

Maastrichtian brachiopods from the chalk of Denmark

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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.

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<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 The study is based on an unpublished prize dissertation awarded the Gold Medal of the University of Copenhagen (Surlyk 1969).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

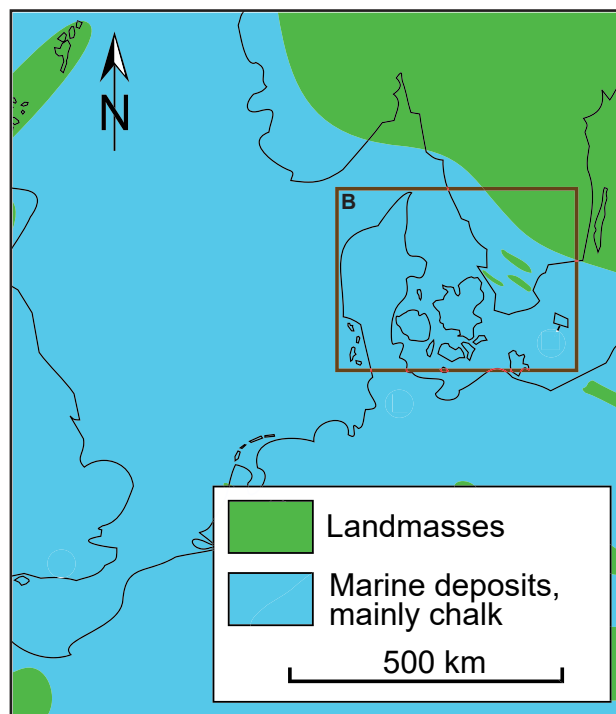


Fig. 1. Map showing the extent of the deep, epeiric Chalk Sea, which covered northern Europe in the Late Cretaceous. Modified from Surlyk *et al.* (2003).

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,

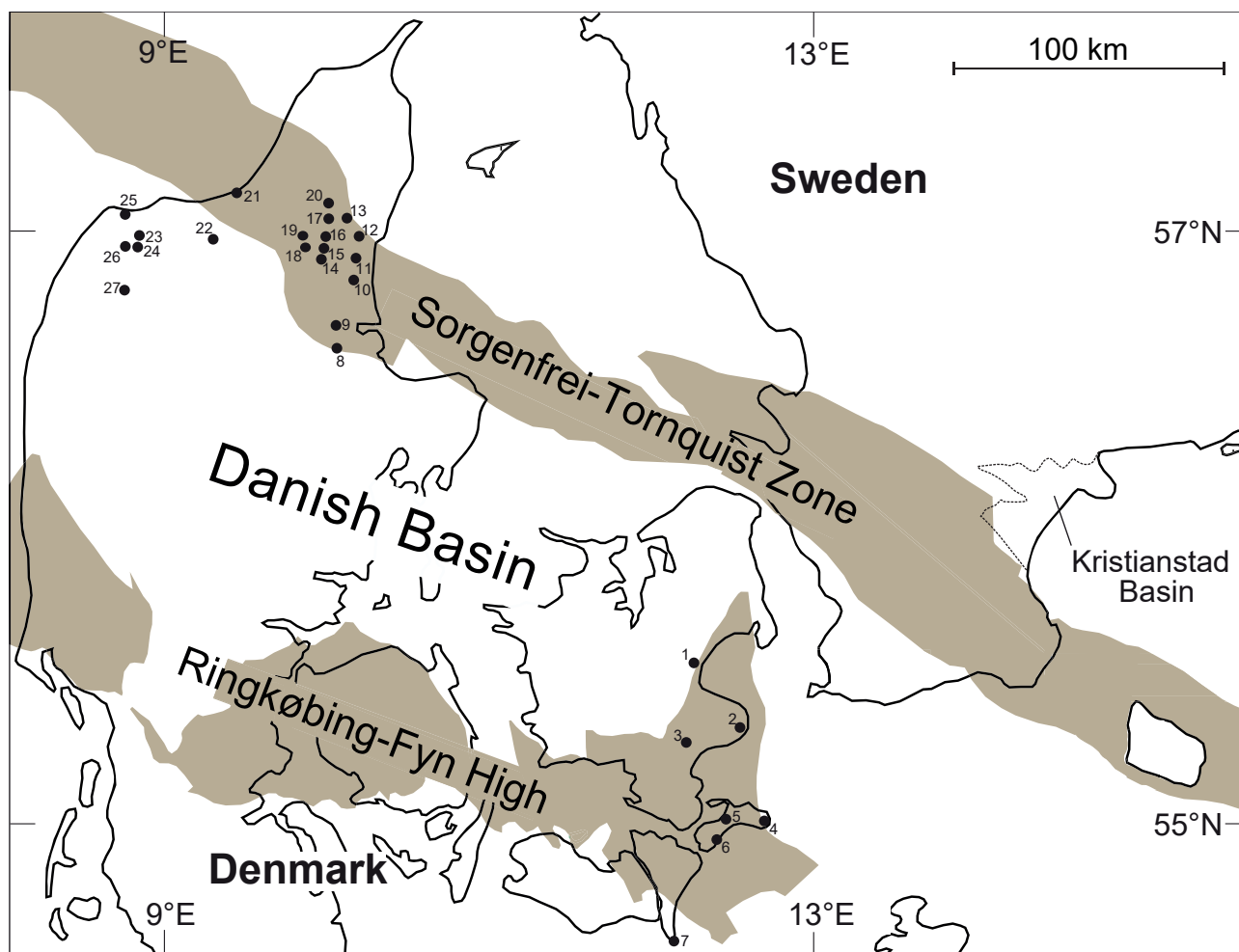


Fig. 2. Map showing the main structural features limiting the Danish Basin and the sample localities, forming the basis for this study. 1. Karlstrup, 2. Stevns Klint, 3. Kongsted, 4. Møns Klint (including 13 sampled thrust sheets), 5. Lille Bissinge, 6. Hvide Klint, 7. Gedser Fyr, 8. Gedser Odde, 9. 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>Neoliothyris obesa</i> Sahni, 1925 (Fig. 28). A, B, C: MGUH 34896.
<i>Neoliothyris fittoni</i> (von Hagenow, 1842) (Fig. 29). A: OESM 10942, B, C: MGUH 34897.
<i>Carneithyris 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

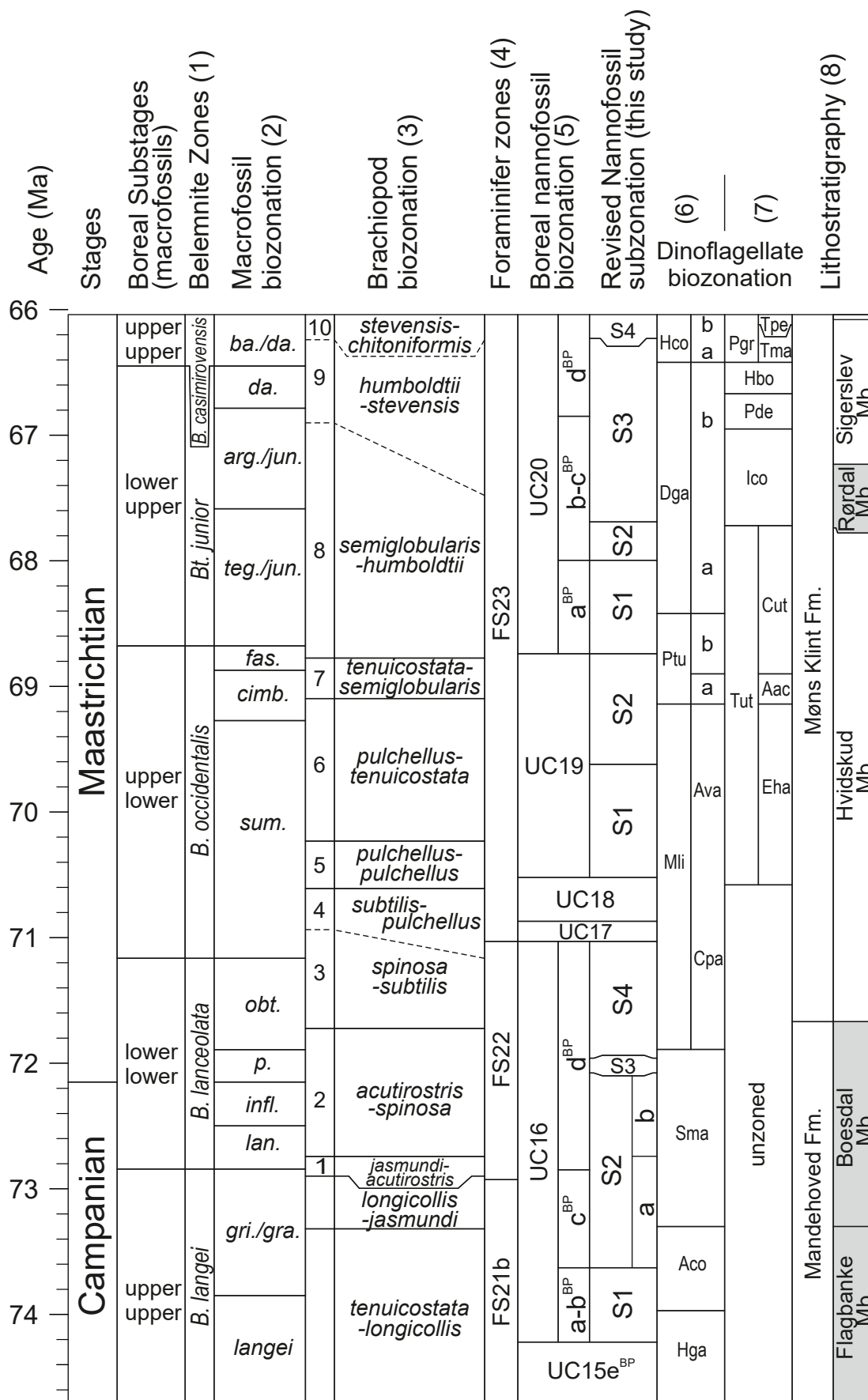
Steinich (1965) was the first to demonstrate that brachiopods obtained by washing of bulk samples were stratigraphically very useful, allowing the recognition of 3 full and 2 partial zones in the lower Maastrichtian chalk of the island of Rügen in NE Germany. Studies of the brachiopods from the Danish 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 uppercase 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 grimmensis*/*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

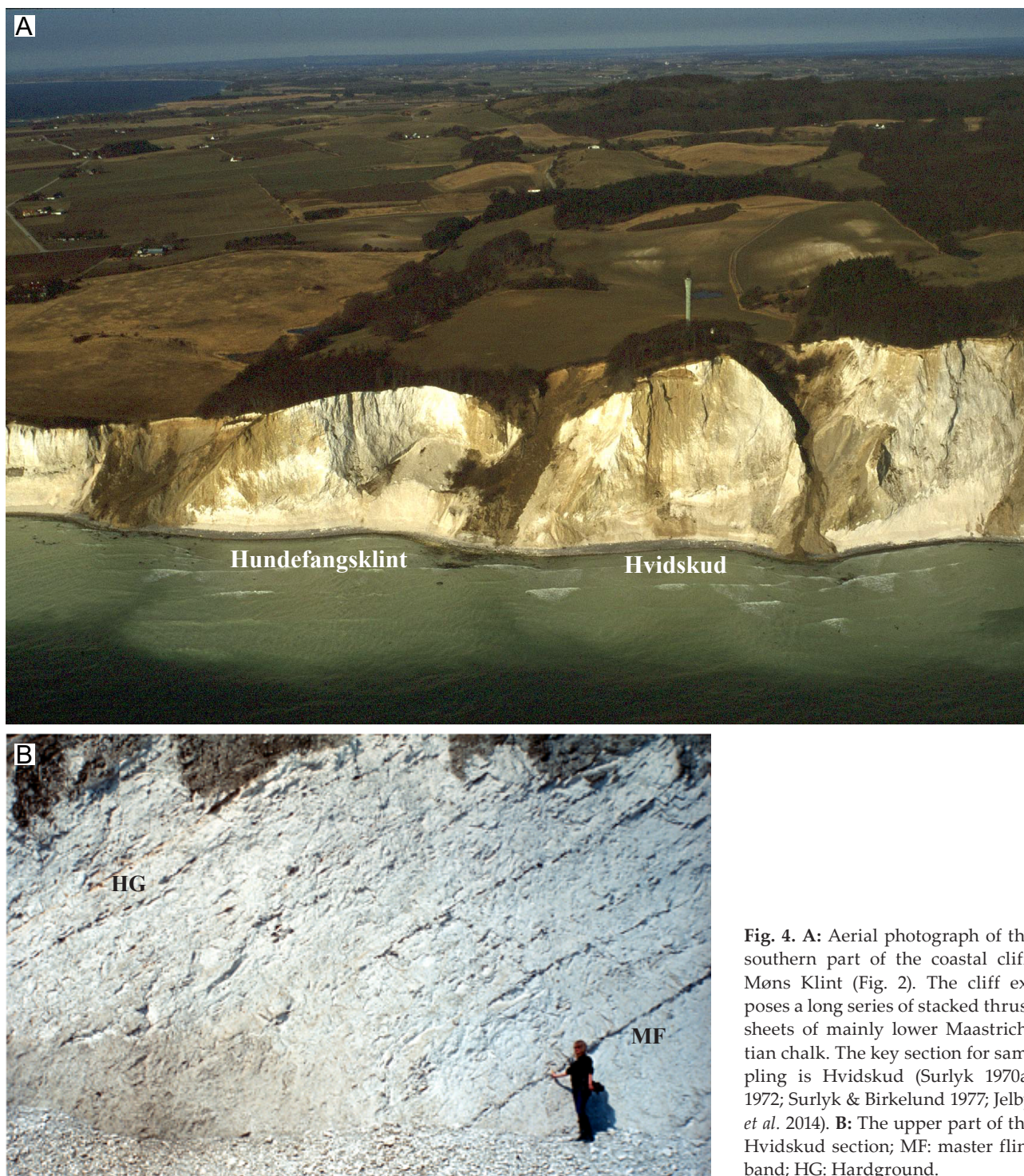


Fig. 4. A: Aerial photograph of the southern part of the coastal cliff, Møns Klint (Fig. 2). The cliff exposes a long series of stacked thrust sheets of mainly lower Maastrichtian chalk. The key section for sampling is Hvidskud (Surlyk 1970a, 1972; Surlyk & Birkelund 1977; Jelby *et al.* 2014). **B:**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

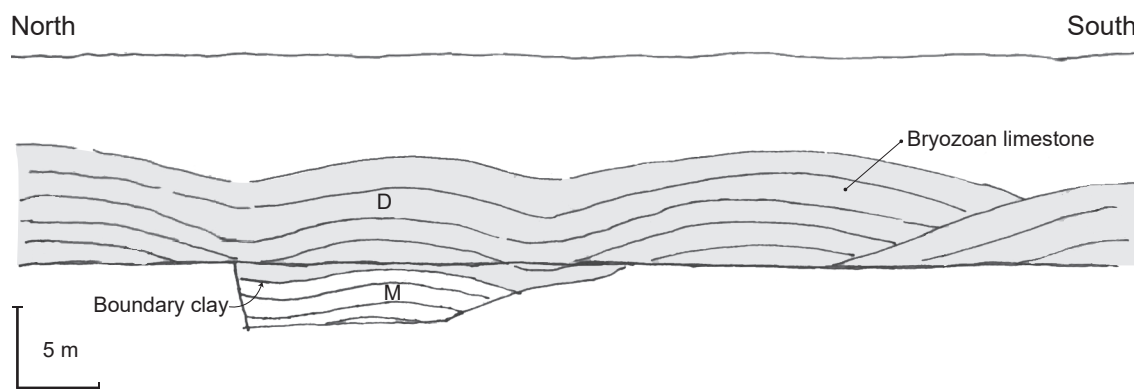
Stevns 3: *I. sendeni*, *Rugia stenius* n. sp., *M. semiglobularis*, *B. stevensis*; *stevensis-chitoniformis* Zone; upper upper Maastrichtian.

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

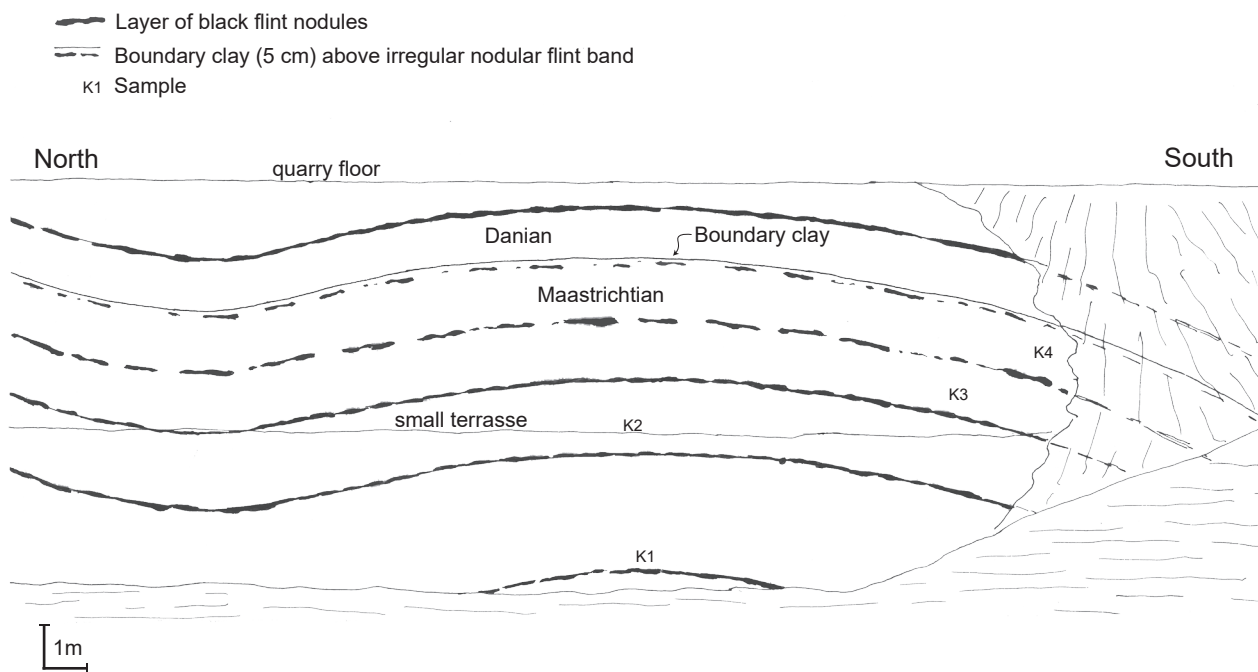


Fig. 5. Field sketches of the Maastrichtian–Danian (K–Pg) boundary at Karlstrup limestone quarry (1 in Fig. 2 and now abandoned). **A:** The lower non-shaded part is upper upper Maastrichtian chalk deposited in overlapping mounds (M). They are draped by the 5 cm thick boundary clay overlain by lower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

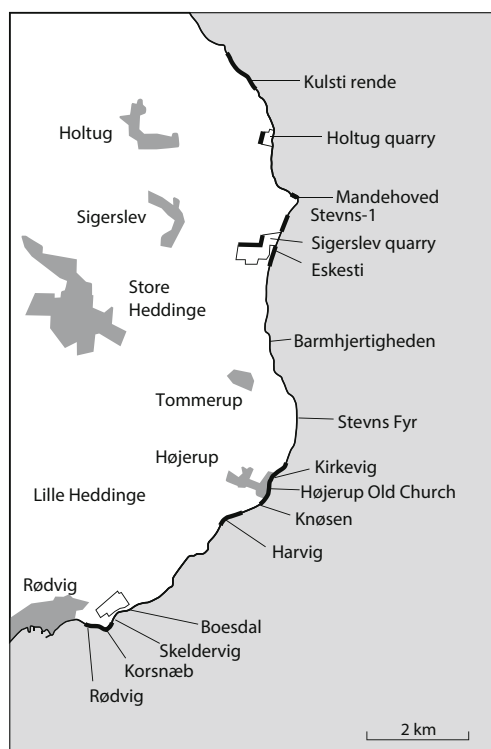


Fig. 6. Map showing the main sample localities along the coastal cliff, Stevns Klint (Fig. 2; From Hansen & Surlyk 2014).

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 barnesiae* 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 Slotsgavlene (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

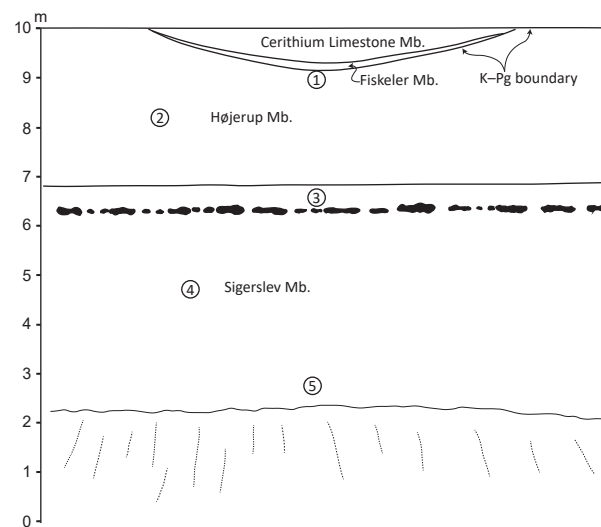


Fig. 7. Field sketch of the Maastrichtian–Danian (K–Pg) boundary succession exposed immediately south of the Højerup old church at Stevns Klint. This is the classical boundary location where Walter Alvarez in 1978 sampled the boundary clay, the Fiskeler Member to check if the iridium anomaly found at 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 Maastrichtian.

