mangyshlak area existed at roughly the same palaeolatitude and experienced similar environmental conditions during this time, including a transgression pulse across the boundary (Schmitz, Keller and Stenvall, 1992; Pardo *et al.*, 1999). However, *P. ravni* disappeared after the boundary at Mangyshlak whilst appearing to continue across the boundary in Danish beds. It has been suggested that the faunal turnover across the boundary at Mangyshlak was caused by a combination of the transgression pulse and extinction event which drove both a migration and extinction of the region's fauna (Jeffery, 1997; Pardo *et al.*, 1999). Specimens of *P. ravni* are identified here as being present in both the shallower waters of Mangyshlak during the uppermost Maastrichtian and deeper waters at Sangstrup during the lowermost Danian, meaning it is unlikely a facies change would have had a significant impact on the species. It may then be assumed that it was the extinction event which was the juncture at which it disappeared at Mangyshlak whilst persisting in Europe.

One potential explanation for this may be the catastrophic collapse of primary productivity during the extinction. Pardo et al., (1999) describe a turnover of ~50% of planktic foraminiferal species across the boundary at this site. Such extreme losses were likely accentuated for sessile benthic organisms which regular echinoids (including *P. ravni*) prefer to feed on by the sharp facies change into more intolerable deeper waters. This would have represented the loss of a significant food source for the species, possibly to the extent that survival was no longer feasible in this region. If such losses were less extreme further west, then it is likely that the consequences would have been similarly reduced. Moreover, as a mobile organism it is also possible that migration may have occurred across these two regions in search of food sources. In Denmark, the growth of bryozoan mounds in the early Danian including those at Sangstrup would have provided an ideal habitat for epifaunal grazers. The abundance of encrusting organisms would have provided a suitable food source for *P. ravni*. Furthermore, later radiation throughout Europe likely also reflects the recovery of ecosystems that the species subsequently became able to occupy. If so, it would also have mixed with previously unencountered species across this region, potentially leading to new ecosystem dynamics.

From Maastrichtian beds of the Mangyshlak area, ~43% of the species were found to be regular whereas only 25% were regular in the Danian (Jeffery, 1997). This decrease disagrees with the trends identified at Stevns and Maastricht. As the most distal region to which comparison was made, this is unsurprising as there were likely different larger scale processes acting here. Additionally, different diagenetic processes could have meant that vulnerable regular echinoid tests were more poorly preserved in this region.

