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EARLY DANIAN SPECIES OF THE ECHINOID GENUS *TYLOCIDARIS* (CIDARIDAE, PSYCHOCIDARINAE) FROM EASTERN DENMARK

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Primary spines of the echinoid genus *Tylocidarid* Pomel, 1883 were formerly widely used as key index fossils for the Danian (Early Palaeocene). In recent years their value as such has been discredited and tylocidarid species distribution has been shown to be diachronous in relation to dinoflagellate biostratigraphy as well as be facies-dependent to the extent that they are missing from important facies types of the Danian. Difficulties in establishing a correlation between the Danian strata of Denmark and southern Sweden have also affected their practical use. A biostratigraphical study based on specimens collected bed by bed at Stevns Klint and additional studies at Karlstrup quarry (both localities situated in the Danian Stage type area, eastern Denmark), have provided evidence that the Early Danian tylocidarid zonation of Denmark and southern Sweden is essentially the same with *T. oedumi* Brünnich Nielsen, 1938 and *T. abildgaardi* Ravn, 1928 being restricted to two distinct zones, and thus not co-occurring as suggested by Brotzen (1959) for the Limhamn locality in Sweden. One major discrepancy between the Danish and Swedish biozonation schemes has thus been eliminated. Material collected at Karlstrup quarry shows that an early Middle Danian rosenkrantz Zone is present at that locality, this zone not having been recorded from Denmark so far. Especially interesting amongst newly collected material are tests of *T. oedumi* and *T. abildgaardi*. Finally, bryozoan mound growth is discussed. It is suggested that the growth of Early Danian mounds was affected by palaeocurrents which swept sediment away from intervening troughs, thus allowing hardground formation to take place there. The troughs must have existed for a considerable time span. At Stevns Klint, a large trough structure shows an impressive series of consecutive (incipient) hardgrounds. In the bryozoan mounds, net growth rate is shown to have been rather slow, allowing typical *T. oedumi* to evolve via 'overlap forms' to *T. abildgaardi* during the formation of the first series of mounds. A new model for tylocidarid evolution in the type Danian is proposed, with the lineage *oedumi*-*'overlap forms'*-*abildgaardi-ravni-bruennichi* becoming extinct in the late Middle Danian, then being replaced by *vexilifera*, originating from a lineage *oedumi-rosenkrantz-vexilifera*.

Key words — Danian, biozonation, Cidaridae (Psychocidarinae), *Tylocidarid*, evolution, bryozoan mounds, Denmark, Sweden.

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INTRODUCTION

For a long time tylocidarids, *i.e.* the disarticulated primary spines of various species of the genus *Tylocidarid* Pomel, 1883, have been considered important key index fossils for the Danian of Den-

mark and southern Sweden. Although still very useful, doubts as to their importance as index fossils have recently been expressed, their place being taken by micro- and/or nannofossils such as foraminifera, dinoflagellates and calcareous nannoplankton.

Two factors have contributed to this situation: — the conclusion that their geographical distribution is diachronous in relation to dinoflagellate biozonation (Hansen, 1977), being evidently facies dependent to the extent that they are missing from many important facies of the Danian; — difficulties related to the definition and identification of species within the genus.

The most recent work on Danian tylocidarids is that of Brotzen (1959), who presented a detailed biozonation for the Limhamn quarry (Skåne, SW Sweden) comprising the following zones:

Tylocidaris herupensis Zone	(= Late Danian) [top]
Tylocidaris brünnichi Zone	(= late Middle Danian)
Tylocidaris rosenkrantzi Zone	(= early Middle Danian)
Tylocidaris oedumi Zone	(= Early Danian) [bottom]

A similar, but different, zonation had already been established in Denmark by Brünnich Nielsen (1938), which was subsequently amended by Rosenkrantz & Wienberg Rasmussen (1960) as follows:

Tylocidaris vexillifera Zone	(= Late Danian) [top]
Tylocidaris bruennichi Zone	(= Middle Danian)
Tylocidaris abildgaardi Zone	(= late Early Danian)
Tylocidaris oedumi Zone	(= early Early Danian) [bottom]

Since their introduction, differences between these zonations have frustrated correlations based on tylocidarids between the Swedish and Danish Danian and have contributed to the view that biostratigraphical dating based on hitherto useful species of this genus is fraught with difficulties.

The discrepancies between Brotzen's (1959) zonation and the Danish zonal scheme were the main reason for a renewed investigation reported upon herein, in the hope of shedding new light on some of the main problems. However, many questions remain, especially since the present paper focuses only on Early Danian tylocidarids. Middle and Late Danian tylocidarid species should be studied along similar lines in the (near) future.

HISTORY OF TYLOCIDARID BIOZONATION

At the beginning of this century, only a single species of *Tylocidaris*, *T. vexilifera* Schlüter, 1892, was recorded from the Danian. Ever since its erection, this species has presented problems. To start with a minor point: Schlüter (1892, p. 126 [54], pl. 17, figs 3, 4) spelt the trivial name as *vexilifera*, while many palaeontologists after him have preferred *vexillifera*.