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-

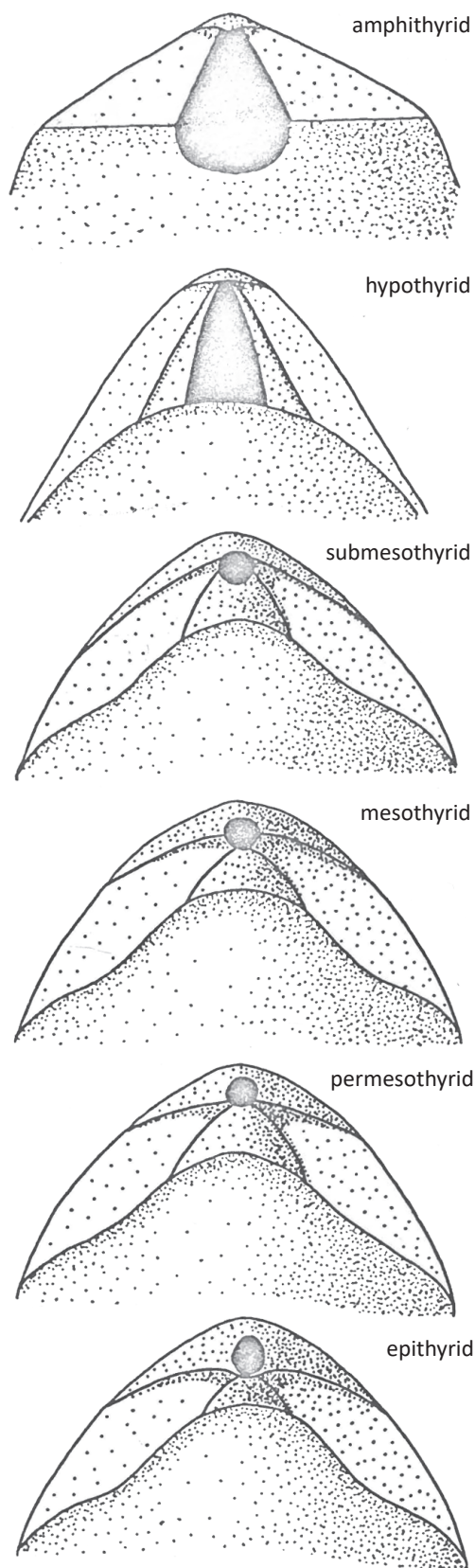


Fig. 8. Terminology describing the relative position of the pedicle opening and the beak ridges. Modified from Williams *et al.* (1997, fig. 318).

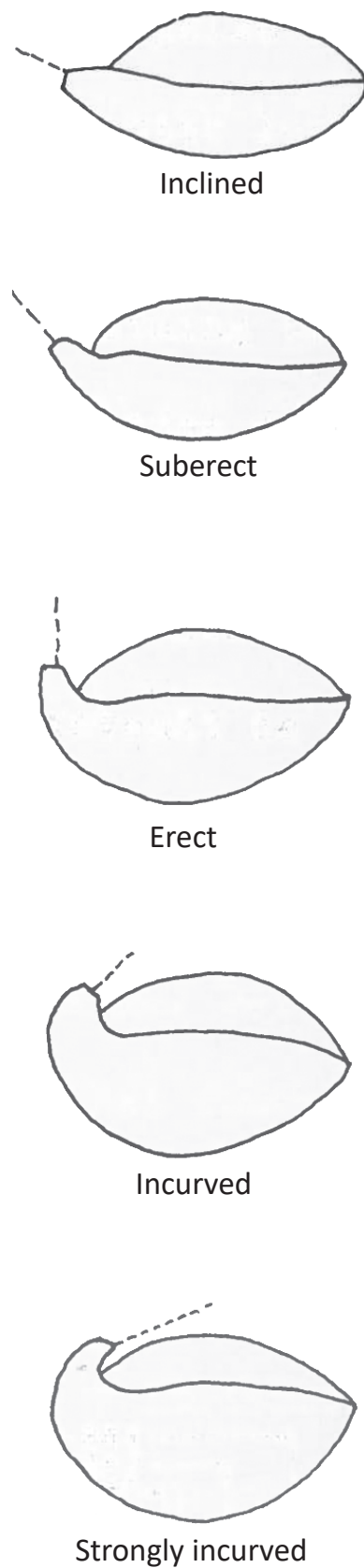


Fig. 9. Terminology describing the position of the pedicle openings relative to the beak ridges. Modified from Williams *et al.* (1997, fig. 318).

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

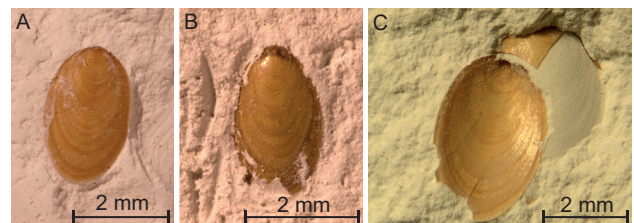


Fig. 10. '*Lingula*' *cretacea* Lundgren, 1885 ventral (A and B) and partially preserved dorsal valve (C). The specimens do not show enough detail of the posterior part around the hinge to allow a safe determination of the genus. Upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone, Sigerslev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

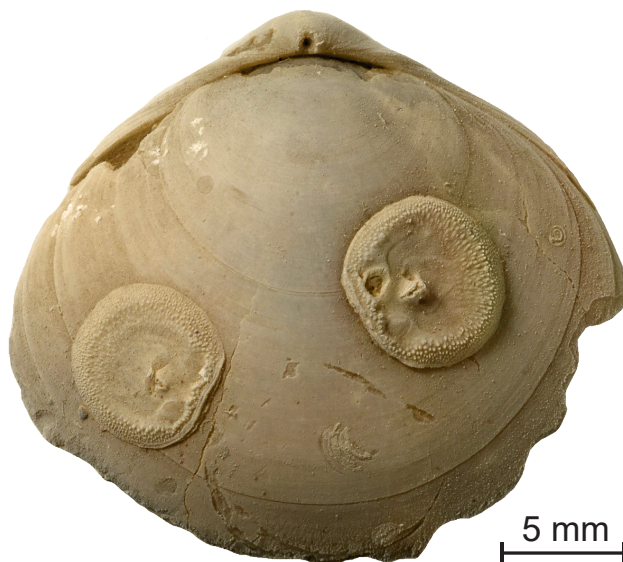


Fig. 11. *Crania craniolaris* Linnaeus, 1758 showing two ventral valves attached to the dorsal valve of the brachiopod *Carneithyris subcardinalis* (Sahni, 1925). The longitudinal axes of the two specimens are directed towards the anterior and lateral margin of the shell of *C. subcardinalis*. This fits 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.

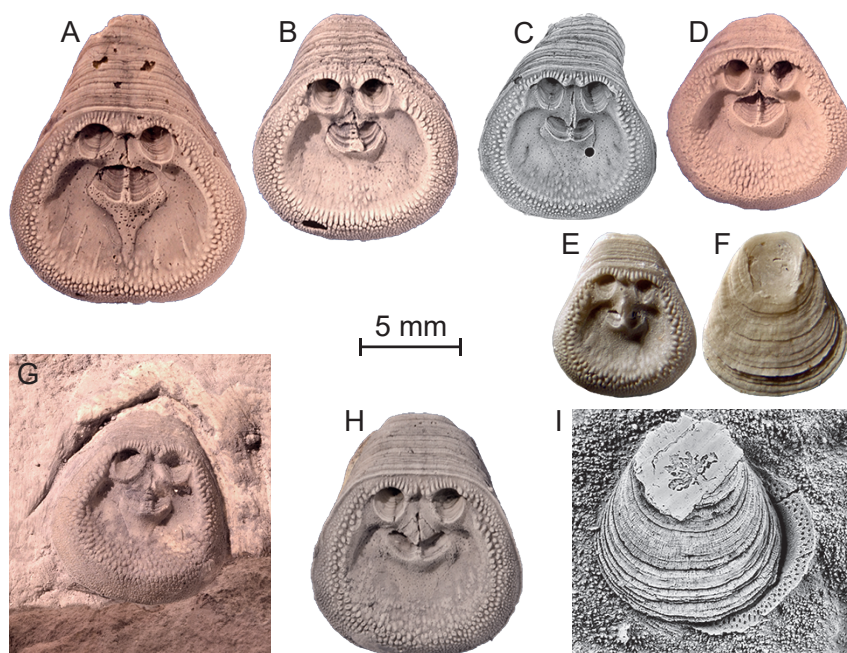


Fig. 12. *Crania antiqua* Defrance, 1818. A, B, C, D, E, G, H: Inside of ventral valve. Note the impressive adductor and pedicle muscle scars, giving the brachiopod a face-like appearance. C: Note the circular gastropod boring. F: External view of same specimen as E, showing attachment scar at posterior end. I: Ventral view of rare complete specimen, probably the only one known from the Danish chalk and designated a Danekræ fossil trove. 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 Maastrichtian, *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 Maastrichtian, *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

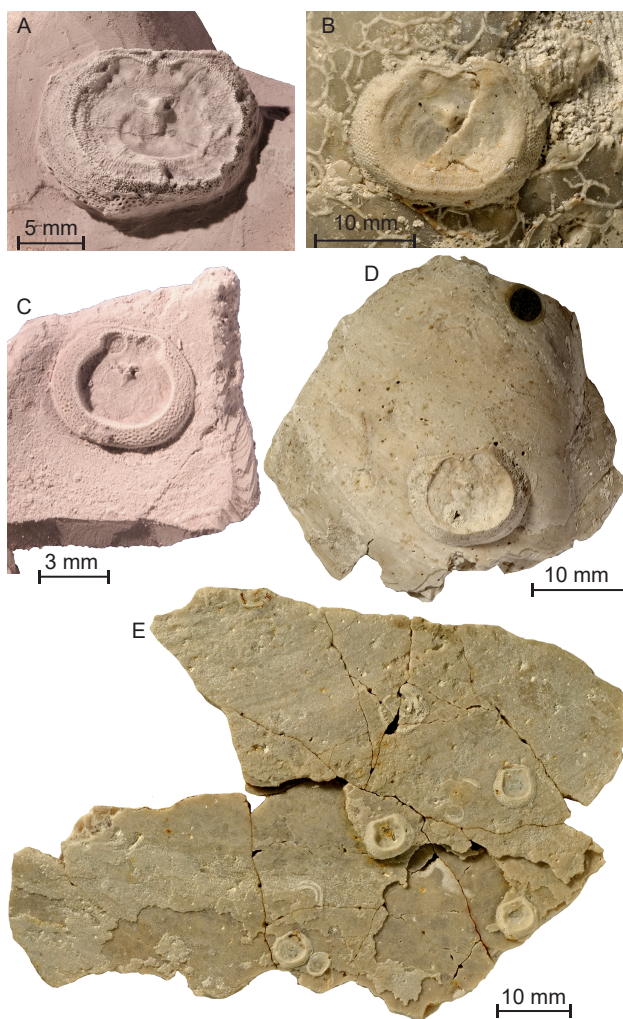


Fig. 13. *Ancistrocrania parisiensis* (DeFrance, 1819). Ventral valves attached with the whole valve to the hard skeletal substrates. **A, B, C:** Sigerslev quarry, Stevns Klint. **D:** Attached to oyster *Pycnodonte vesicularis* (Lamarck, 1806), Dania. **E:** Five specimens attached to inoceramid shell,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

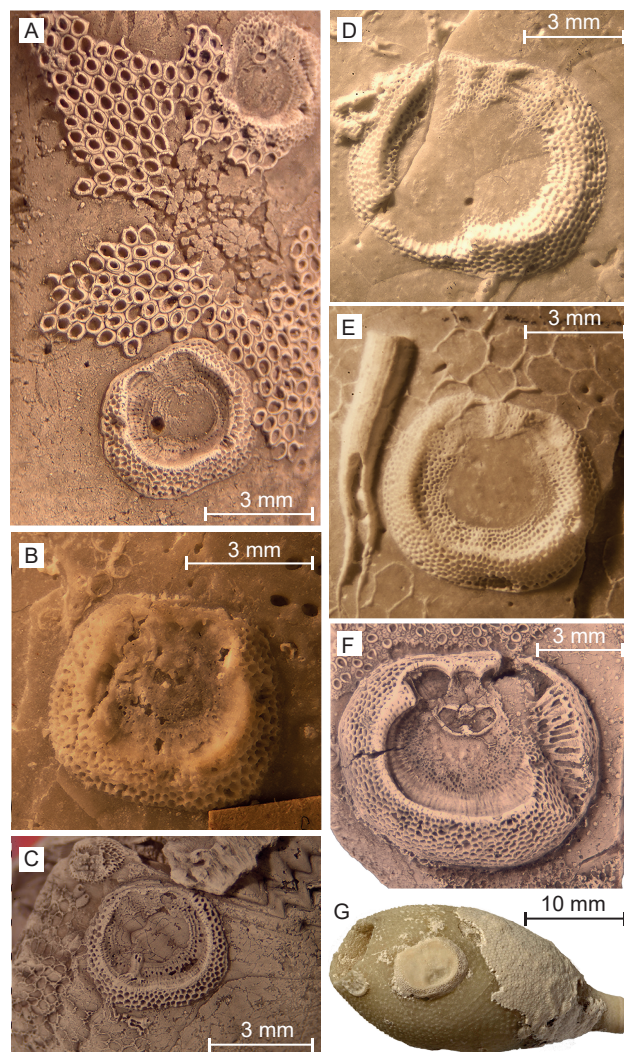


Fig. 14. *Ancistrocrania tubulosa* (Nielsen, 1909). **A–G:** Ventral valves attached to large hard substrates. Note the tubular pores of shell margin. **G:** Attached with the whole valve to the bulbous spine of the regular echinoid *Tylocidaris baltica* together with a microporid cheilostome bryozoa, probably *Micropora* sp., to the right (E. Håkansson, pers. comm. 2024). Upper upper Maastrichtian, *stevensi*–*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-

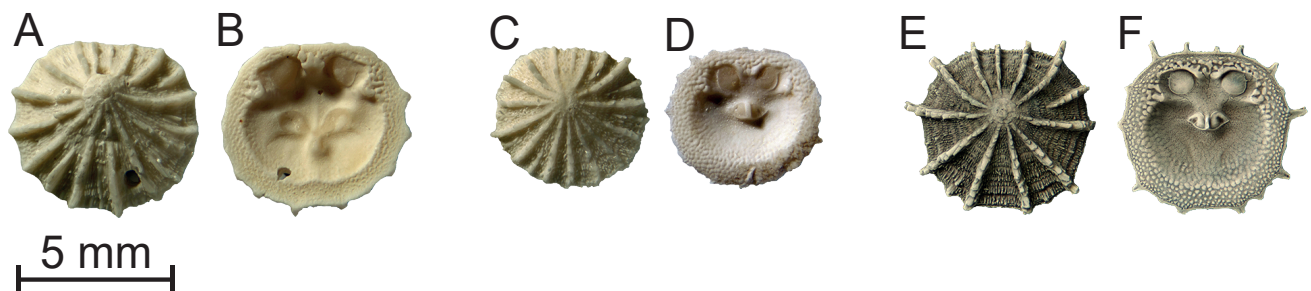


Fig. 15. *Isocrania costata* (J. Sowerby, 1823). External and internal views of ventral valves. Note the low number of laterally curving costellae which extend somewhat beyond the margin of the valve. The interstices have a sculpture of elongate knobs, each ending at a growth line. Note that the protegulum 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 *stevensis*–*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-

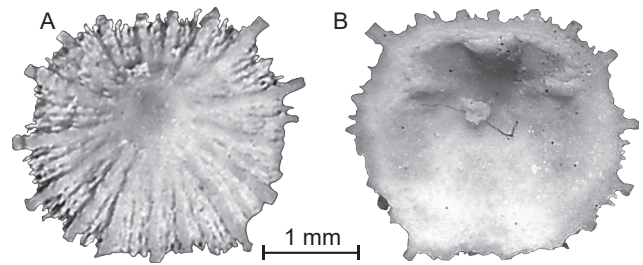


Fig. 16. *Isocrania sendeni* Simon, 2007. **A:** Dorsal valve, external view. Note large number of costellae and small size. **B:** Internal view of same specimen. Upper upper Maastrichtian, *stevensis*–*chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Fig. 2, 6).

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, *stevensis*–*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.

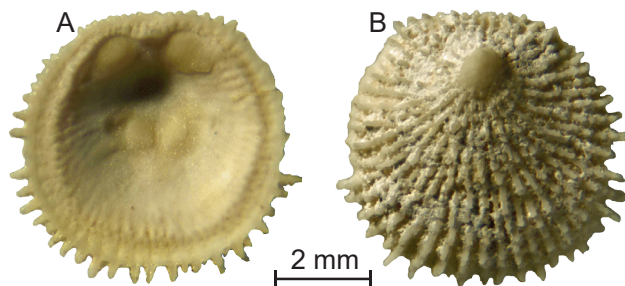


Fig. 17. *Isocrania barbata* (von Hagenow, 1842). Dorsal valve. **A:** Internal view. **B:** External view. Note the large number of laterally curved costellae, which extend beyond the valve margin and possess a characteristic saw-like knobby ornamentation. Lower Maastrichtian. Møns Klint (Fig. 2).

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

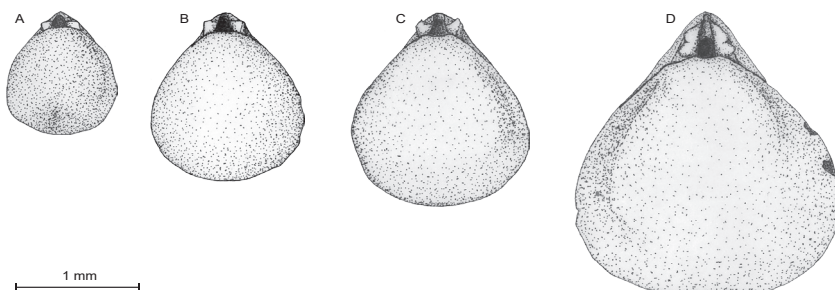


Fig. 18. *Cretirhynchia* sp. Juvenile specimens, probably all belonging to *C. retracta*. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

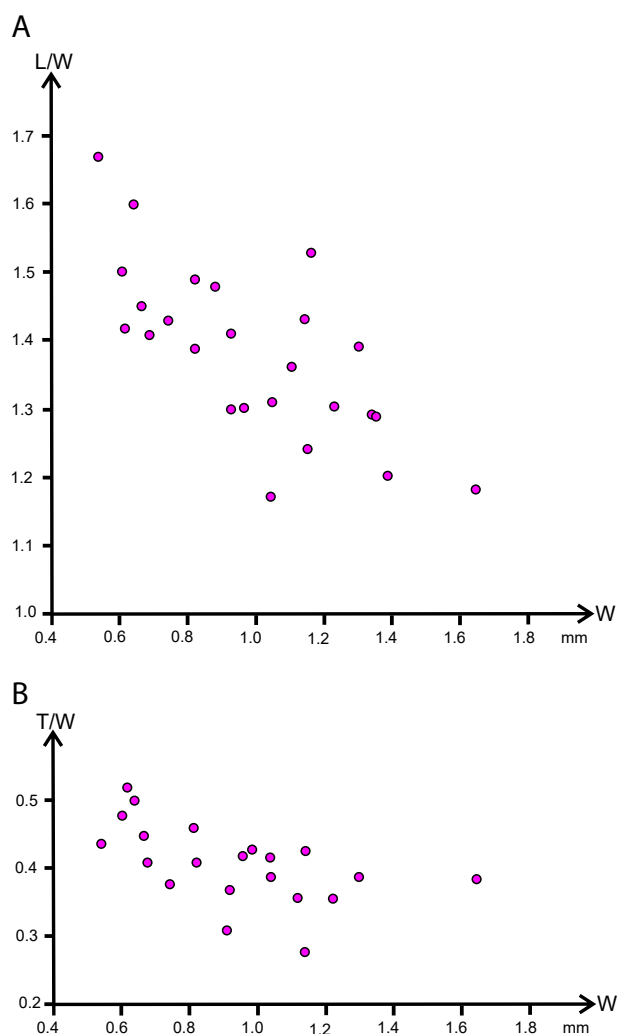


Fig. 19. *Cretirhynchia* sp. Scatter diagrams.