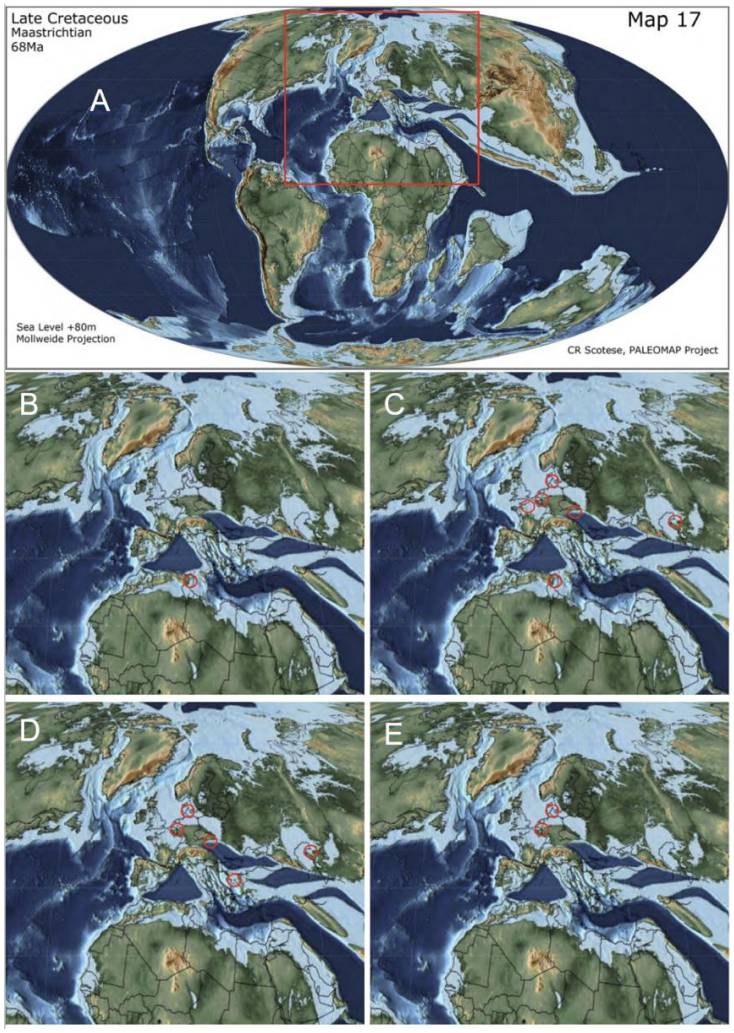

Figure 10. *Modified map from (Scotese, 2014) showing in red (A) highlighted area of comparisons; recorded Eurasian occurrences of Adelopneustes montainvillensis in the (B) upper Maastrichtian (before the boundary) and (C) lower Danian (after boundary); recorded occurrences of Phymosoma ravni in the (D) upper Maastrichtian and (E) lower Danian.*

Conclusions and Outlook

Conclusion

Despite existing as part of the same bryozoan mound sequence as Stevns Klint, diagenetic differences point to different redox conditions, which in turn may suggest a position further offshore. A diverse selection of echinoid species was found at Sangstrup Klint which provides an interesting point of comparison to other sites across Eurasia. Species identified at Sangstrup are all present across numerous Europe sites during this time, with many having distributions even further afield. Species are also distributed temporally, indicating migration patterns. *Phymosoma ravni* disappears at the Mangyshlak peninsula whilst persisting in Denmark across the boundary, potentially caused by the extinction event disrupting food systems across these regions. Its later radiation also possibly reflects the subsequent recovery of ecosystems following the event. *Adelopneustes montainvillensis* appears to migrate from northern Africa, but the exact causes could not be determined in this study. Despite similar environmental conditions, the Maastricht type area may have been geographically isolated from Sangstrup, giving rise to different assemblages at the species level, a point accentuated by the differential development of successors to *Echinocorys scutata* across these two sites after its demise. Almost all the sites of comparison display similar trends in changing regular to irregular ratios across the boundary to Sangstrup. Mangyshlak, however, displays a decrease in the proportion of regular echinoids across the boundary. Such differences highlight the different impacts of the extinction event across a larger scale.

This study confirms that recovery trends following the extinction event were consistent throughout Denmark, with the initially surviving echinoid species also continuing on later into the Danian. The migration and mobility of other species such as *A. montainvillensis* highlights the importance of migration as a reaction to catastrophic events, which can be shown here to occur over relatively rapid timescales. Similar movements can thus be assumed to occur for marine biota under rapidly increasing modern anthropogenic stresses, though tracing such movements may be more difficult than in the case of terrestrial biota. Identifying suitable and accessible environments for stressed biota, as Sangstrup and other areas of the Danish basin were for echinoids during the K-Pg boundary, is essential to understanding what modern migration patterns may arise.

Outlook

Owing to time restrictions, a comparatively small collection of species was created for Sangstrup Klint. With the quality of specimen preservation at this site, future work should continue to seek specimens from here as well as contact the numerous amateur collectors based in this region. Moreover, as Stevns Klint and Møns Klint were recently granted 'UNESCO Heritage status', Sangstrup may provide a useful alternative for those wishing to collect lower Danian samples from the same bryozoan mound sequence. That such interesting distribution patterns can already be drawn from the relatively small collection documented in this study should encourage further work on investigating distributions across the boundary. More detailed assemblages should continue to be built for different regions to allow a more complete picture to emerge that reveals the true complexity of the turmoil in the aftermath of the extinction event.

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Figures

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Fig. 10: Image modified from Scotese, C.R. (2014) *Atlas of Late Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 16 – 22, Mollweide Projection*. Evanston.

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