Much more serious confusion arose from the fact that Schlüter stated that his species originated from the Maastrichtian white chalk of Stevns Klint, which is an error, the species being typical of the

Danian. Rosenkrantz (1965) presented compelling arguments in support of the view that Schlüter's specimens must have come from the former quarry at Herfølge, south of Køge (eastern Sjælland) and thus must be of Late Danian age.

In 1909, Brünnich Nielsen was the first to point out that the various forms of *T. vexilifera* Schlüter occurring in the Danian might be useful as index fossils. It was not until 1926 that Ødum subdivided Schlüter's species into three 'forms', viz. forma beta (= *T. vexilifera* Schlüter, 1892 s. str.), forma alpha (= *T. abildgaardi* Ravn, 1928), and forma gamma (= *T. oedumi* Brünnich Nielsen, 1938).

Ravn (1928) proposed the following division of Schlüter's species: forma typica (= *T. vexilifera* Schlüter, 1892 s. str.), var. *Brünnichi* (= *T. bruennichi* Ravn, 1928), and var. *Abildgaardi* (= *T. abildgaardi* Ravn, 1928 and *T. oedumi* Brünnich Nielsen, 1938). Ravn's var. *Brünnichi* was newly introduced and is now known to characterise the Middle Danian. In his var. *Abildgaardi*, Ravn grouped not only the Early Danian species now known under that name but also Ødum's (1926) forma gamma (= *T. oedumi*). Later, Brünnich Nielsen (1938) presented the following zonation:

Late Danian	<i>Tylocidaris vexilifera</i> Schlüter (sensu Ravn, 1928)
	<i>Tylocidaris bruennichi</i> Ravn, 1928
Early Danian	<i>Tylocidaris abildgaardi</i> Ravn, 1928
	<i>Tylocidaris oedumi</i> Brünnich Nielsen, 1938 (based on forma gamma Ødum, 1926)

This new zonation was also used in the virtually simultaneous paper by Rosenkrantz (1938) on the stratigraphy and tectonics of the Danian of eastern Sjælland. Wind (1953, 1954), without any justification, referred *T. oedumi* to the late Turonian-?late Santonian *T. (T.) clavifera* (Mantell, 1822) as a subspecies and *T. abildgaardi*, *T. bruennichi* and *T. vexilifera* to the Campanian-Maastrichtian *T. pomifer* (Leymerie, 1851) [now referred to the genus *Sardocidaris* Lambert, 1907; see Smith & Wright, 1989] also as subspecies, viz. *T. p. pomifer*, *T. p. Brünnichi* and *T. p. herupensis* Wind, 1954, respectively. Wind's taxonomy has not been adopted by later workers, with the exception of Brotzen (1959), who used the name *Tylocidaris herupensis* Wind, 1954 for *T. vexilifera* Schlüter, 1892.

Brotzen's paper on the tylocidarid biozonation of the Danian of Limhamn is of prime importance; three new species were erected, *viz.* *T. windi* (Early Danian), *T. rosenkrantzi* and *T. ravni* (both early Middle Danian). According to Brotzen, the Danian of Limhamn shows the following pattern in tylocidarid distribution:

- Late Danian herupensis Zone
[species represented: *T. herupensis* (= *T. vexilifera*)]
- late Middle Danian bruennichi Zone
[species represented: *T. bruennichi*]
- early Middle Danian rosenkrantzi Zone
[species represented: *T. rosenkrantzi*, *T. ravni*, and *T. abildgaardii*]
- Early Danian oedumi Zone
[species represented: *T. oedumi*, *T. windi*, and *T. abildgaardii*]

As mentioned above, this zonal scheme differs from the biozonation used then and now for the Danian of Denmark. The main problems concern the Early Danian, where Danish palaeontologists distinguish a separate earliest Early Danian oedumi Zone, overlain by the late Early Danian abildgaardii Zone. The Middle Danian in the Danish zonal scheme comprises but a single zone, that of *T. bruennichi*, since *T. rosenkrantzi* has not yet been recorded from the Danish Middle Danian (see below).

Hansen (1977) complicated matters even more by showing tylocidarid distribution to be diachronous in relation to the proposed dinoflagellate biozonation. To this may be added, that from my own field work and a study of the literature, it has become apparent that tylocidarids are extremely rare in or even absent from some of the major facies types of the Danian, such as many of the micritic and biomicritic limestones known collectively under informal or old names as 'blegekridt', 'slamkalk', 'kalksandskalk' or 'Saltholmskalk', thus diminishing further their value as key index biota. Tylocidarid species most commonly occur in bryozoan limestone facies.

The aim of the present paper is to investigate the extent to which tylocidarid species may still be used as key index biota for the Early Danian of eastern Denmark. It was considered essential to attempt to

resolve the discrepancies between eastern Denmark and southern Sweden. Two localities in eastern Denmark (Karlstrup and Stevns Klint) were selected for this purpose, and compared with Limhamn (SW Sweden) on opposite sides of the Øresund. All three localities are situated in the type area of the Danian Stage (compare Brotzen, 1959, fig. 1) and are thus of prime importance in biostratigraphical studies of the type Danian. Detailed descriptions and sections of Limhamn quarry may be found in Brood (1973), Cheetham (1971), Holland & Gabrielson (1979) and Holland (1982).