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

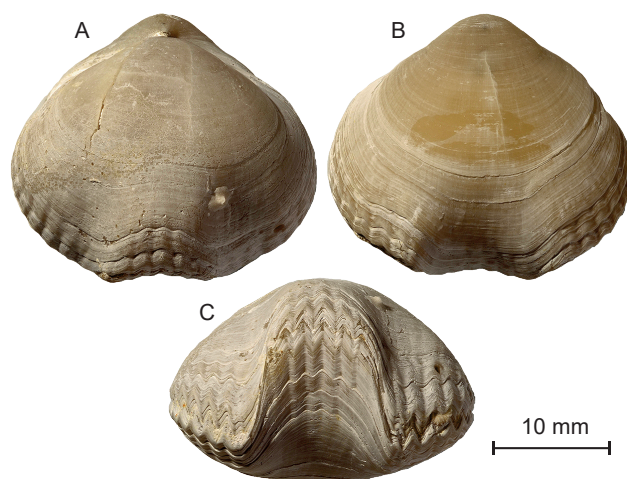


Fig. 20. *Cretirhynchia retracts* (Roemer, 1841). A, B, C: Dorsal, ventral and anterior views, respectively of the same specimen. Note the closed foramen (A), indicating a free-living mode-of-life (Surlyk 1972). Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint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

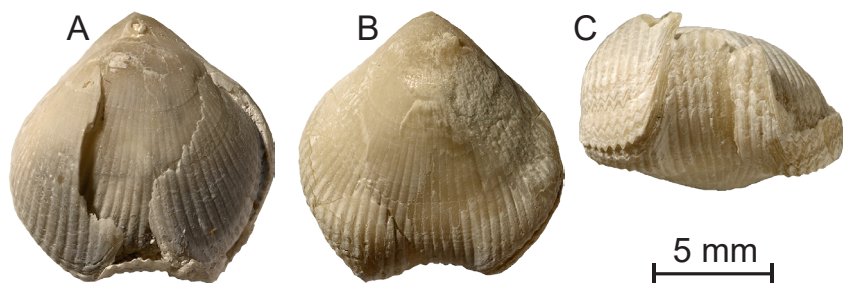


Fig. 21. *Cretirhynchia plicatilis* (J. de C. Sowerby, 1818). Dorsal, ventral, and anterior views, respectively of the same specimen. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6).

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).

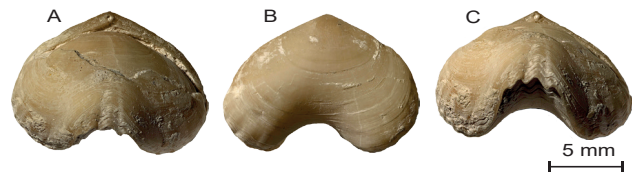


Fig. 22. *Homaletarhynchia limbata* (von Schlotheim, 1813), **A:** Dorsal view. Note very small foramen which may have been closed in larger specimens, indicating a free-living mode-of-life (Surlyk 1972). **B:** Same specimen in ventral views. **C:** Dorsal view of another specimen. Lower Maastrichtian,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

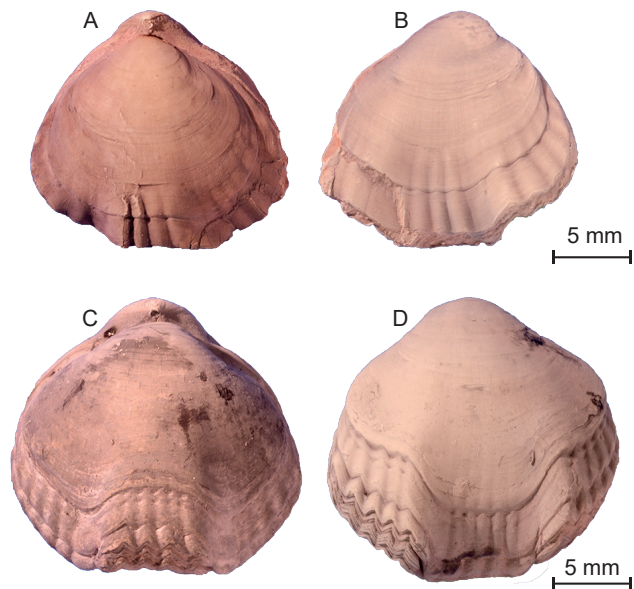


Fig. 23. *Homaletarhynchia limbata* (von Schlotheim, 1813), **A, B:** Dorsal and ventral views, respectively. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Sigerslev quarry, Stevns Klint (Figs 2, 6). **C, D:** Dorsal and ventral views, respectively. Sigerslev quarry. Upper upper Maastrichtian,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

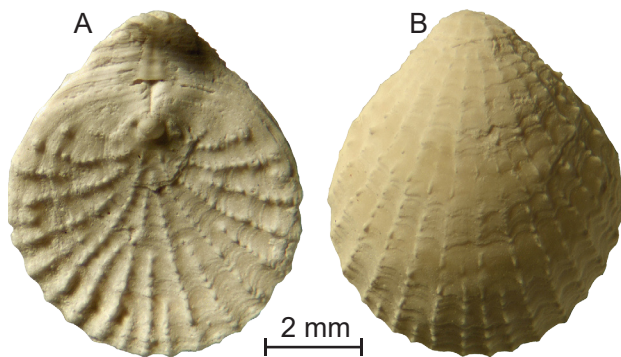


Fig. 24. *Thecidea papillata* (von Schlotheim, 1813). **A:** Dorsal view. **B:** Ventral view of same specimen. Note the circular outline of the dorsal valve and the laterally curved costellae. New ones added by intercalation. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Kulsti Rende, Stevns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

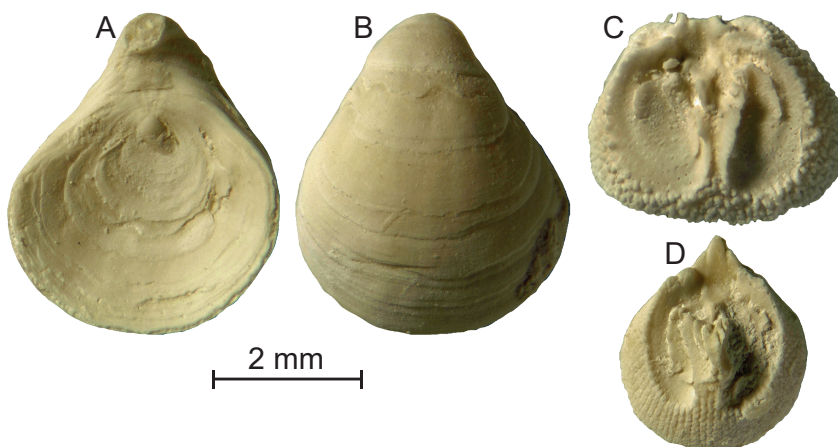


Fig. 25. *Thecidea recurvirostra* Defrance, 1828. **A:** Dorsal view. Note the incurved beak, smooth shell surface and the circular outline of the dorsal valve. **B:** Same specimen in ventral view. **C, D:** Inner side of ventral valves. Uppermost Maastrichtian, *stevensis-chitoniformis* Zone. Holtug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

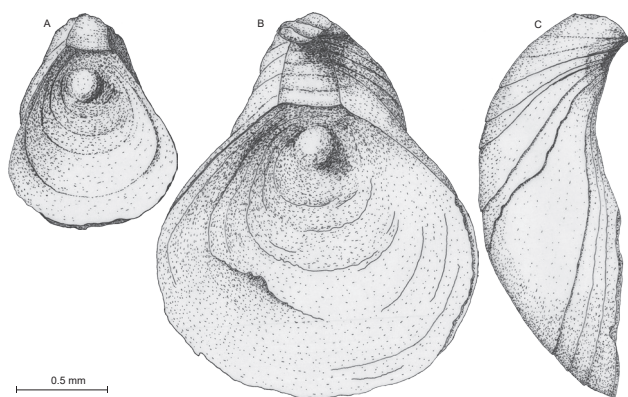


Fig. 26. *Thecidea recurvirostra* Defrance, 1828. Two growth stages. **A:** Dorsal view. **B, C:** Dorsal and lateral views. Uppermost Maastrichtian, *stevensis*–*chitoniformis* Zone. Højerup, Stevns Klint (Figs 2, 6).

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, *stevensis*–*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

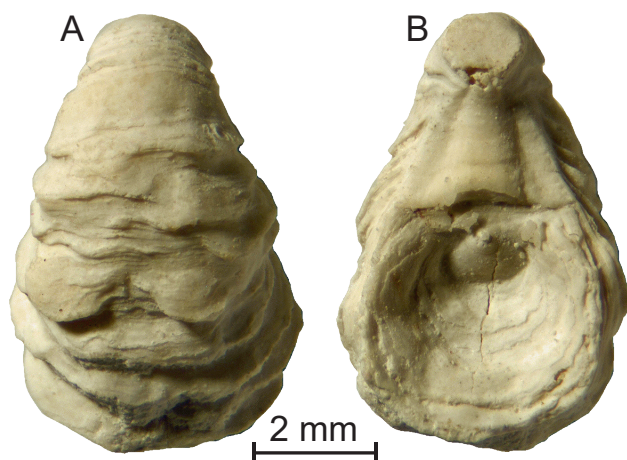


Fig. 27. *Vermiculothecidea vermicularis* (von Schlotheim, 1813). **A:** Ventral view, showing marked step-like growth lines. **B:** Dorsal view of same specimen. Note the strongly posteriorly extended rostrum making the ventral valve almost the double length of the dorsal valve. Both valves are very 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 *Neoliothyrina* Sahni, 1925

Type species *Neoliothyrina obesa* Davidson, 1852

Neoliothyrina 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

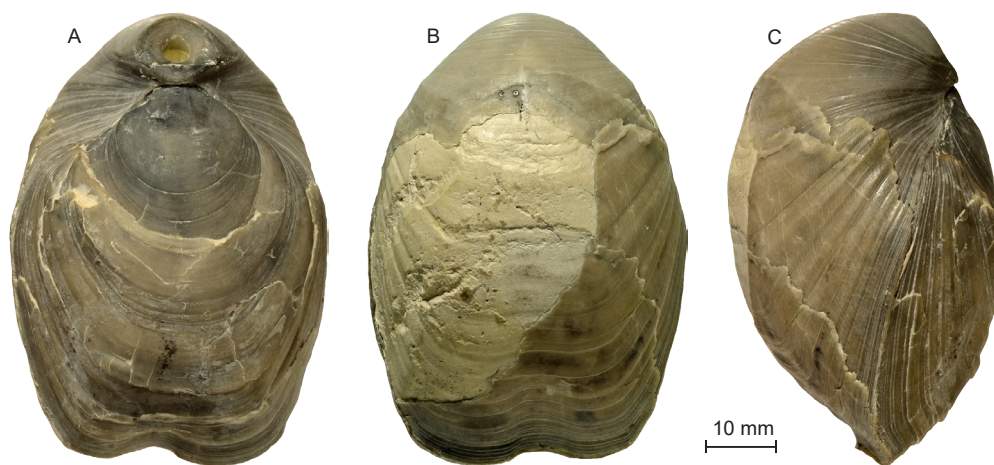


Fig. 28. *Neoliothyrina obesa* Sahni, 1925. **A:** Dorsal view of an unusually well-preserved specimen of this thin-shelled species. *N. obesa* is the largest brachiopod species found in the Danish chalk. Note medial anterior sinus. **B** and **C:** Same specimen in ventral and lateral views, respectively.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

Neoliothyra fittoni (von Hagenow, 1842)

Fig. 29

This species is in many respects similar to *Neoliothyra 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

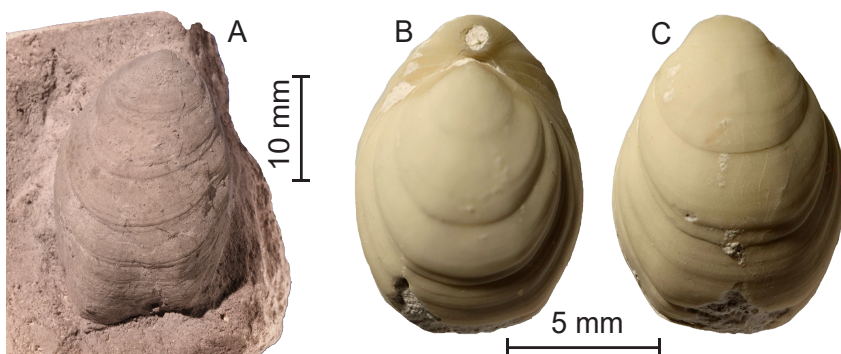


Fig. 29. *Neoliothyra fittoni* (von Hagenow, 1842). **A:** Ventral view. **B** and **C:** Another specimen in dorsal and ventral views, respectively. Note the marked growth lines. Lower upper Maastrichtian. Store Stejlebjerg, Møns Klint (Fig. 2).

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,

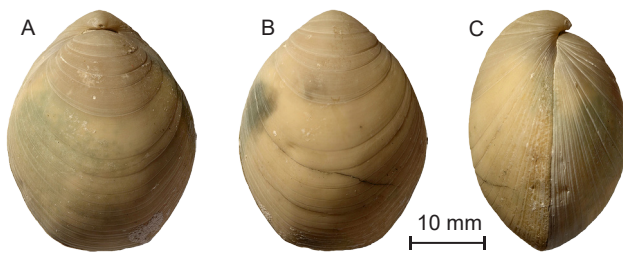


Fig. 30. *Carneithyris subcardinalis* (Sahni, 1925), an unusually well-preserved specimen of this thin-shelled species. Note the very small, essentially closed foramen, indicating a free-living mode-of-life of the older stages of this species (Surlyk 1972). **A, B, C:** Dorsal, ventral and lateral views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

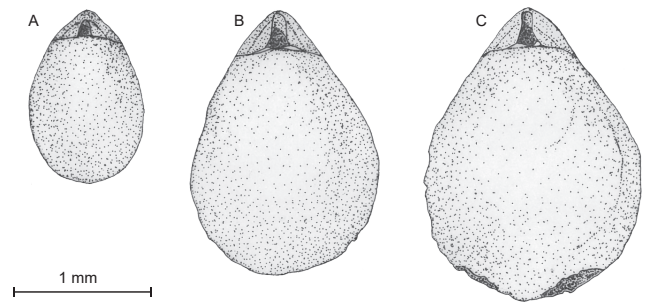


Fig. 31. *Carneithyris subcardinalis* (Sahni, 1925). **A, B, C:** Juvenile growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

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

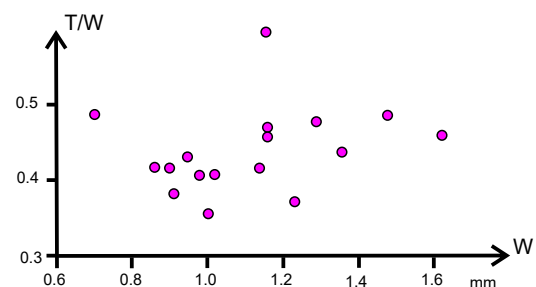
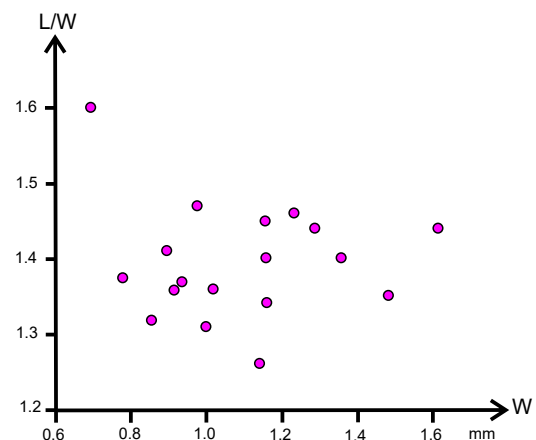


Fig. 32. *Carneithyris subcardinalis* (Sahni, 1925), scatter diagrams of juvenile specimens. L=length, W= width, T=thickness.

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 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 hypothyrid below $W=1$ mm, and changes to submesothyrid and further to mesothyrid 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

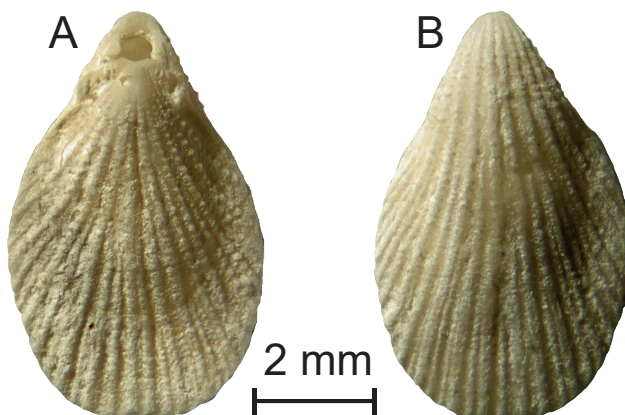


Fig. 33. *Terebratulina chrysalis* (von Schlotheim, 1813). **A:** Dorsal view. **B:** Same specimen in ventral view. Note the numerous fine costellae where new ones are formed by intercalation. Uppermost Maastrichtian, *stevensi*–*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

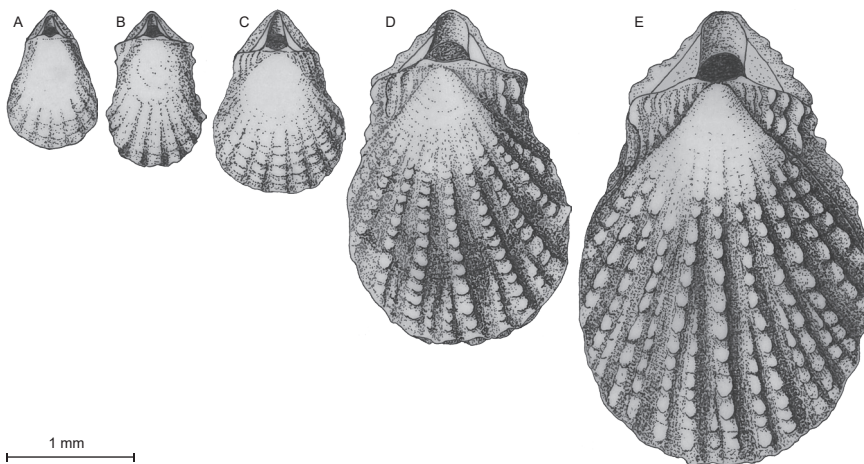


Fig. 34. *Terebratulina chrysalis* (von Schlotheim, 1813). Growth stages, showing the formation of new costellae by intercalation (D, E). Upper lower Maastrichtian. Hundefangsklint, Møns Klint (Figs 2, 4).

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 $W=2.5-3$ 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*.

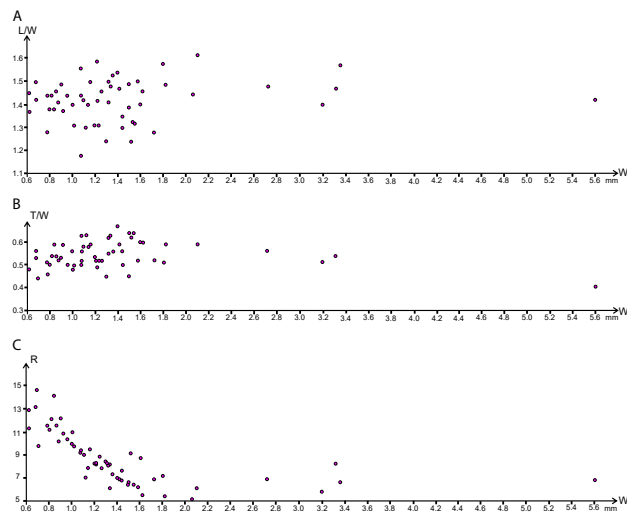


Fig. 35. *Terebratulina chrysalis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width, R=number of ribs/costellae.

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 $W=0.3$ mm. They become stronger dur-

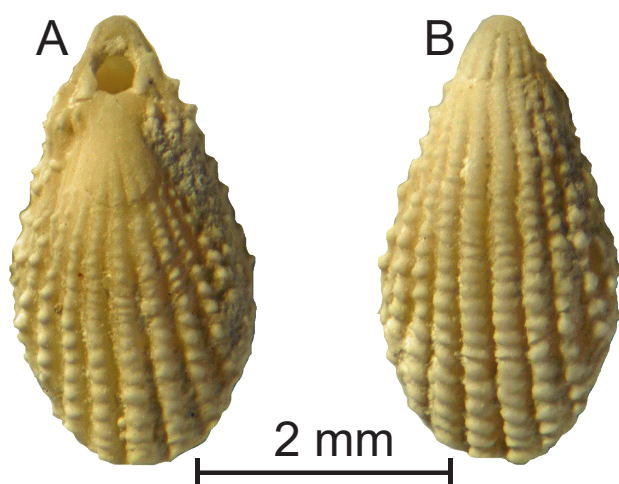


Fig. 36. *Terebratulina longicollis* Steinich, 1965. **A:** Dorsal view. **B:** Same specimen in ventral view. Note the coarse, undivided, straight, strongly ornamented, costae. Lower Maastrichtian. Møns Klint (Fig. 2).

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

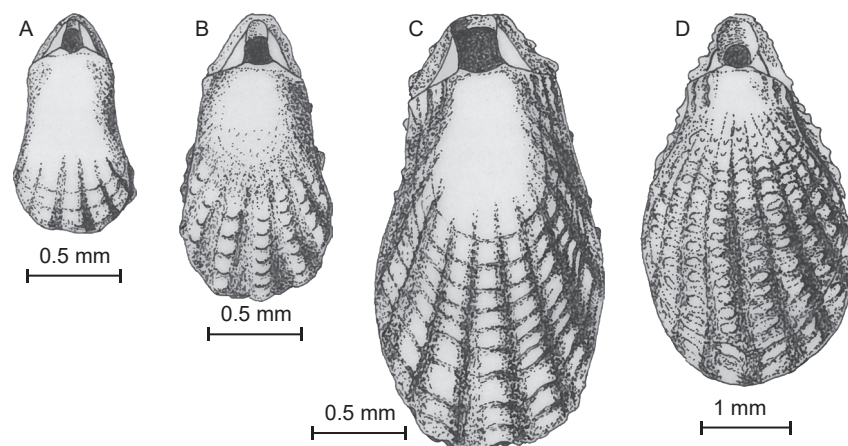


Fig. 37. *Terebratulina longicollis* Steinich, 1965. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

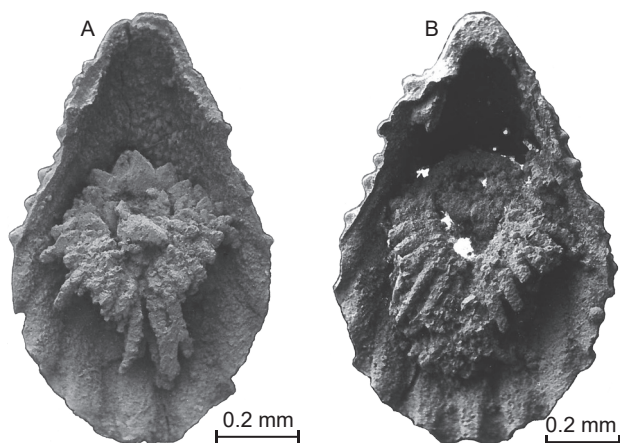


Fig. 38. *Terebratulina longicollis* Steinich, 1965. SEM photographs of opened ventral valves, showing the well-preserved spicular skeletons of the lophophore arms. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

(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).

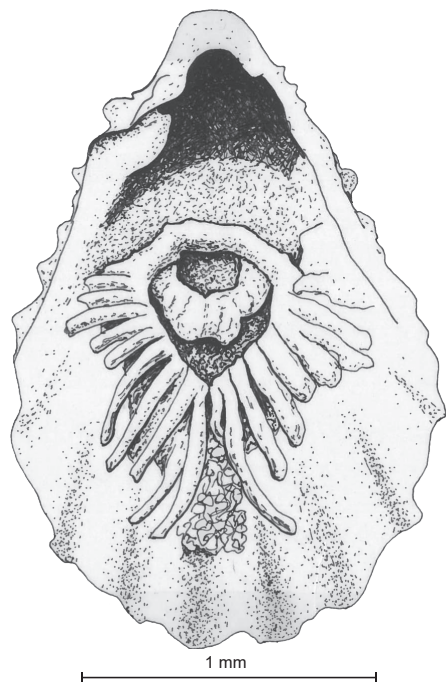


Fig. 39. *Terebratulina longicollis* Steinich, 1965. Opened ventral valve, showing the spicular skeleton of the plectolophous lophophore, Lower upper Maastrichtian, Gudumholm (Fig. 2).

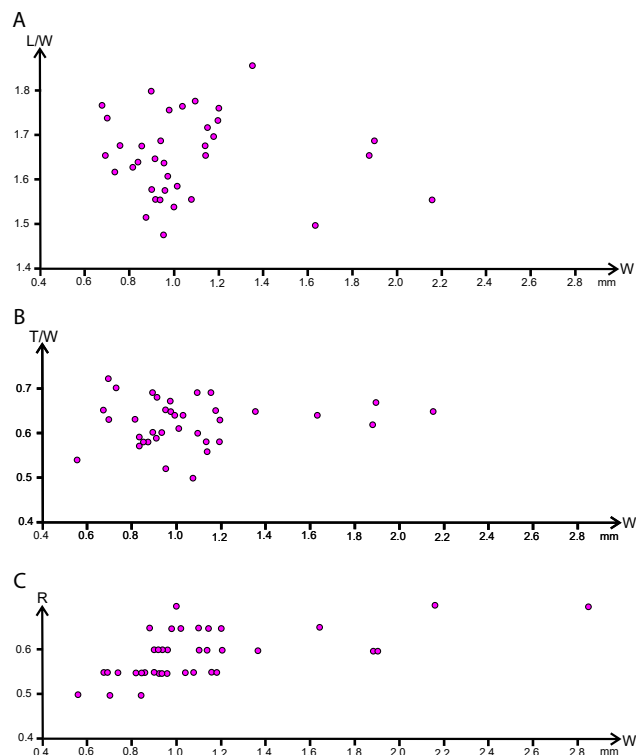


Fig. 40. *Terebratulina longicollis* Steinich, 1965. Scatter diagrams. L=length, W=width, R=number of ribs/costae. *T. longicollis* can always be distinguished from the other species of the Danish chalk by the high L/W.

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.

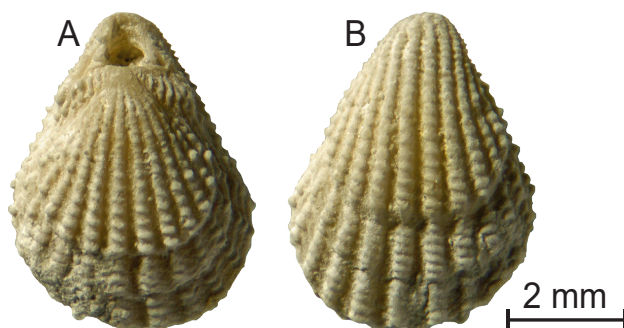


Fig. 41. *Terebratulina faujasii* (Roemer, 1841). A: Dorsal view. B: Same specimen in ventral view. Note the straight undivided costae with a strong sculpture of half-ring tubercles. The tubercles are somewhat similar to, but much stronger than those of *Gisilina jasmundi* Steinich, 1965. Lower Maastrichtian.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

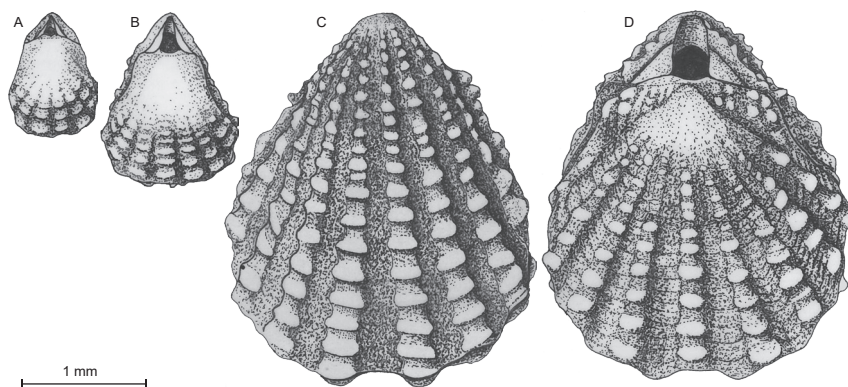


Fig. 42. *Terebratulina faujasii* (Roemer, 1841). Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

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 hypothyrid 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

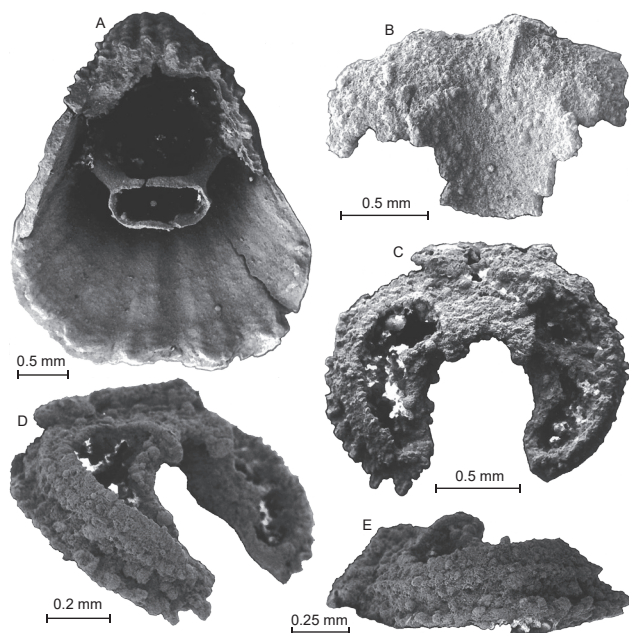


Fig. 43. *Terebratulina faujasii* (Roemer, 1841). A: Opened specimen, showing the ring of the brachidium. B: Spicular skeleton of the anterior body wall. C, D and E: Spicular skeleton of the plectolophous lophophore in dorsal, oblique and lateral views, respectively. Møns Klint (4 in Fig. 2).

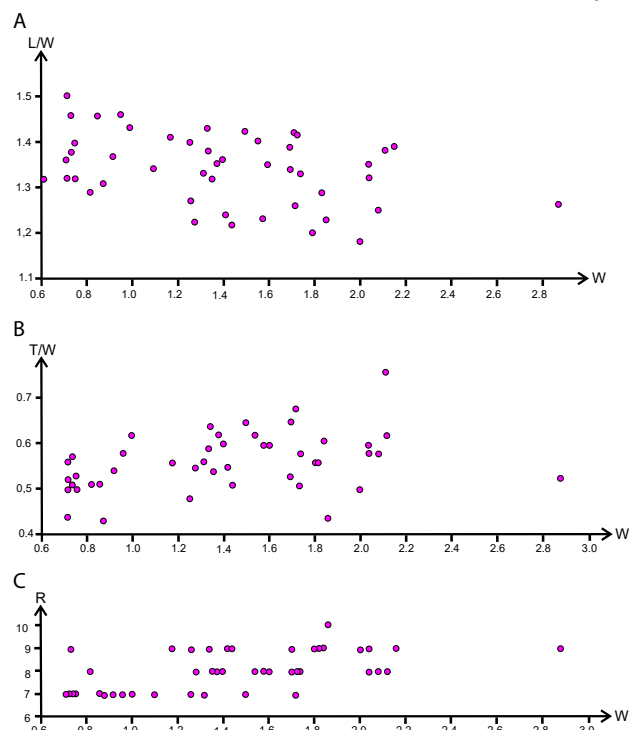


Fig. 44. *Terebratulina faujasii* (Roemer, 1841). Scatter diagrams. L=length, W= width, T=thickness, R=number of ribs/costae.

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

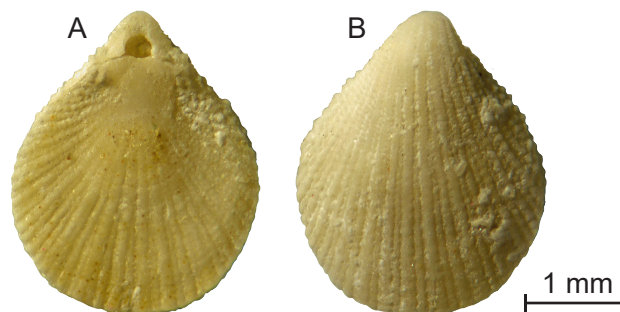


Fig. 45. *Terebratulina subtilis* Steinich, 1965. **A:** Dorsal view. **B:** Same specimen in ventral view. Note the large number of very fine costellae with only a weak knobby ornamentation. New costellae are formed by intercalation. Lower Maastrichtian. Møns Klint (Fig. 2).

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 hypothyrid but changes to submesothyrid 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.

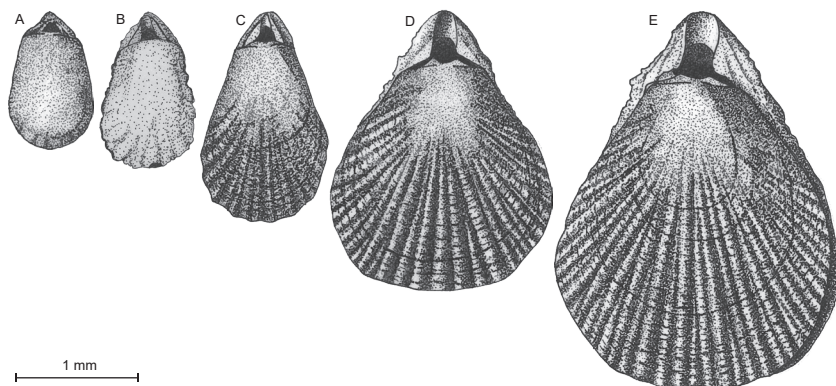


Fig. 46. *Terebratulina subtilis* Steinich, 1965. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

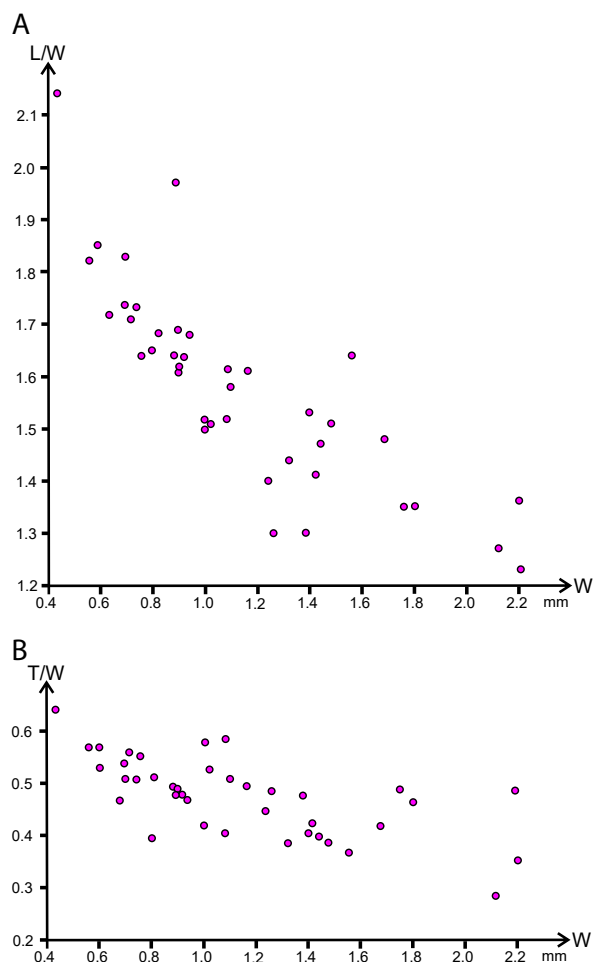


Fig. 47. *Terebratulina subtilis* Steinich, 1965. Scatter diagrams. L=length, W= width, T=thickness.

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

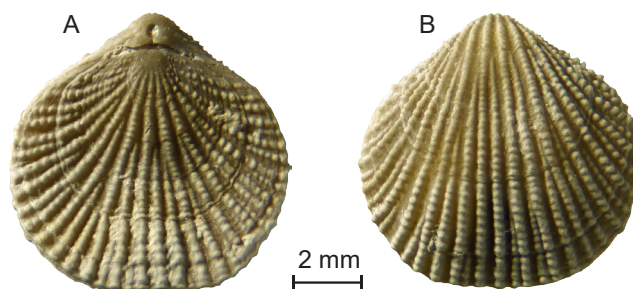


Fig. 48. *Gyrosoria gracilis* (von Schlotheim, 1813). A: Dorsal view. B: Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

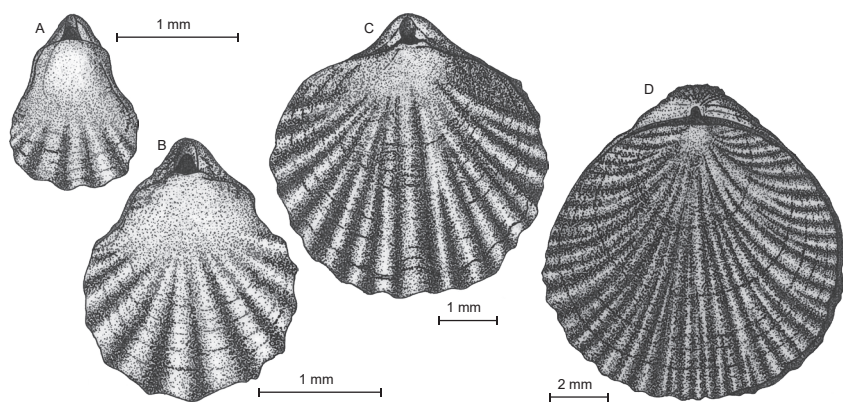


Fig. 49. *Gyrosoria gracilis* (von Schlotheim, 1813). Growth stages.

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).

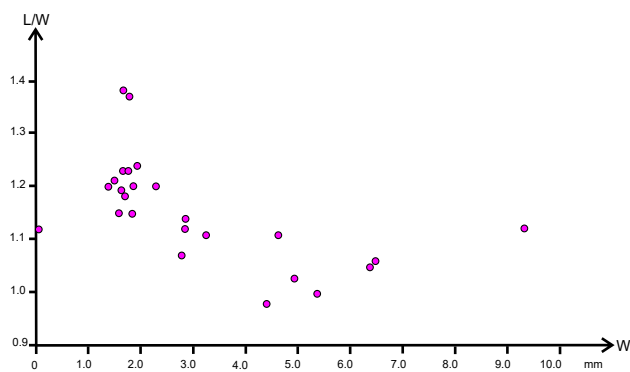


Fig. 50. *Gyrosoria gracilis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width.

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

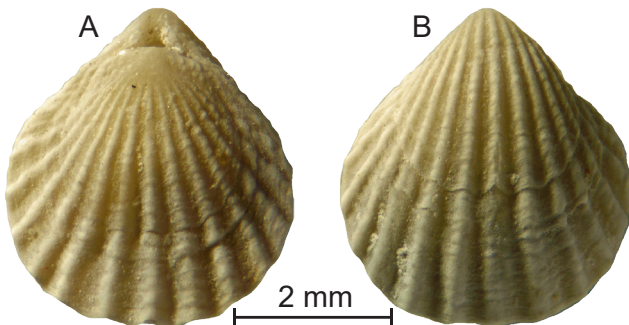


Fig. 51. *Gisilina gisii* (Roemer, 1841). A: Dorsal view. Note the straight only weakly knobbed costae where new costae are formed at the shell ears. B: Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

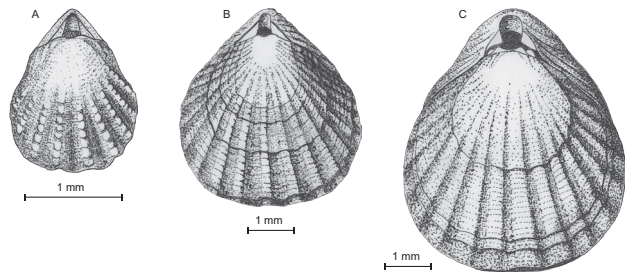


Fig. 52. *Gisilina gisii* (Roemer, 1841). Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

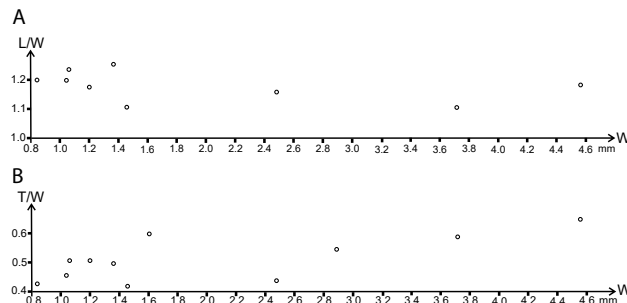


Fig. 53. *Gisilina gisii* (Roemer, 1841). Scatter diagrams. L=length, W=width, T=thickness.

the ventral valve during growth. It is initially hypothryd, but changes to submesothryd and finally to mesothryd. 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 mesothryd 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

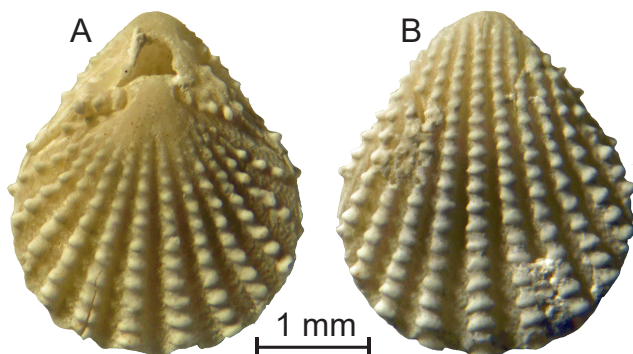


Fig. 54. *Gisilina jasmundi* Steinich, 1965. **A:** Dorsal view. Note the straight costae with a characteristic knobby sculpture, which are not as strongly developed than the half-ring knobs of rather similar *Terebratulina faujasii*. **B:** Same specimen in ventral view. Lower Maastrichtian. Møns Klint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

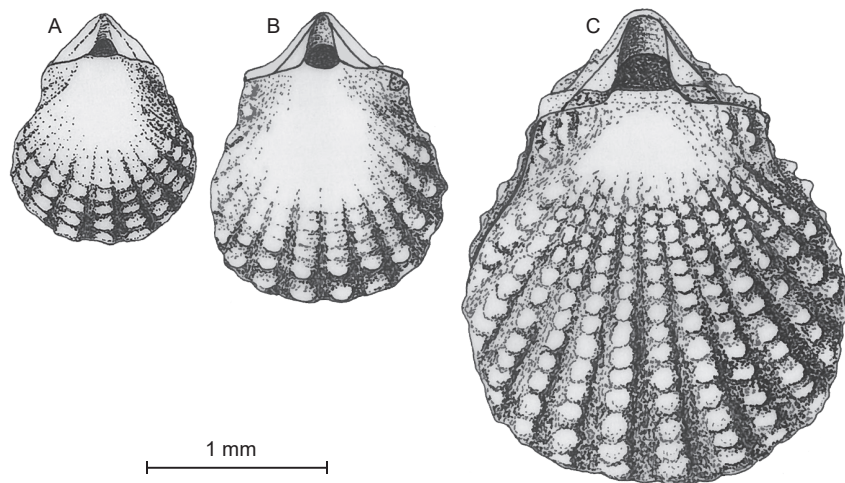


Fig. 55. *Gisilina jasmundi* Steinich, 1965. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

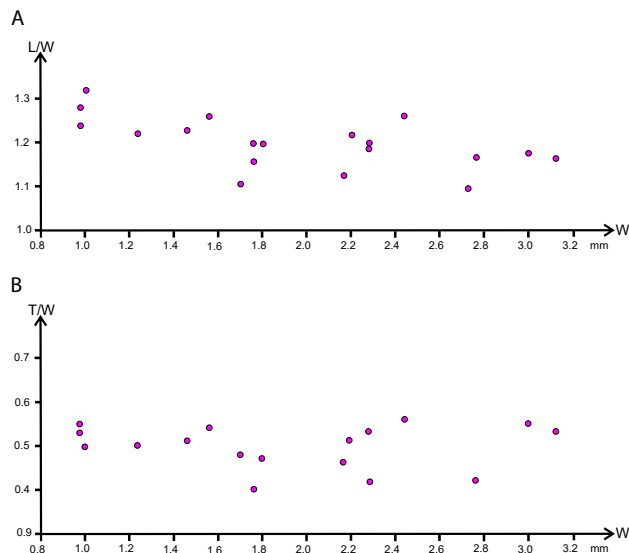


Fig. 56. *Gisilina jasmundi* Steinich, 1965. Scatter diagrams. L=length, W=width, T=thickness.