LOCALITIES

1. Karlstrup quarry

The quarry at Karlstrup (formerly Kagstrup) is situated in eastern Sjælland, c 10 km north of Køge, south of Copenhagen. Quarrying was ceased in the mid-1970s. The deeper part of the quarry, exhibiting more than 14 m of Late Maastrichtian white chalk, is now flooded; the remaining part is in the process of becoming overgrown. Along the sides of the water there are still fine sections exposing the Cretaceous/Tertiary boundary (see Gravesen, 1983; Ekdale & Bromley, 1984). Bryozoan limestones of the Early Danian oedumi and abildgaardii Zones are still beautifully exposed at the W, N, and E quarry faces.

Karlstrup quarry thus exposes a series of strata more or less identical to that seen at Stevns Klint. The presence at Karlstrup of early Middle Danian strata is discussed in detail below. The sequence is as follows:

— white chalk

This unit [latest Maastrichtian, equivalent of Brotzen's (1959) 'Stevnsian', brachiopod zone 10 of Surlyk (1970, 1972), *Belemnella casimirovensis* Zone in belemnite terms and *Pseudotextularia elegans* Zone of foraminiferal biozonation], comprises a 'normal' white chalk facies with some bryozoans and a diverse macrofauna [list in Gravesen, 1983; see also Surlyk (1979a, p. 47)].

— Fish Clay (Fiskeler)

This unit comprises a finely laminated marl with a maximum thickness of 10 cm. It contains many remanié Late Maastrichtian fossils.

— Cerithium Limestone

This is a 30-100 cm thick soft limestone reminiscent

of the white chalk facies. At the present locality, it is referred to as 'streaky chalk', on account of the many streaks of greyish marl. On microfaunal evidence (foraminifera) it is assigned to the *Eoglobigerina danica* Zone (Bang in Gravesen, 1983). Two spines herein referred to as *Tylocidaris* aff. *oedumi* are the only ones known to date from the Cerithium Limestone in Denmark (see discussion below).

— 'Karlstrup Chalkstone'

Resting upon the Cerithium Limestone and separated from that unit by a flint band is a 25-40 (-50) cm thick indurated limestone of hardground type with thalassinoid burrows and common siliceous sponges (*Aphrocallistes* cf. *alveolites* Roemer, 1841). Aragonitic biota are preserved as external moulds and include gastropods and bivalves. Echinoids are found locally. Spines of *T. oedumi* demonstrate that this unit forms the base of the *oedumi* Zone at this locality.

— Early Danian bryozoan limestones

These limestones display well-developed biohermal structures, which lithologically are similar to those found at Stevns Klint and contain the same macrofaunas, including echinoids, crinoids, asteroids, bivalves, brachiopods, gastropods, octocorals and sponges. In addition to the two Early Danian species *T. oedumi* and *T. abildgaardi* also spines occur that are attributable to 'overlap forms' (see below) as found at Stevns Klint and spines referred to as *T. aff. rosenkrantzi* and *T. ravni*, both indicative of the early Middle Danian.

Originally, it was intended to select the bryozoan limestone sections at Karlstrup for detailed bed-by-bed collections of tylocidarids; because of a lack of stability of quarry faces this plan had to be abandoned. The emphasis of the field work was therefore shifted to the Korsnæb section at Stevns Klint described below.

The Karlstrup section is of particular importance in having yielded the first tylocidarid spines from the Cerithium Limestone of Denmark known to date (see Pl. 1, Figs 1, 2). Because of this limited number of specimens their specific assignment is far from clear; they are here referred to as *T. aff. oedumi*. *Ex situ abildgaardi*-like spines with diminutive crowns appear to characterise the transition from *T. abildgaardi* to the Middle Danian coronate forms of *T. bruennichi*; they are best referred to *T. ravni*

Brotzen, 1959. In addition, from scree at the foot of the northern quarry face a number of spines probably coming from the uppermost parts of the section exposed have been collected. These are here referred to as *T. aff. rosenkrantzi* (Pl. 4, Figs 5-11). The occurrence of both '*T. ravni*' and *T. aff. rosenkrantzi* at this locality indicate the presence at the northern quarry face of earliest Middle Danian strata referable to the *rosenkrantzi* Zone.

2. Stevns Klint

This well-known and classic locality was first properly described by Abildgaard (1759) and has since remained very important not only to local Danish geology, but also internationally because of the Cretaceous/Tertiary (K/T) boundary strata being well exposed along this cliff section. For a historical review of the research of Stevns Klint the reader is referred to Gravesen (1979a). Detailed discussions may be found in Forchhammer (1825), Ravn (1903), Milthers (1908), Brünnich Nielsen (1917), Rosenkrantz (1924, 1940, 1966), Andersen (1944), Rosenkrantz & Wienberg Rasmussen (1960), Berthelsen (1962), Berggren (1964), Wienberg Rasmussen (1967, 1971), Håkansson (1971), Christensen *et al.* (1973), Birkelund & Bromley (1979), Bromley (1979b), Floris (1979) and Surlyk (1979b, 1984).