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 plectophe. 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. Kjølbygård: 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

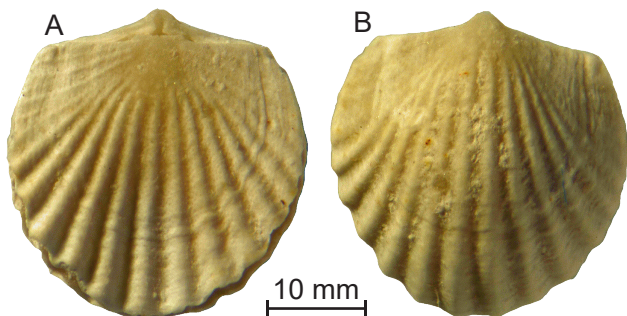


Fig. 57. *Meonia semiglobularis* (Posselt, 1894). A: Dorsal view. B: Same specimen in ventral view. Møns Klint (4 in Fig. 2).

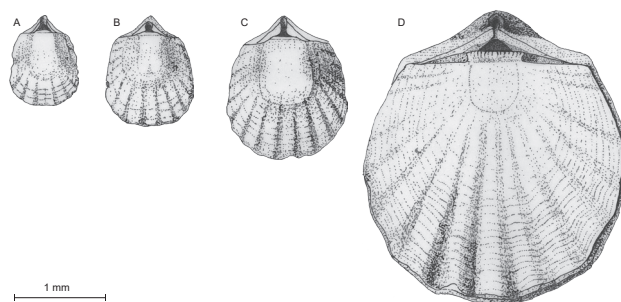


Fig. 58. *Meonia semiglobularis* (Posselt, 1894). Growth stages. Lower upper Maastrichtian. Nørre Flødal (Fig. 2).

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

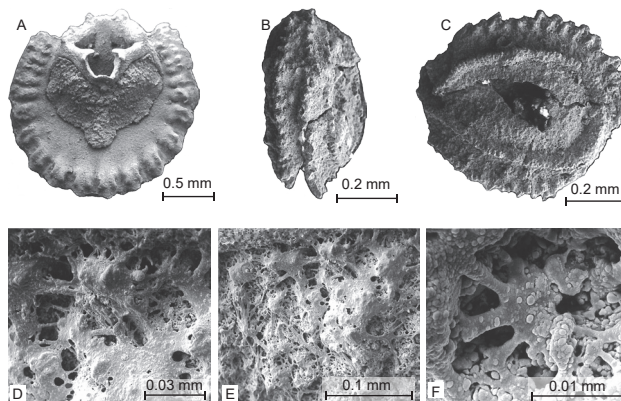


Fig. 59. *Meonia semiglobularis* (Posselt, 1894). Spicular skeletons. A: Anterior body wall. B and C: Frontal and lateral views of schizolophous lophophore. The lower panel shows details of spicular meshwork of the body wall.

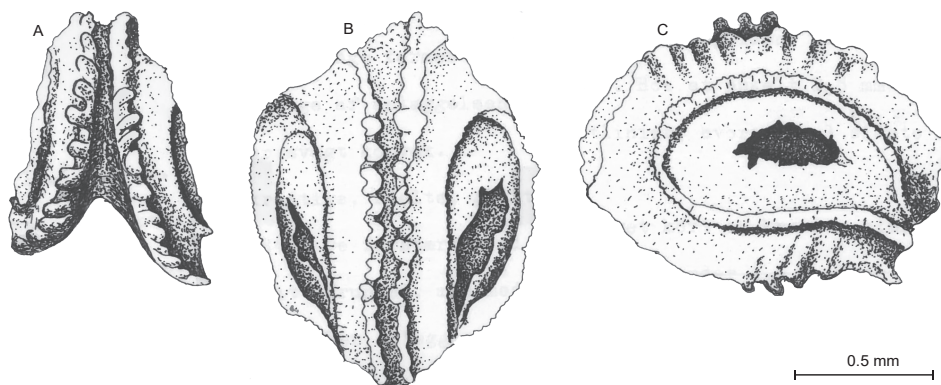


Fig. 60. *Meonia semiglobularis* (Posselt, 1894). Spicular skeletons of schizolophous lophophore. A, B and C: Frontal, dorsal and lateral views, respectively. Lower upper Maastrichtian, Gudumholm (Fig. 2).

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

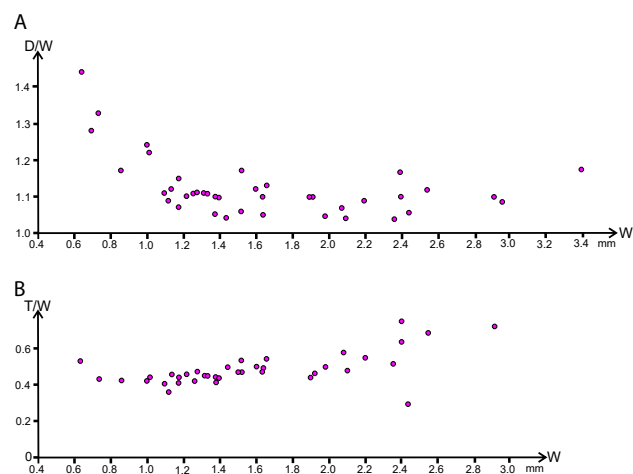


Fig. 61. *Meonia semiglobularis* (Posselt, 1894). Scatter diagrams. W=width, T=thickness, D=diameter of foramen.

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 $W=0.6$

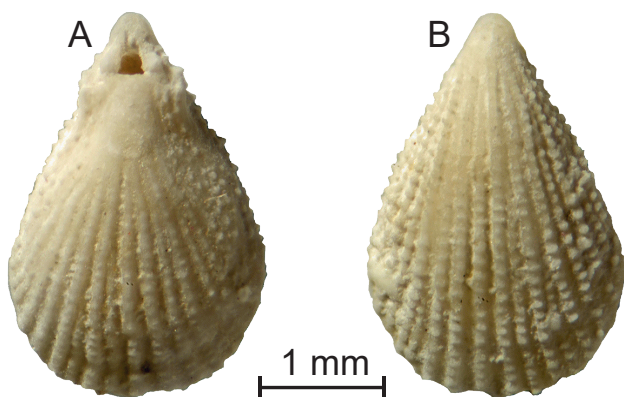


Fig. 62. *Rugia tenuicostata* Steinich, 1963. A.: Dorsal view. B: Same specimen in ventral view, showing the scales on the costellae giving them a fretsaw like appearance. Lower Maastrichtian. Møns Klint (Fig. 2).

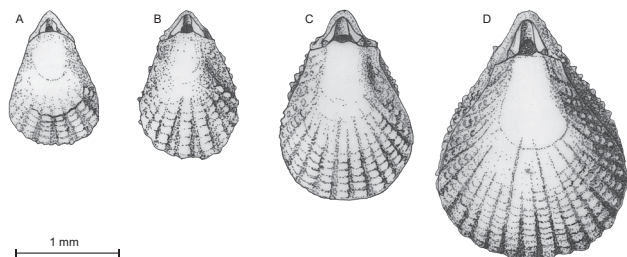


Fig. 63. *Rugia tenuicostata* Steinich, 1963. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 7).

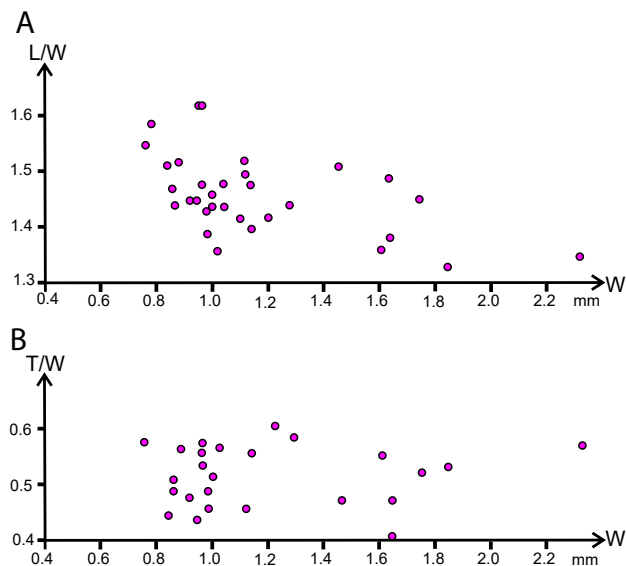


Fig. 64. *Rugia tenuicostata* Steinich, 1963. Scatter diagrams. L=length, W=width, T=thickness.

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 hypothyril. 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

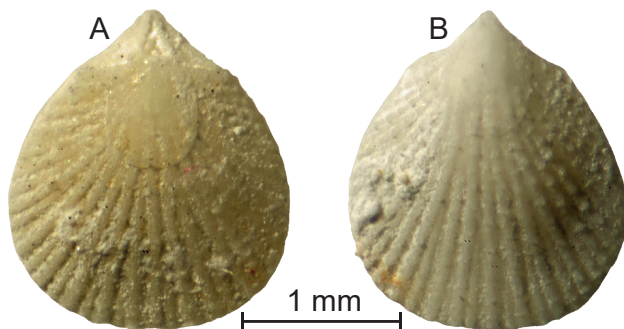


Fig. 65. *Rugia acutirostris* Steinich, 1965. **A:** Dorsal view. Note pointed rostrum and numerous, laterally curved, fairly smooth costellae. New costellae formed by intercalation. **B:** Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

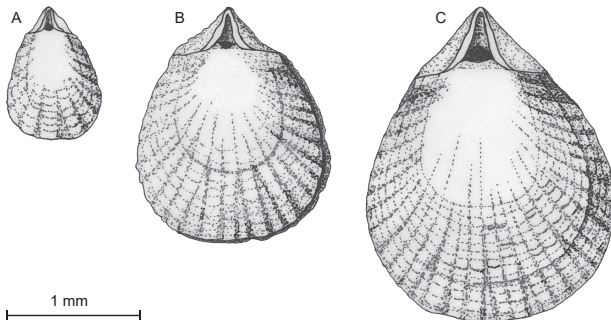


Fig. 66. *Rugia acutirostris* Steinich, 1965. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

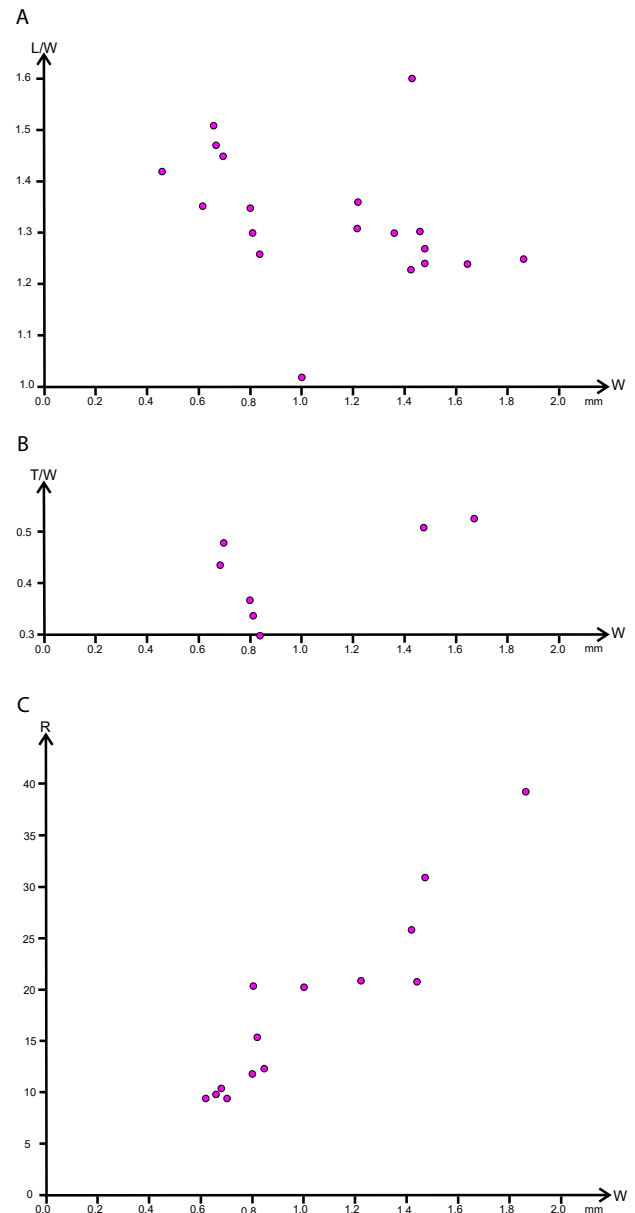


Fig. 67. *Rugia acutirostris* Steinich, 1965. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Upper lower Maastrichtian, Møns Klint (Fig. 2).

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

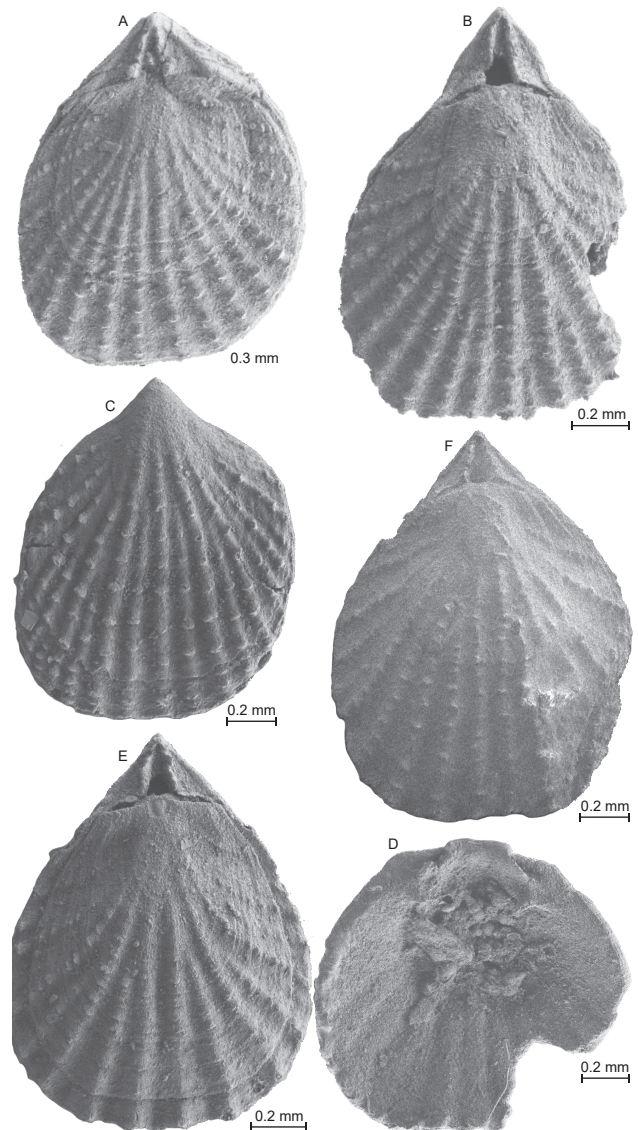


Fig. 68. *Rugia stenius* n. sp. A: Holotype. B, C, E, F: Paratypes. D: Dorsal valve, inside view. Sample Karlstrup 2. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. All specimens from sample Karlstrup 2, Karlstrup (Figs 2, 5B).

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

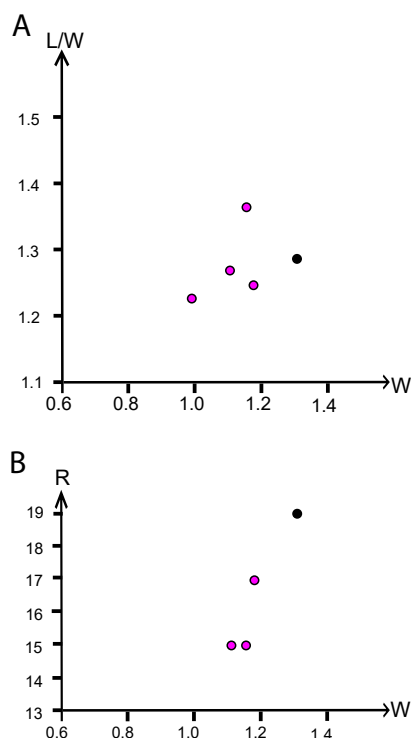


Fig. 69. *Rugia stenius* n. sp. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Sample Karlstrup 2. Upper upper Maastrichtian, *stevensis-chitoniformis* Zone. Karlstrup (Figs 2, 5B).

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-

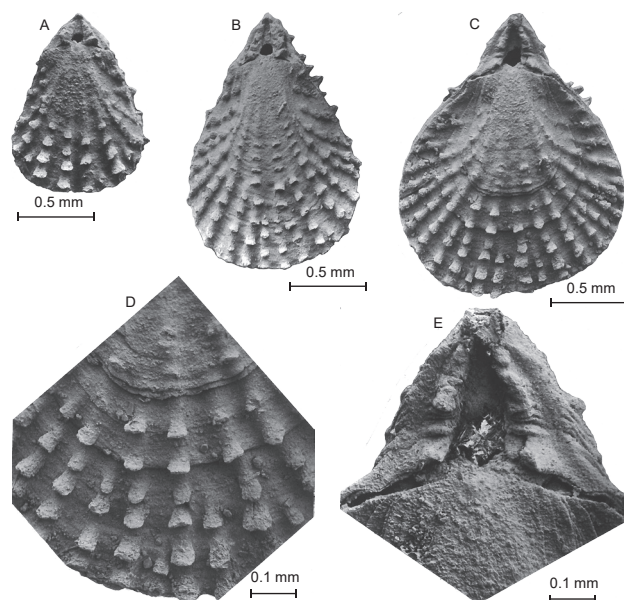


Fig. 70. *Rugia tegulata* Surlyk, 1970. A–C: Growth stages. C. Dorsal view of the holotype. D: Details of the scale-like tubercles of the costellae. E: Details of the foramen and deltidial plates. Lower upper Maastrichtian, *semiglobularis-humboldtii* Zone. Lindholm (19 in Fig. 2).

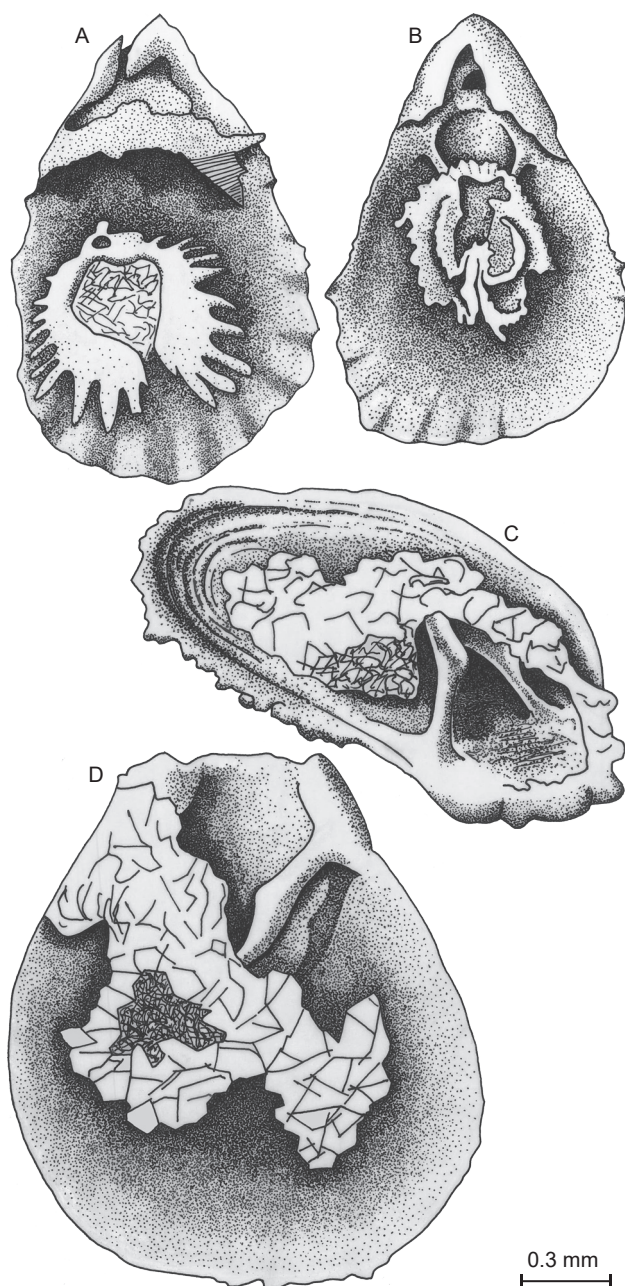


Fig. 71. *Rugia tegulata* Surlyk, 1970. **A, B:** Schizolophous lophophore in dorsal view. **C, D:** Brachidium and strongly recrystallized spicular skeleton of lophophore. Lindholm (16 in Fig. 2).

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. Sættepeklint: 3.

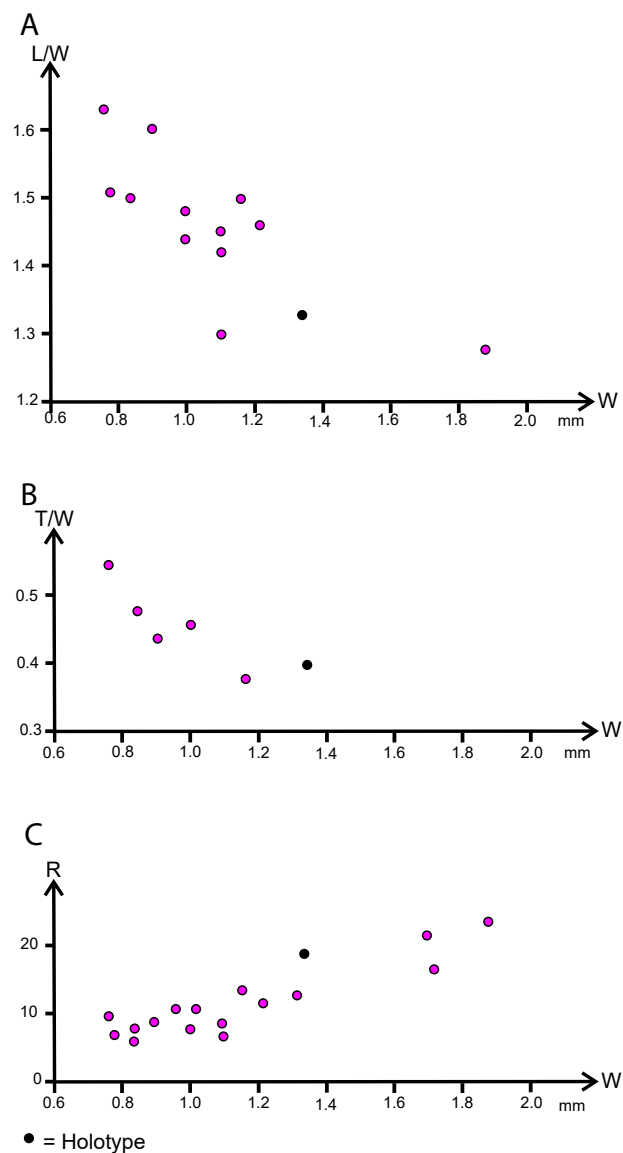


Fig. 72. *Rugia tegulata* Surlyk, 1970. Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs. Lindholm (19 in Fig. 2).

Chronostratigraphy in Denmark. Upper lower Maastichtian – lower upper Maastichtian, 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

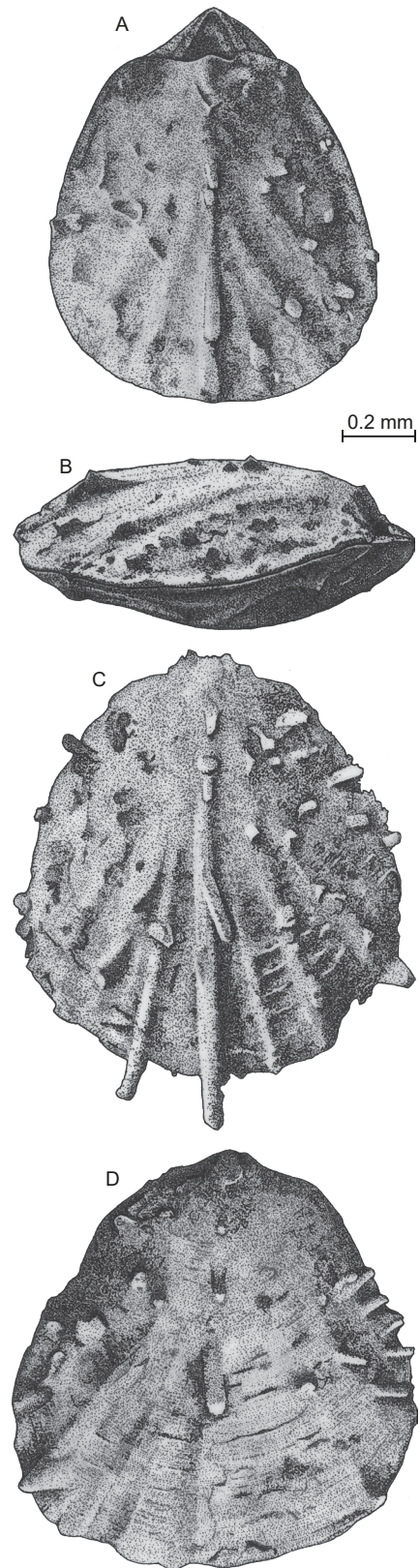


Fig. 73. *Rugia spinosa* Surlyk, 1970. **A, B:** Dorsal and slightly oblique lateral views of holotype, respectively. **C, D:** Dorsal valves. Lower lower Maastrichtian, *spinosa*–*subtilis* Zone, Gedser Fyr (Fig. 2).

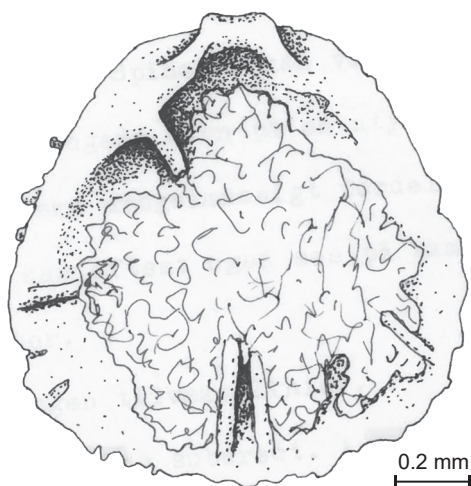


Fig. 74. *Rugia spinosa* Surlyk, 1970. Internal view of dorsal valve, showing internal ribs. Lower lower Maastrichtian, *spinosa-subtilis* Zone, Gedser Fyr (Fig. 2).

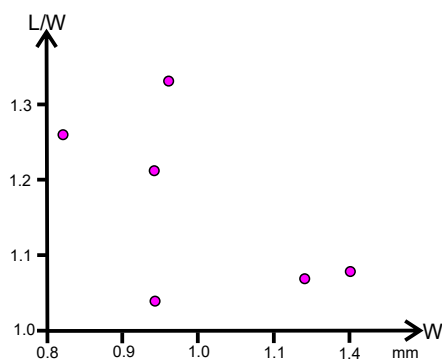


Fig. 75. *Rugia spinosa* Surlyk, 1970. Scatter diagram. L=length, W=width.

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.

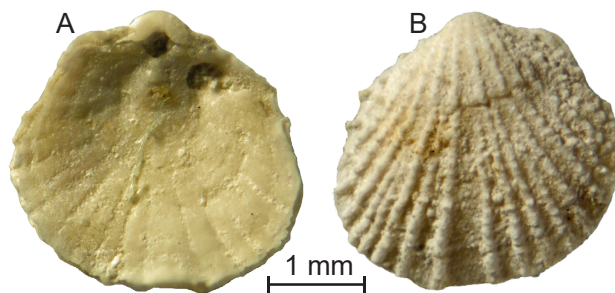


Fig. 76. *Dracius carnifex* Steinich, 1967. **A:** Dorsal view. Note the weak, irregular costellae. **B:** Same specimen in ventral view. Note the irregular, knobbed costae and intercalated costellae. Lower Maastrichtian. Møns Klint (Fig. 2).

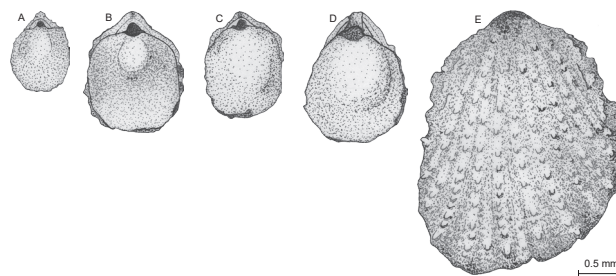


Fig. 77. *Dracius carnifex* Steinich, 1967. Growth stages. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

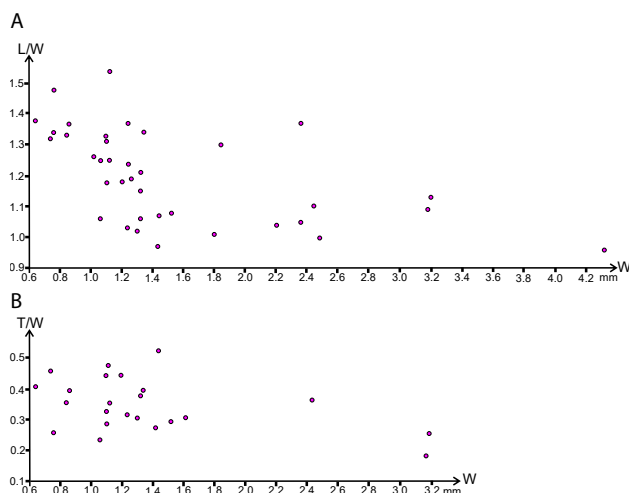


Fig. 78. *Dracius carnifex* Steinich, 1967. Scatter diagrams. L=length, W=width, T=thickness.

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.

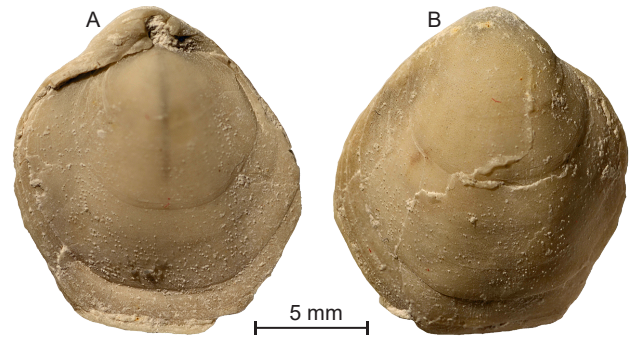


Fig. 79. *Kingena pentangulata* (Woodward, 1833). **A:** Dorsal view. **B:** Same specimen in ventral view. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 4).

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).

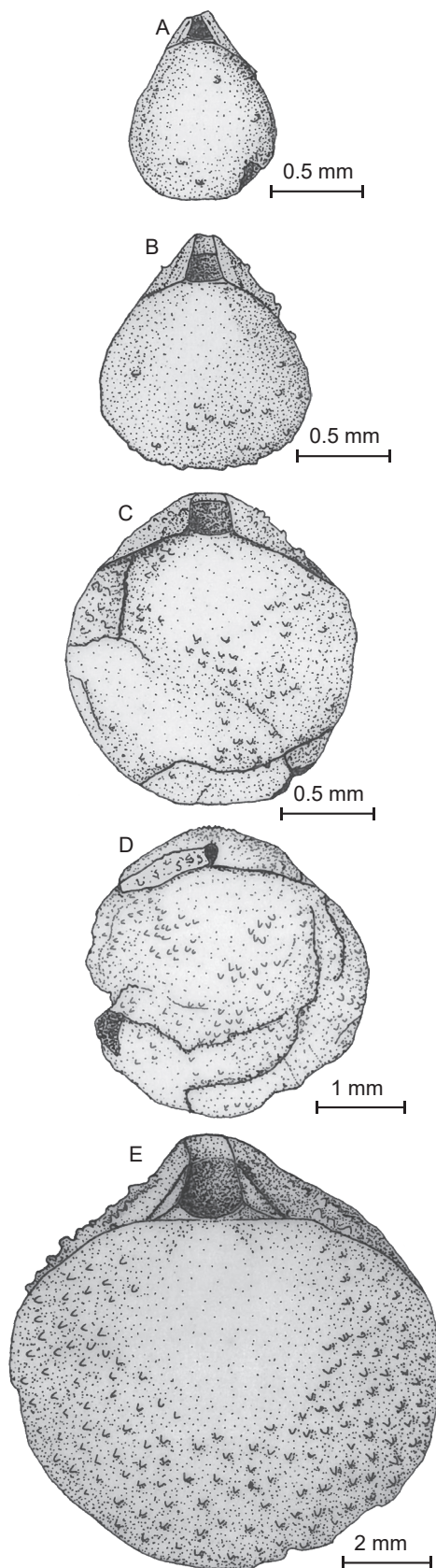


Fig. 80. *Kingena pentangulata* (Woodward, 1833). Growth stages. Lower Maastrichtian, Møns Klint (Fig. 2).

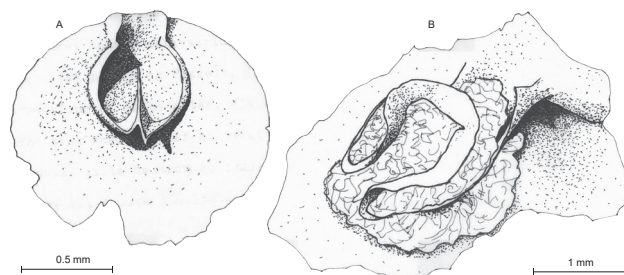


Fig. 81. *Kingena pentangulata* (Woodward, 1833). Details of septum and brachidium in juvenile (A) and adult (B) specimens. Lower upper Maastrichtian, Lindholm (Fig. 2).

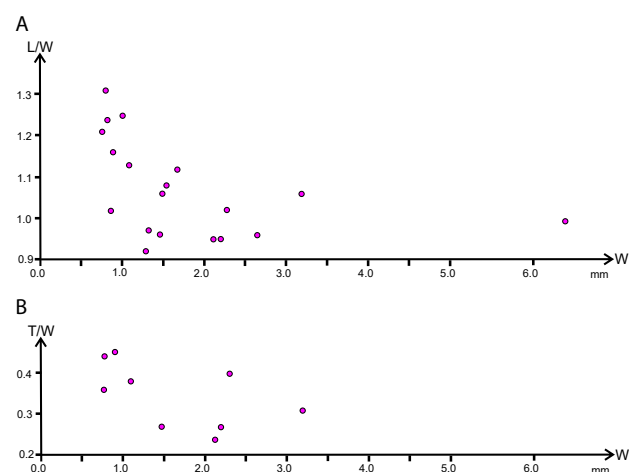


Fig. 82. *Kingena pentangulata* (Woodward, 1833). Scatter diagrams. L=length, W=width, T=thickness.

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

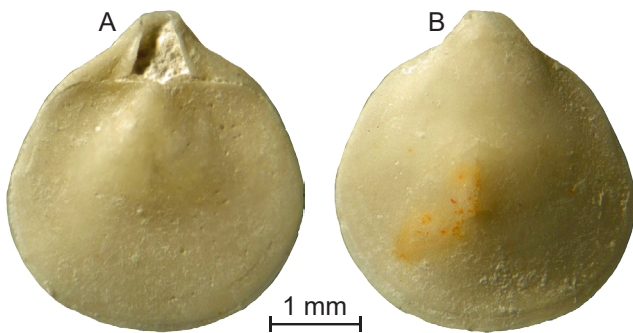


Fig. 83. *Dalligas nobilis* Steinich, 1968. A: Dorsal view. Note the straight hinge line and large truncated triangular foramen. B: Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

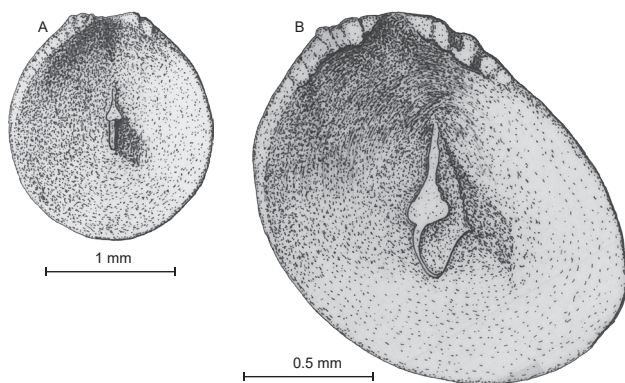


Fig. 84. *Dalligas nobilis* Steinich, 1968. Internal views of inner side of dorsal valve, showing details of the dorsal median septum. Lower upper Maastrichtian. Gudumholm (Fig. 2).

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

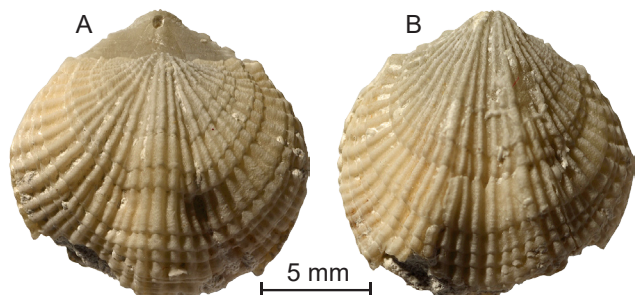


Fig. 85. *Ruegenella humboldtii* (von Hagenow, 1842). A: Dorsal view. B: Same specimen in ventral view. Upper upper Maastrichtian. Kulsti Rende, Stevns Klint (Figs 2, 6).