— Korsnæb section

For the present study this part of Stevns Klint was chosen because here the Cretaceous/Tertiary boundary is closer to beach level than anywhere else along the cliff, which makes the earliest Early Danian strata more easily accessible. Because of this easy access at the Korsnæb section, it was possible to collect specimens bed by bed.

The Korsnæb section is part of the southernmost exposure of Stevns Klint, situated east of Rødvig (Figs 1, 2). It encompasses the easternmost 400 m of the cliff, ending in the prominent point (headland) by the name of Korsnæb.

The section exposes well the Early Danian bryozoan limestones with well-developed biohermal structures. In some parts of the section, the Late Maastrichtian white chalk and the Cretaceous/Tertiary boundary strata are also exposed.

The sequence exposed here is as follows:

a - Late Maastrichtian white chalk

This unit most probably corresponds entirely to the 'grey chalk' ('Gråkridt') as exposed at the classic

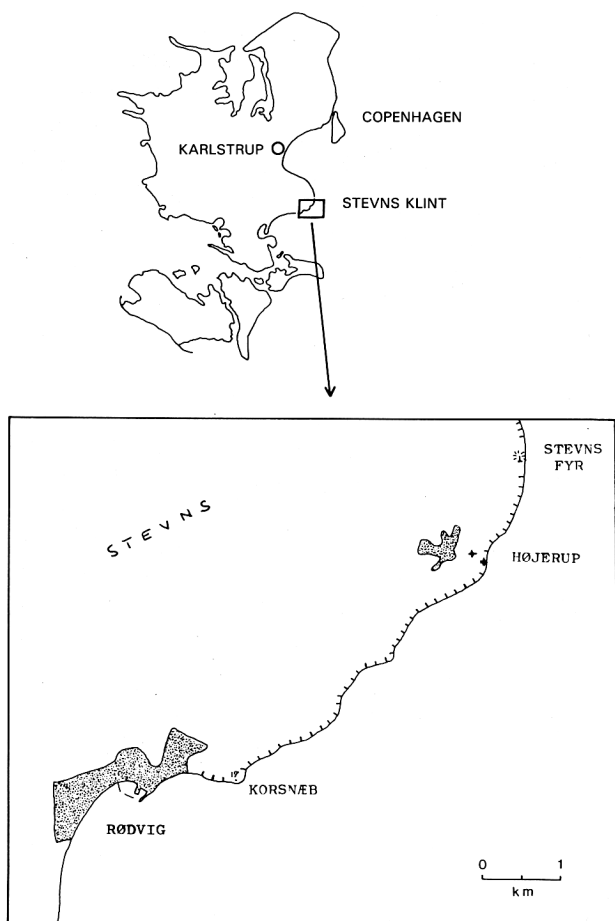


Fig. 1. Maps showing location of Karlstrup, Stevns Klint and the Korsnæb headland; the Korsnæb section is situated directly west of Korsnæb.

section at Højerup a few kilometres to the north. This is a white chalk with bryozoans, nodular and tabular flints, grey marly streaks and burrows with marly infill. For a detailed lithological description of this facies at Højerup, the reader is referred to Håkansson *et al.* (1974). This unit yields in the Korsnæb section a varied macrofauna. As at Højerup, the top parts (between the depressions of the Fish Clay) are indurated to form the so-called 'Indurated white chalk' with aragonitic fossils preserved as internal and external moulds. Together with the earliest Danian Cerithium Limestone the 'Indurated white chalk' forms part of the complex hardground at the Maastrichtian/Danian boundary (see *e.g.* Surlyk, 1979b).

b - Fish Clay

This unit may reach thicknesses of 35 cm locally at Stevns Klint (Christensen *et al.*, 1973). In the

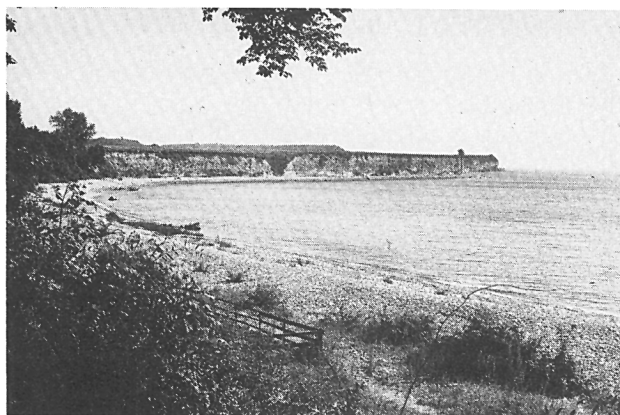


Fig. 2. The Korsnæb section seen from the beach at Rødvig (summer of 1984).