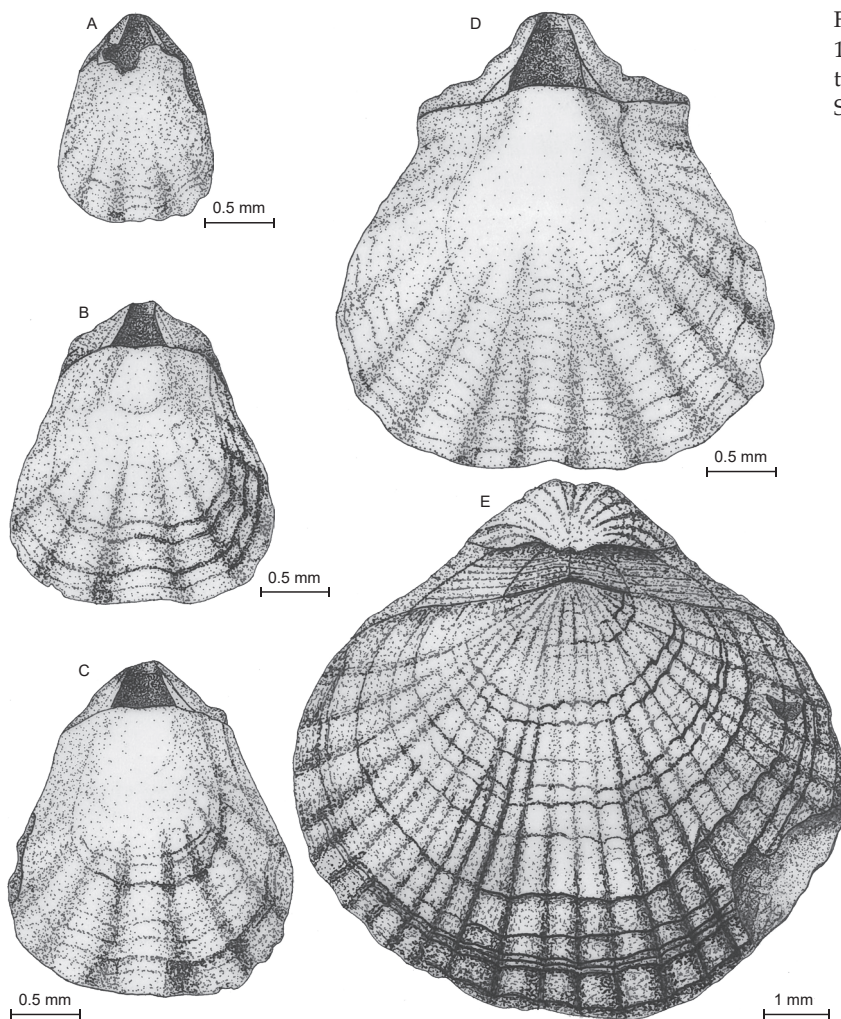


Fig. 86. *Ruedgenella humboldtii* (von Hagenow, 1842). Growth Stages. Upper upper Maastrichtian, *stevensis*–*chitoniformis* brachiopod Zone. Stevns Klint (Fig. 2).

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 $W=2.5$ – 3 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 $W=0.7$ – 0.8 mm. They are wide, flat and rapidly become stronger. The median costae start to split at $W=1.2$ – 1.7 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 $W=3.0$ mm. these become collar-like during

growth and fuse medially. The pedicle collar is very long in small specimens. The foramen is submesothyrid and circular in fully grown specimens. Development of the brachidium starts at $W=0.8$ – 1.0 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 $W=2$ 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).

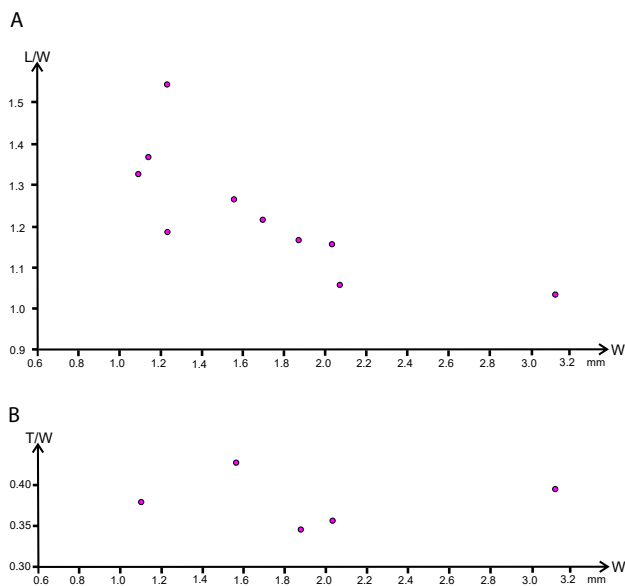


Fig. 87. *Ruegenella humboldtii* (von Hagenow, 1842). Scatter diagrams. L=length, W=width, T=thickness.

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-

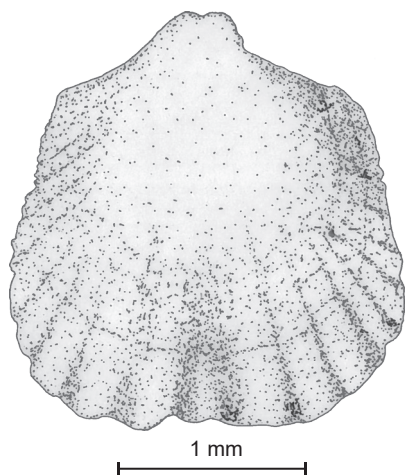


Fig. 88. *Ruegenella* sp. Rørdal-1, core 1. Ventral valve. Note the relatively large number of costae and greater width at hinge line compared to specimens of *Ruegenella humboldtii* of the same size. Rørdal (Fig. 2).

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

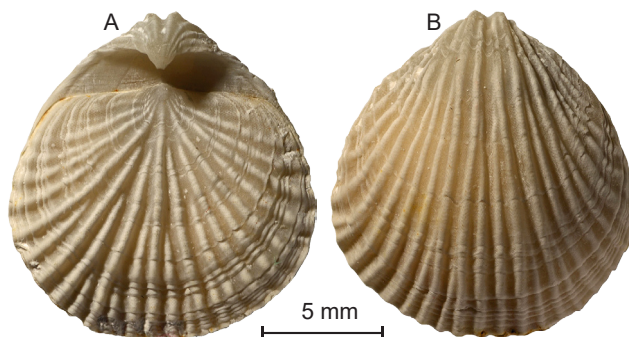


Fig. 89. *Trigonosemus pulchellus* (Nilsson, 1827). **A:** Dorsal view. Note the incurved rostrum, the closed foramen, and the strong, laterally curved costellae where new ones are added by intercalation. **B:** Same specimen in ventral view. Upper lower Maastrichtian, *pulchellus–pulchellus* Zone. Møns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

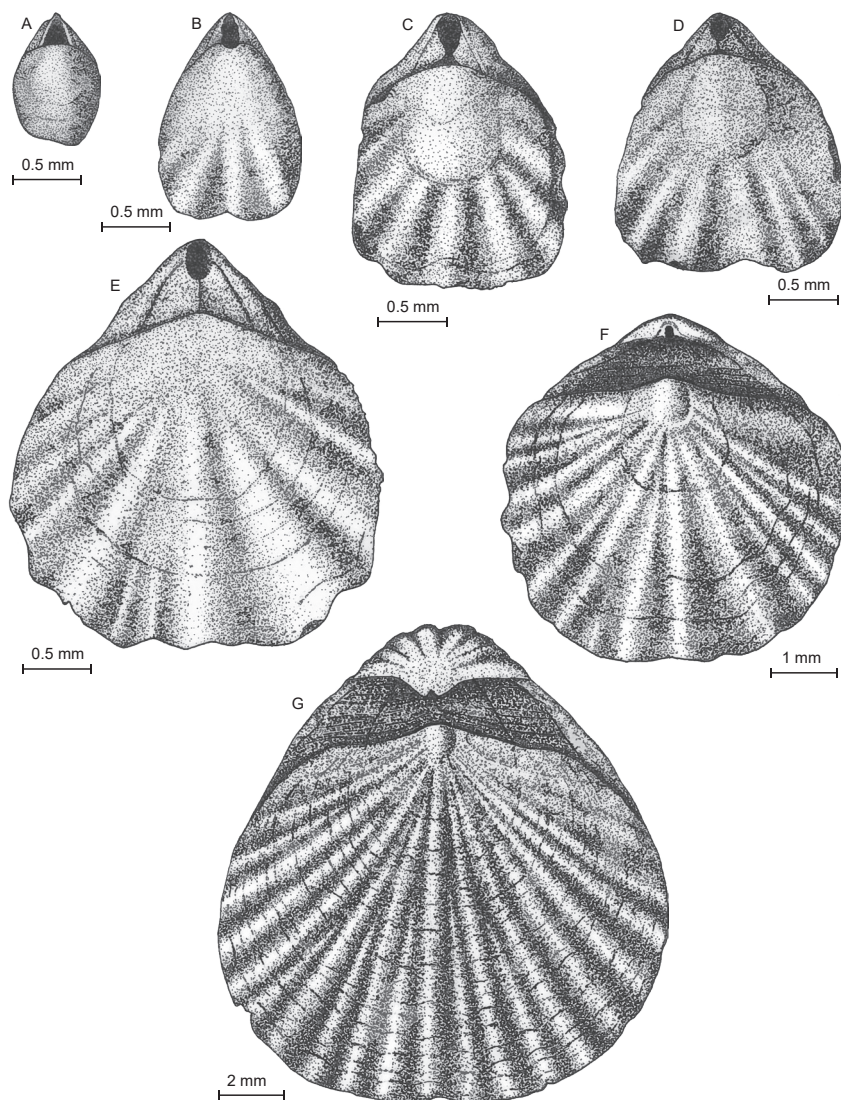


Fig. 90. *Trigonosemus pulchellus* (Nilsson, 1827). Growth stages. Upper lower Maastrichtian, *pulchellus-pulchellus* Zone. Hvidskud, Møns Klint (Figs 2, 4).

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 *Argyrothea* or *Bronnothyris* of the same size. *T. pulchellus* is, however, more elongate and is commonly somewhat asymmetrical.

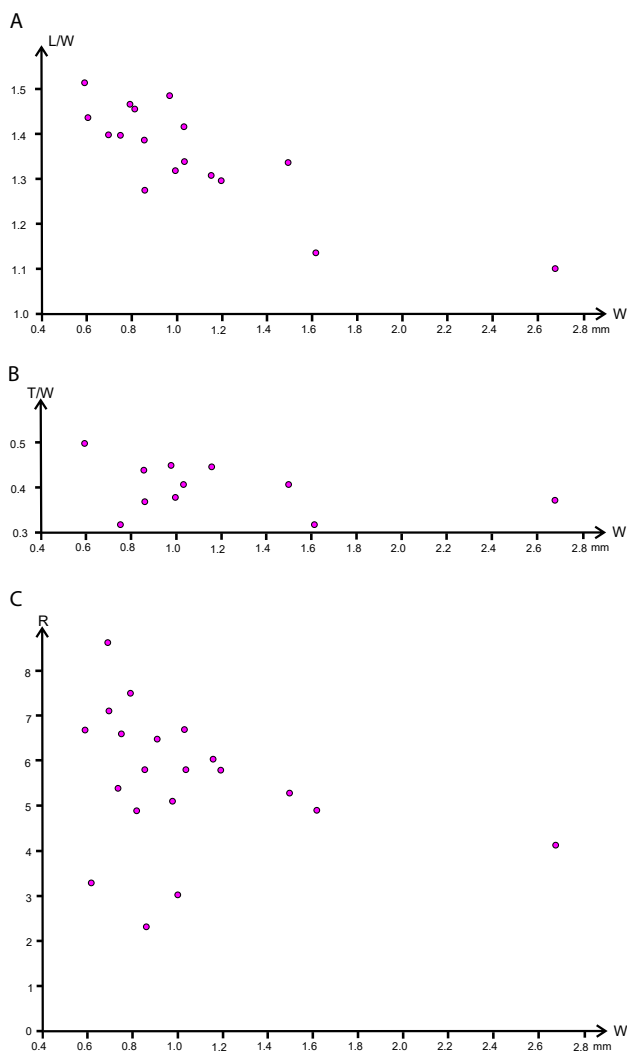


Fig. 91. *Trigonosemus pulchellus* (Nilsson, 1827). Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs/costellae. Upper lower Maastrichtian, *pulchellus*–*pulchellus* Zone.

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 subtriangu-
lar. 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 pre-
sent 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 in-
crease 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 com-
monly 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 pos-
teriorly 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 char-
acterized by the subtriangular outline and inflated
ventral valve. It is possible that *Bronnothyris obsti-
nata* (Steinich 1965) should be referred to *A. hirundo*.
Steinich (1965) had relatively few specimens of *B. ob-
stinata* at his disposal and his illustrated specimens

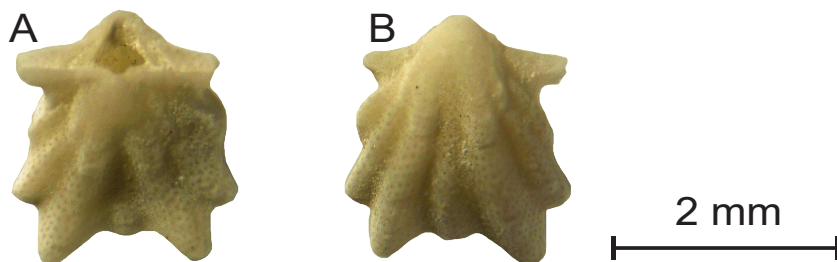


Fig. 92. *Argyrotheca hirundo* (von Hage-
now, 1842). **A:** Dorsal view. Note the lat-
erally diverging costae and the onset of
a new one in the median sinus. **B:** Same
specimen in ventral view. Lower Maas-
trichtian. Møns Klint (Fig. 2).

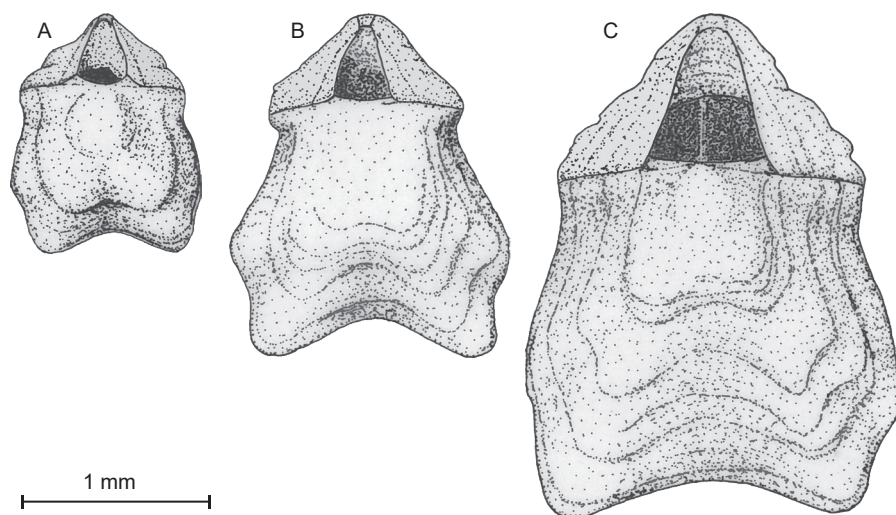


Fig. 93. *Argyrotheca hirundo* (von Hagenow, 1842). Growth stages. Lower upper Maastrichtian, *semiglobularis-humboldtii* Zone. Ferslev (Fig. 2).

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

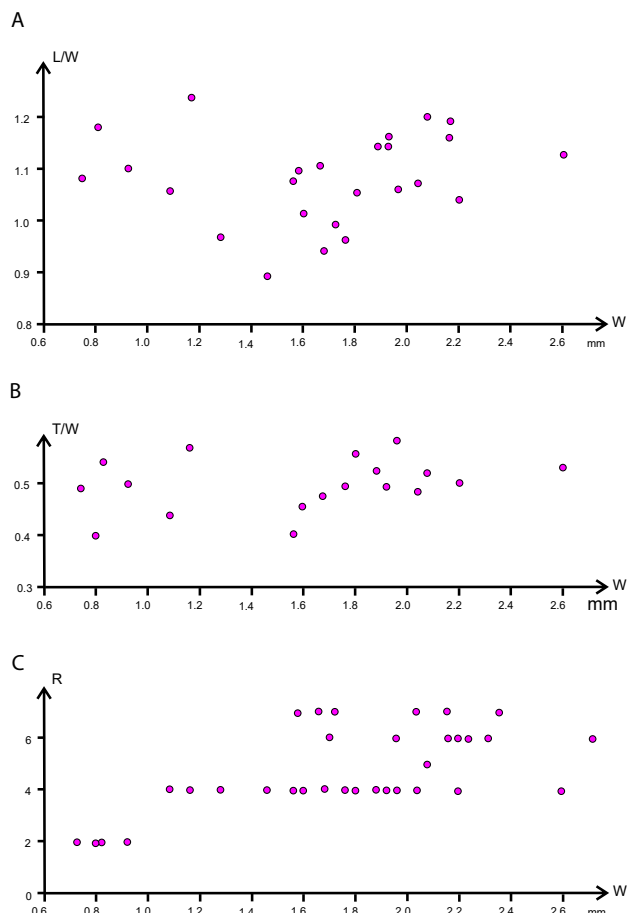


Fig. 94. *Argyrotheca hirundo* (von Hagenow, 1842). Scatter diagrams. L=length, W=width, T=thickness, R=number of ribs/costae.

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

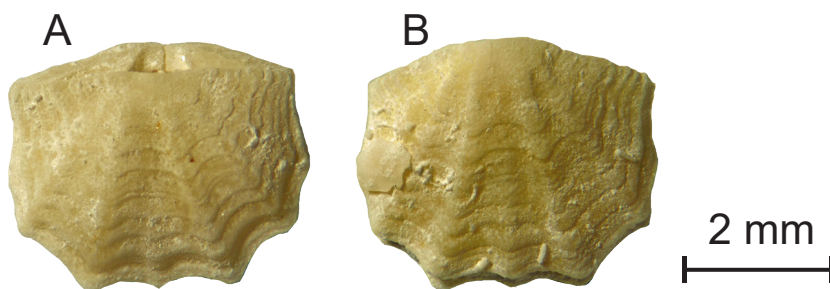


Fig. 95. *Bronnothyris bronnii* (Roemer, 1841). **A:** Dorsal view. **B:** Same specimen in ventral view, Uppermost Maastrichtian, *stevensis*-*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

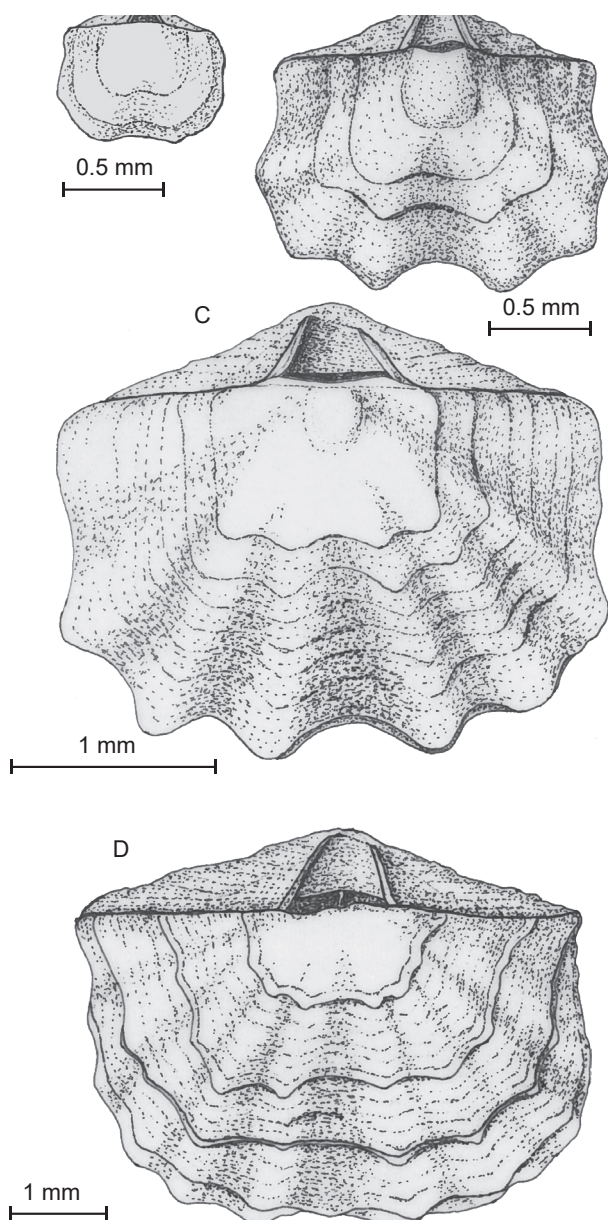


Fig. 96. *Bronnothyris bronnii* (Roemer, 1841). Growth stages. Upper lower Maastrichtian. Hundefangsklint, Møns Klint (Figs 2, 4).

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

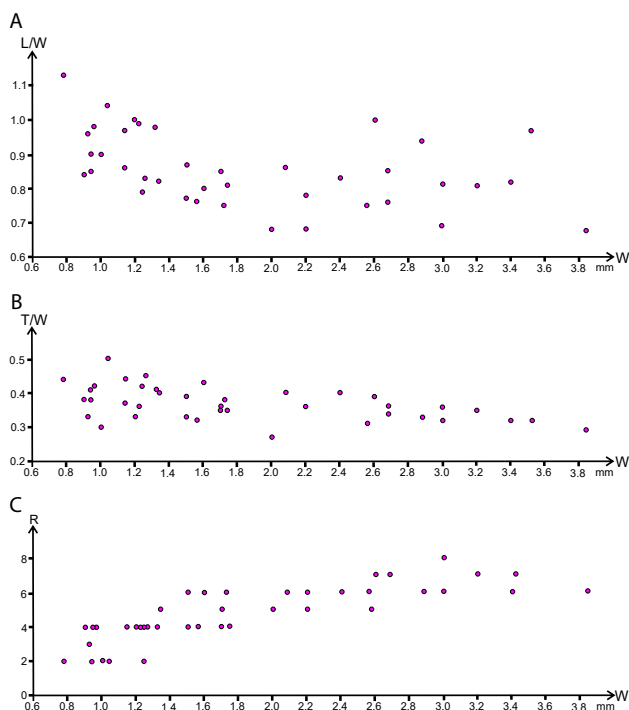


Fig. 97. *Bronnothyris brononii* (Roemer, 1841). Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae. Lower Maastrichtian. Møns Klint (Fig. 2).