Korsnæb section it is generally thinner (maximum thickness often only *c.* 10 cm or even as thin as one to a few centimetres). Due to wave action it is often washed out leaving an empty fissure in the cliff face.

c - Cerithium Limestone

In the Korsnæb section this unit generally attains a thickness of *c.* 20-40 cm; in the western part of the section it is much thicker, up to 70 cm, which is about the maximum thickness encountered at Stevns Klint. Where it is thickest, it consists of two different lithological entities merging imperceptibly into each other.

The lower part is a whitish, chalk-like, and soft sediment with numerous streaks of grey marl. The upper part is a yellowish or yellowish-white, hard limestone with numerous *Thalassinoides* burrows and is developed as a typical hardground, in places showing well-developed slickensides. Within this hardground, aragonitic fossils are preserved as external and internal moulds, showing fine details of ornament. The macrofauna includes gastropods, solitary corals, siliceous sponges and echinoids.

The marginal parts of the *Thalassinoides* burrows are often converted into tubular flints, corresponding to the original shape of the burrows. Internally these flints often contain unconsolidated sediment with bryozoans and extremely well-preserved Early Danian fossils, *e.g.* the shallow-burrowing echinoid *Brissopneustes danicus* Schlüter, 1897 (referred to the genus *Cyclaster* Cotteau, 1856 by Asgaard, 1976), in other parts of Stevns also spines of *T. oedumi*, gastropods and bivalves. This fauna appears to match that found in the lowest beds of the overlying bryozoan limestone.

Reference point	Height	Reference point	Height
KO -175	367	KO -45	251
KO -165	343	KO -35	202
KO -155	315	KO +10	194
KO -145	312	KO +20	190
KO -135	285	KO +30	204
KO -120	244	KO +40	190
KO -115	255	KO +50	178
KO -110	248	KO +60	143
KO -65	231	KO +90	203
KO -60	244	KO +95	226
KO -55	246	KO +100	193
KO -50	255		

Table 1. Height of lower boundary of bryozoan limestone at the Korsnæb section, Stevns Klint (vertical height in centimetres above beach level on 27 July 1985; leveling by Peter Toft and Palle Gravesen).

d - Early Danian Bryozoan Limestone

This unit (Table 1) has a sharp lower boundary (probably an originally erosive contact formed under submarine conditions, compare Surlyk, 1979b, p. 169; Birkelund & Håkansson, 1982, p. 375). As may be seen in Table 2, this lower boundary is situated at different levels above the present beachline even over a short distance of 400 m, as occupied by the Korsnæb section. If this boundary plane can be assumed to have been originally reasonably even, the present variation in vertical position must be attributed to a slight folding of the strata in post-Danian times (compare Rosenkrantz, 1938).

The Bryozoan Limestone (Fig. 3) typically consists of numerous skeletal fragments of benthic biota, mostly bryozoans, in a micritic matrix. Its benthic fauna may make up as much as *c* 40 % of the sediment (Birkelund & Håkansson, 1982, p. 375), but still the fabric remains in large part mud-supported (Bromley, 1979a, p. 17). A closer look reveals the presence of a wide range of subfacies: marly layers, incipient as well as well-developed typical hardgrounds, the latter being the so-called 'Krabbelag' of Brünnich Nielsen (1917; compare also Rosenkrantz, 1966, p. 724), echinoderm 'coquinas' with winnowed micrite, comprising solely skeletal debris, on the flanks of some bioherms, etc. (see Surlyk 1979b, p. 170). The coquinas may consist of randomly orientated echinoid tests of epifaunal *Echinocorys sulcata* (Goldfuss, 1829) [at Karlstrup also of epifaunal *Phymosoma* aff. *granulosum*

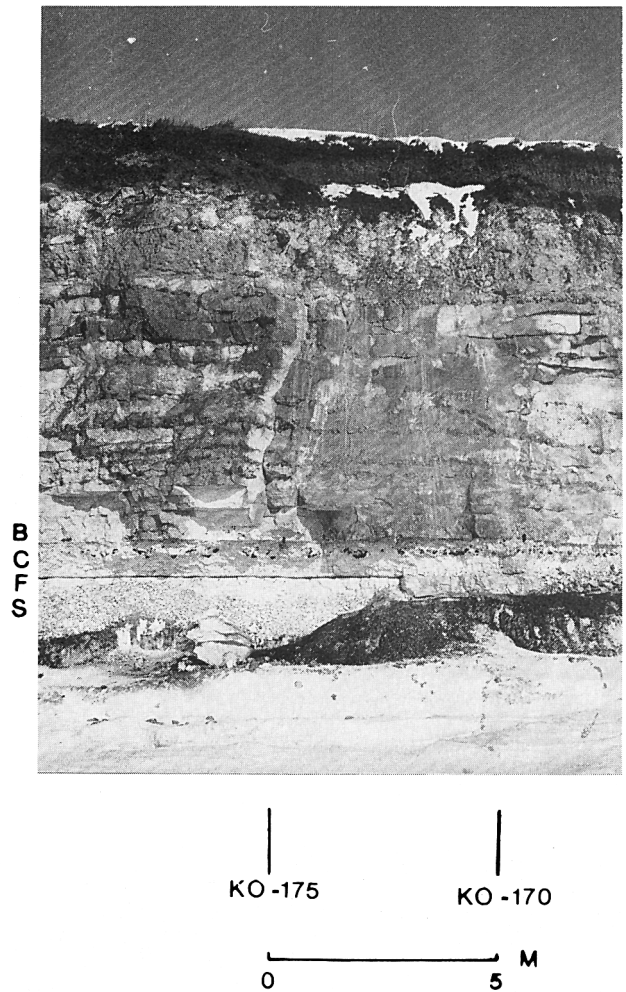


Fig. 3. The westernmost part of Korsnæb section showing Late Maastrichtian white chalk and K/T boundary strata (March 1987). For horizontal co-ordinates see text. B - lowermost part of Early Danian Bryozoan Limestone forming bulk of cliff (marked is the base of the oedumi Zone); C - Cerithium Limestone (earliest Danian); F - Fish Clay (basal Danian marl); S - Late Maastrichtian white chalk (baltica Zone).

(Goldfuss, 1829) and infaunal *Brissopeustes danicus* Schlüter, 1897].

A closer look also reveals the presence of finely laminated limestones (with little apparent bioturbation) as opposed to limestones where bioturbation seems to have disturbed much of whatever primary lamination there might have been. In places, *Thalassinoides* forms complex networks (Figs 11, 12; see also Bromley, 1979a, p. 27). A detailed sedimentological study comprising an analysis of the ichnofauna is bound to yield a wealth of new information on the details of formation of these bryozoan limestones.

Biostratigraphically, these limestones have traditionally been divided into two tylocidarid zones: that of *T. oedumi* in the lowermost beds and that of *T. abildgaardi* in the remaining part. The macrofauna of these two zones appears to be more or less identical. The lower beds of the Bryozoan Limestones are almost horizontal, and only some metres higher do typical biohermal structures start to appear. Having once started to form, however, they must have grown into impressive bioherms standing out several metres above the sea floor at that time with deep, current-swept, elongated troughs between them (see discussion below). The bryozoan limestones contain a number of distinct and impressive flint bands which have all been numbered and used in the course of the present investigation.

METHODS

The field work at the Korsnæb section (Figs 4, 5) was conducted along the following lines:

- 1 - preparation of a drawing of the entire section (Fig. 8a, b);

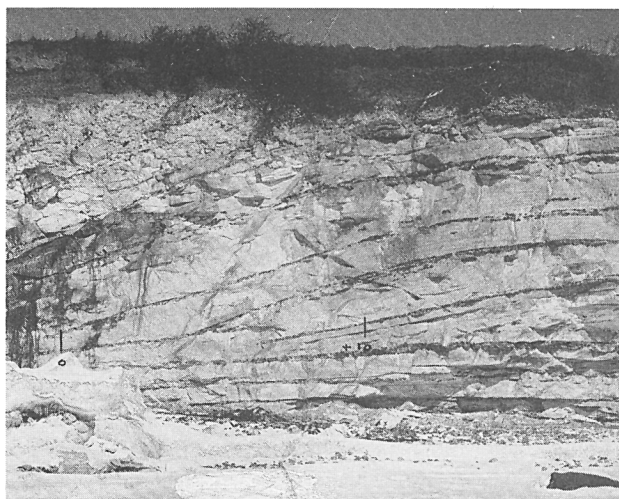


Fig. 4. The Korsnæb section: western flank of a large biohermal structure in Early Danian bryozoan limestones (March 1987). For horizontal co-ordinates see text.

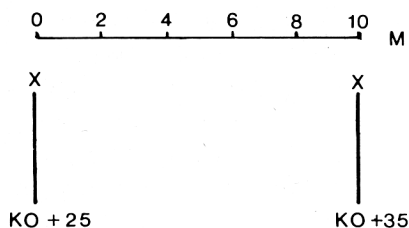
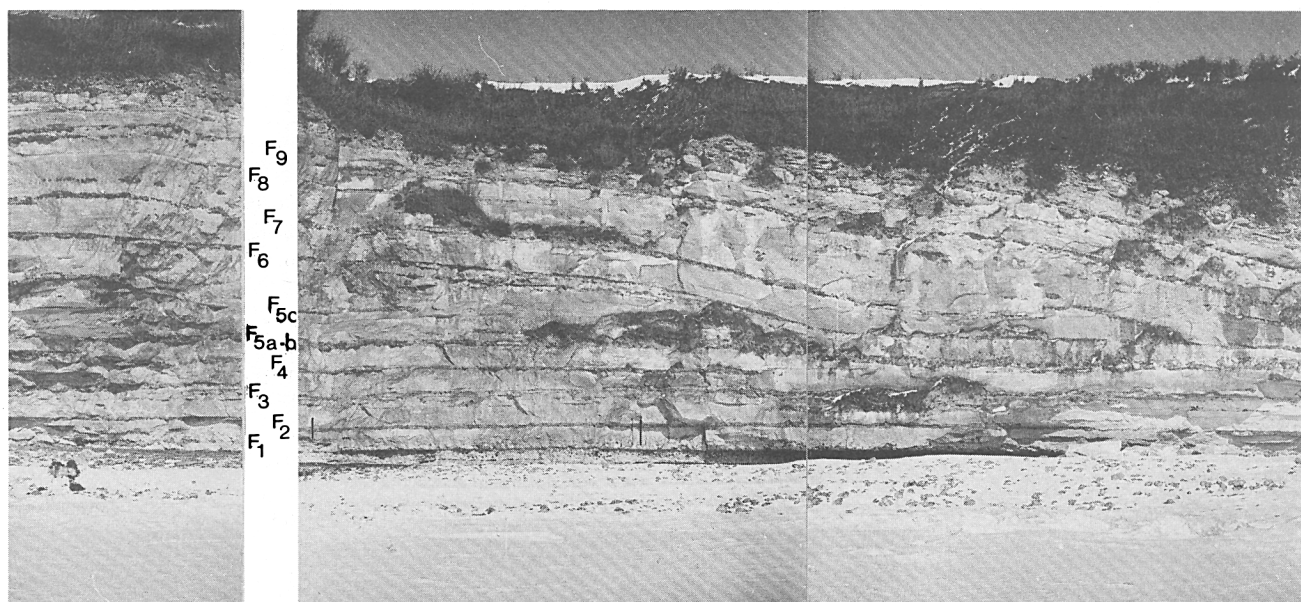