& Schrøder 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-

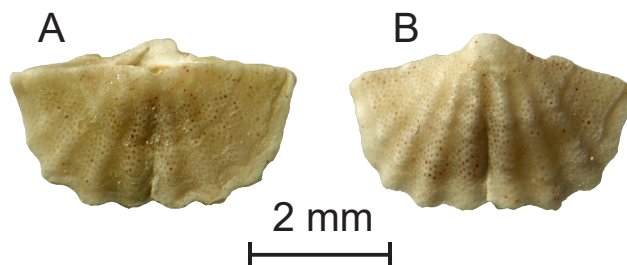


Fig. 98. *Bronnothyris coniuncta* Steinich, 1965. A: Dorsal view. B: Ventral view of same specimen. Upper lower Maastrichtian. Hvidskud Møns Klint (Figs 2, 4).

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

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

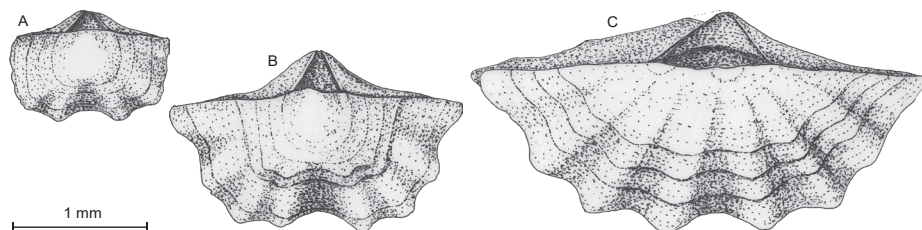


Fig. 99. *Bronnothyris coniuncta* Steinich, 1965. Growth stages. Upper lower Maastrichtian. Hvidskud Møns Klint (Figs 2, 4).

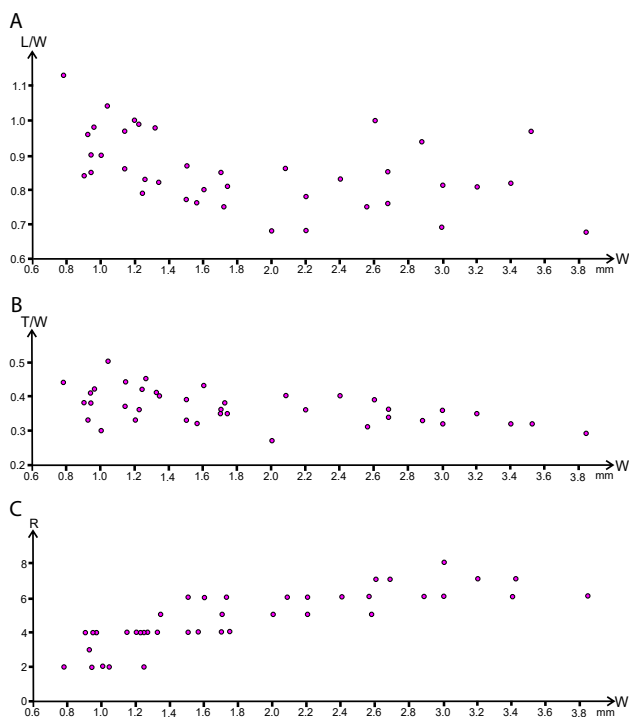


Fig. 100. *Bronnothyris coniuncta* Steinich, 1965. Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae.

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

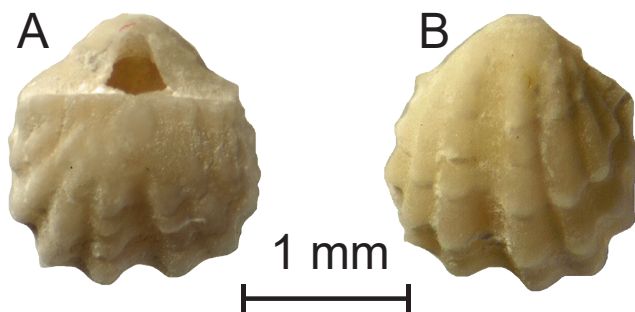


Fig. 101. *Bronnothyris stevensis* (Nielsen, 1928). **A**: Dorsal view. **B**: Same specimen in slightly oblique ventral view. Note the characteristic arrangement of two bundles each comprising three costae. Upper upper Maastrichtian, *stevensis*-*chitoniformis* Zone. Kulsti Rende, Stevns Klint (Figs 2, 6).

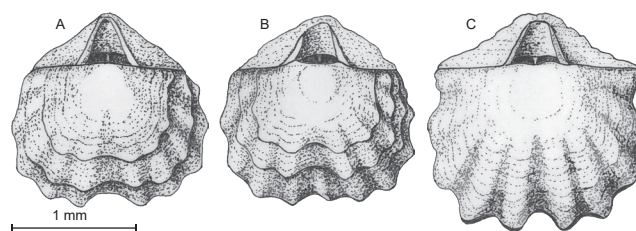


Fig. 102. *Bronnothyris stevensis* (Nielsen, 1928). Growth stages. Upper upper Maastrichtian, *stevensis*-*chitoniformis* brachiopod Zone. Stevns Klint (Fig. 2).

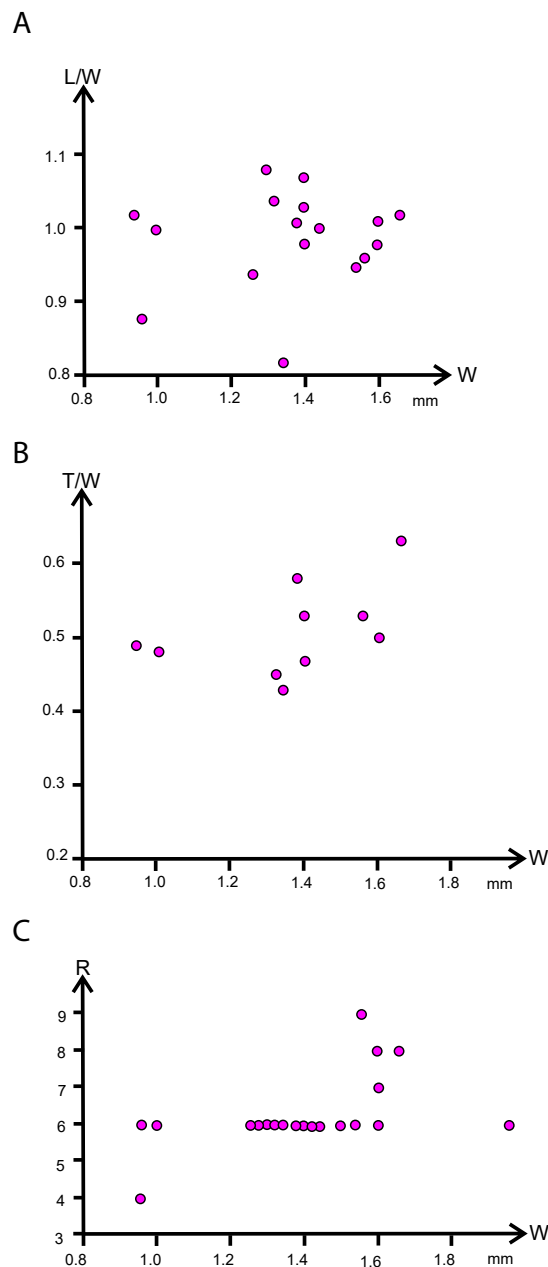


Fig. 103. *Bronnothyris stevensis* (Nielsen, 1928). Scatter diagrams. L=length, w=width, T=thickness, R=number of ribs/costae.

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



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).

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-

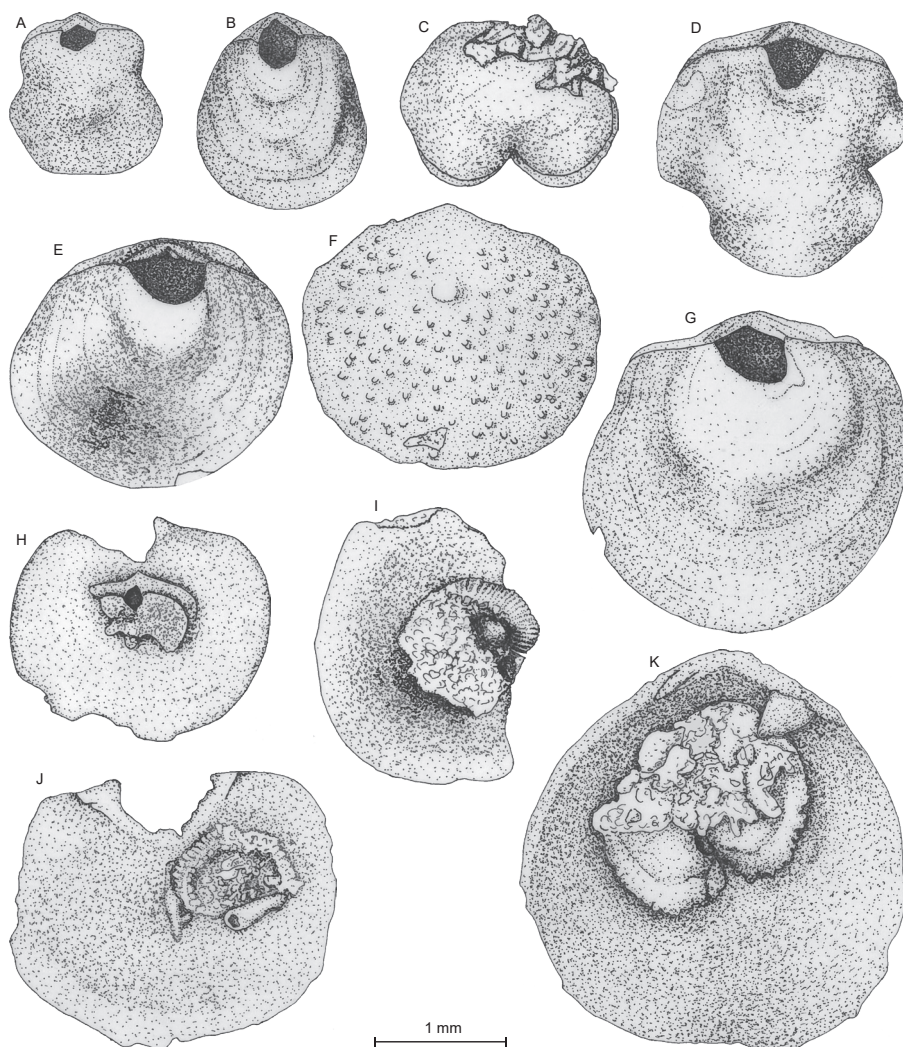


Fig. 105. *Aemula inusitata* Steinich, 1967. A, B, D, E, G: Growth stages in dorsal view, showing the characteristic outline of the shell with irregular indentations of anterior margin. C: Ventral view. F: Ventral valve showing the sculpture comprising small tubercles. H: Spicular skeleton, showing circular 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.

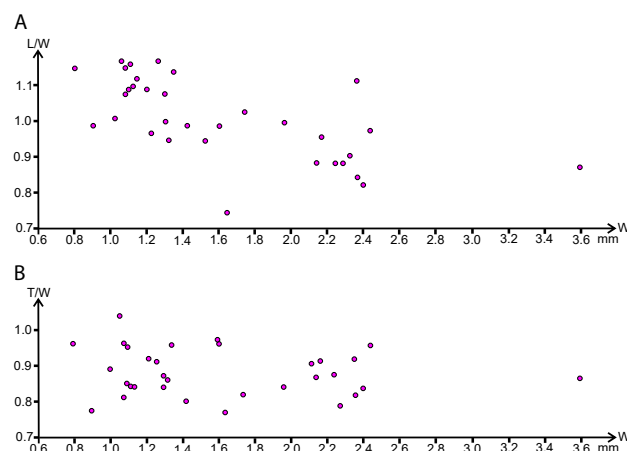


Fig. 106. *Aemula inusitata* Steinich, 1967. Scatter diagrams. L=length, W=width, T=thickness.

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

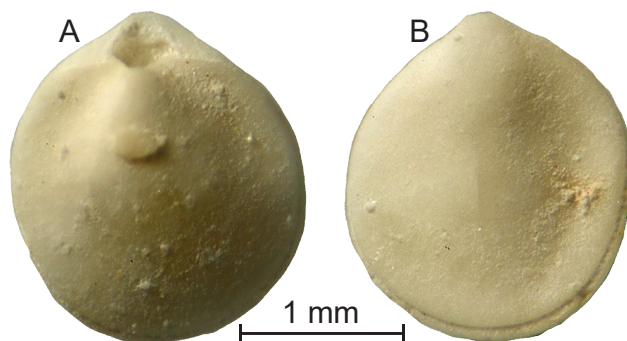


Fig. 107. *Scumulus inopinatus* Steinich, 1968. **A:** Dorsal view. Note the amphithyrid foramen. **B:** Same specimen in ventral view. Lower Maastrichtian. Møns Klint (Fig. 2).

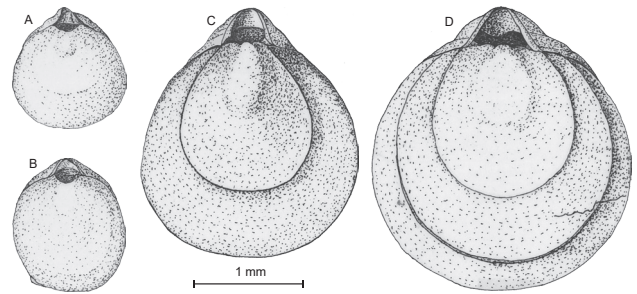


Fig. 108. *Scumulus inopinatus* Steinich, 1968. Growth stages. Note that the foramen changes during growth from amphithyrid to hypothyrid in adult forms. Upper lower Maastrichtian. Hvidskud, Møns Klint (Figs 2, 7).

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*

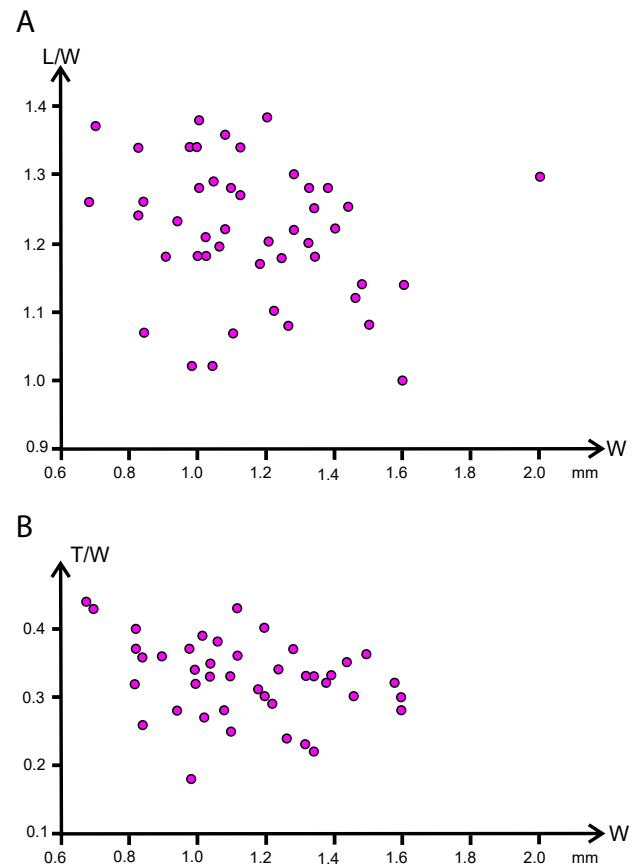


Fig. 109. *Scumulus inopinatus* Steinich, 1968. Scatter diagrams. L=length, W=width, T=thickness

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; Kjølbygård: 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

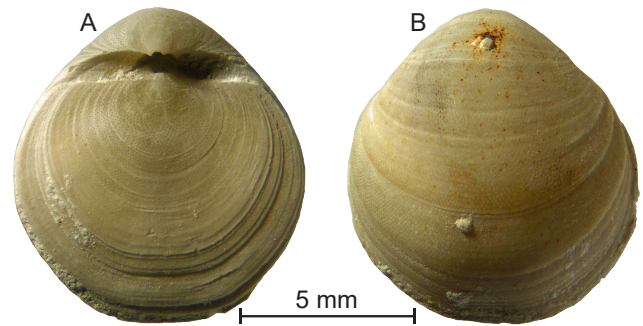


Fig. 110. *Magas chitoniformis* (von Schlotheim, 1813). **A:** Dorsal view. Note the strongly incurved rostrum, which almost closes the foramen; Adult *M. chitoniformis* thus belongs to the highly characteristic group of hemispherical species in the Maastrichtian chalk (Surlyk 1972). **B:** Same specimen 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-

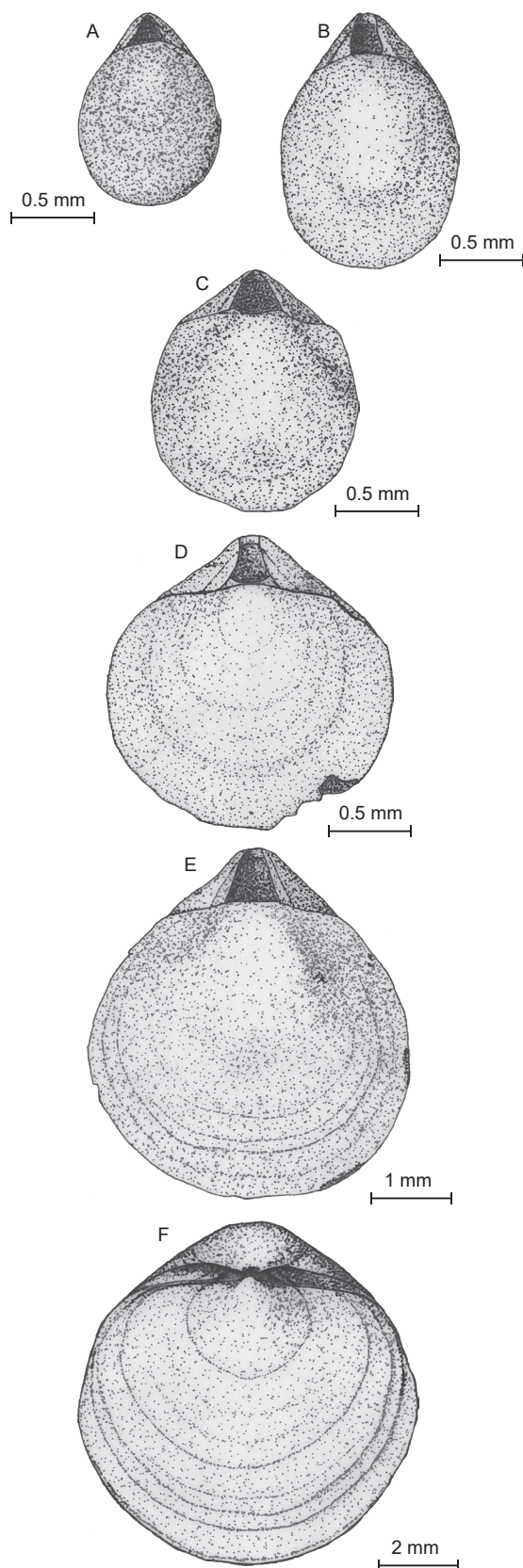


Fig. 111. *Magas chitoniformis* (von Schlotheim, 1813). Growth stages. A–D. Nørre Flødal and E. Gudumholm. Lower upper Maastrichtian. F. Møns Klint, upper lower Maastrichtian (Fig. 2).

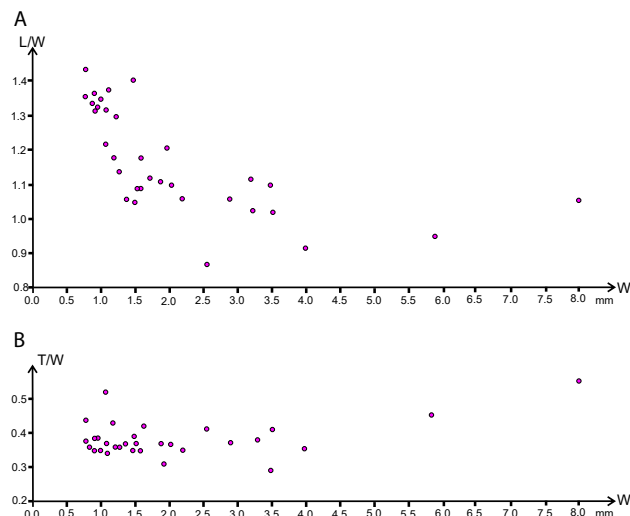


Fig. 112. *Magas chitoniformis* (von Schlotheim, 1813). Scatter diagrams. L=length, W=width, T=thickness.

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. Forchammers 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, *Neoliothyryna 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 Kerterminde 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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