Fig. 5. The Korsnæb section: part of biohermal structure in section KO +25, illustrating the practical use of the co-ordinate system described in the text (March 1987). Flint bands are numbered consecutively.

- 2 - numbering of all flint bands so as to have a set of marker horizons for bed-by-bed collection (Table 2);
- 3 - establishment of a co-ordinate system covering the entire cliff face of the section;
- 4 - measurement of detailed sections at twenty different locations as high up the cliff face as possible, making use of 4 or 6 m long ladders.

Some of these sections are shown in Figs 11-15.

Points 2 and 3 are in need of further explanation: Due to the complexity of the biohermal structures occurring in this bryozoan limestone unit, bed-by-bed collecting presents problems immediately. In passing from one biohermal structure to the other, individual limestone beds and flint bands tend to either thin out and disappear or merge with other beds or flint bands; also, new limestone beds and flint bands may be intercalated. A closer look, however, reveals a pattern of marker horizons, flint bands in particular, but also marly horizons and hardgrounds, which can be traced from one biohermal structure to an adjacent one, some of them even over long distances. Tracing these marker horizons results in a first tentative basis for correlation of individual beds from one structure to the next. Numbering the individual limestone beds and flint bands is possible only within each separate bioherm. This necessitates the establishment of a number of different reference systems, each of which can only be used within the individual bioherm for which it has been worked out. This appears to be the only practical solution to the problem.

Within each individual biohermal structure a numbering system for limestone beds and flint bands was established, in practice focusing on flint bands, numbered consecutively from bottom to top F1, F2, F3 and so on. Bed-by-bed collecting can then be undertaken with reference to this system and specimens collected may be documented as follows:

- + 13 cm above top of F3 ..., or,
- 17 cm below base of F4

However, because of extreme lateral variations seen in biohermal structures a vertical reference does not suffice. To be able to tell exactly from where within a biohermal structure (top, flank, intervening troughs etc.) a specimen has been collected, a means of referring to the horizontal plane is also needed. To this end, a horizontal division was also established starting from an arbitrary zero point referred

Section	Local flint band numbering
KO +25	KO +25/F6
KO +75	KO +75/F6
KO +100	KO +100/F10
KO +130	KO +130/F7
KO +150	KO +150/F4
KO +185	KO +185/F6

Table 2. Example of numbering of a marker horizon within various sections of the Korsnæb section, Stevns Klint (here, the flint band marking the lower boundary of the *abildgaardi* Zone).

to as KO 0 [short for KO(rsnaeb)]. From this point, distances were measured horizontally to the right (positive figures) and to the left (negative figures). Using the vertical and horizontal reference systems, a co-ordinate system was effectively spread out over the cliff face. The individual sections were named after their position along the horizontal axis in the following way:

- 1 - section KO -150 (from KO -175 to KO -115)
- 2 - section KO - 90 (from KO -115 to KO - 70)
- 3 - section KO - 30 (from KO - 70 to KO - 10)
- 4 - section KO + 25 (from KO - 10 to KO + 70)
- 5 - section KO + 75 (from KO + 70 to KO + 85)
- 6 - section KO +100 (from KO + 85 to KO +120)
- 7 - section KO +130 (from KO +120 to KO +140)
- 8 - section KO +150 (from KO +140 to KO +170)
- 9 - section KO +185 (from KO +170 to KO +210)
- 10 - section KO +220 (from KO +210 to KO +223)

In this way, the 400 m long Korsnæb section was divided into ten individual sections of unequal length to conform with the individual biohermal structures.

Thus, each section has its own individual numbering system for limestone beds and flint bands. As the numbers of these do not correspond from one section to the other, a flint band may be numbered '4' in one section and '6' in another where more flint bands are developed (see Table 2). To avoid confusion as to which particular flints bands are meant, all bands should be indicated both by a 'section index' (e.g. KO -30) as well as the number. Flint no. 4 (counted from below) within section KO -30 should then be indicated as KO -30/F4.

A combination of the horizontal reference system with the individually numbered flint bands within the different sections provides a co-ordinate system for the entire Korsnæb section, enabling the collec-

tion of specimens along the entire section and a reference to the precise location of specimens, e.g.:

- horizontal parameter: KO -30,76 m; vertical parameter: + 18 cm above top of flint KO -30/F3, or,

- horizontal parameter: KO +220,24 m; vertical parameter: - 5 cm below base of flint KO +220/F7.

All bed-by-bed collecting at the Korsnæb section has been done using this co-ordinate system.

SYSTEMATIC DESCRIPTIONS

Introductory remarks — The genus *Tylocidarid* was erected for cidarid echinoids with clavate or glandiform primary spines and imperforate primary tubercles. Like most other regular echinoids, tylocidarid tests tend to disintegrate rapidly upon death resulting in fossil assemblages consisting of scattered spines, dissociated lantern elements and tests mostly consisting of a single row of interambulacral plates with two adjacent rows of ambulacra or even single plates. For a full discussion of the various stages of disintegration of regular echinoids see e.g. Schäfer (1971), Smith (1984) and especially Kidwell & Baumiller (1990).

As Danian species of *Tylocidarid* are almost exclusively found in bryozoan limestone facies, which to a large degree consists of more or less broken skeletal parts of bryozoans, crinoids, asteroids, brachiopods, irregular and regular echinoids etc., it is not surprising that the tylocidarid remains are mostly found in a state of advanced disintegration (loose spines, lantern elements and test plates). Complete tests are rare; tests associated with spines such as the specimen figured by Ravn (1928, pl. 4, fig. 35) or the specimen figured herein (see Pl. 2, Fig. 7) are rarities.

However, during field work it appeared that test segments (interambulacral segment with adjacent ambulacral columns) are fairly common in the Early Danian bryozoan limestones both at Karlstrup and at Stevns Klint and also that complete tests (without spines) are not quite as rare as previously thought. A dozen or so complete tests of *T. abildgaardii* have been collected at Karlstrup and at Stevns Klint. Of *T. oedumi*, however, only a single complete test has so far been encountered (see Pl. 2, Figs 1-3).

Danian tylocidarid spines show a wide range of variation as far as morphology is concerned; this has led to the erection of several 'species' (Brotzen, 1959). The primary spines of some taxa are so dis-

tinctive that they may be immediately identified to species; this applies to fully-grown spines of e.g. *T. oedumi*, *T. abildgaardii*, *T. bruennichi*, and *T. vexilifera*, which explains why they have been held to represent good index fossils for the Danian. However, there are serious problems. In practice, it is often difficult to identify individual spines, and, as shown below, there is a level ('overlap zone') at the boundary of the oedumi and abildgaardii Zones at Stevns Klint where a proper assignment of spines is difficult. In my opinion, the individual populations ('species') of *Tylocidarid* within the Danian can only be defined statistically, meaning that a single or a few spines may not be an adequate basis for the identification of a species.

Morphotype analysis — Putting the various shapes of the Danian tylocidarid spines into a scheme that can be treated statistically presents a problem. In practice, I ended up with the following method (Table 3) based on an assessment of the form of the spines (= morphotypes) according the groupings shown in Fig. 6 and described below:

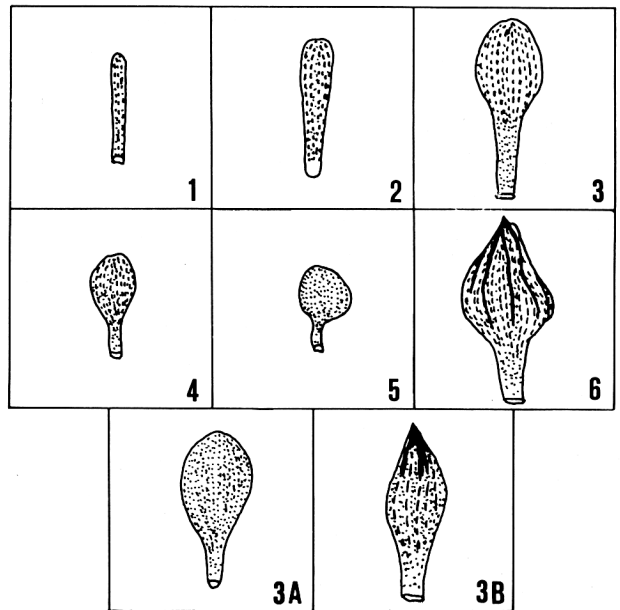


Fig. 6. Morphotypes of tylocidarid primary spines as here defined: type 3 - typical *T. oedumi*; type 4 - overlap forms; type 5 - *T. abildgaardii*; type 6 - *T. vexilifera*; type 3a - *T. baltica*; type 3b - *T. rosenkrantzi*. See text for details.

- morphotype 1: elongate clavate, sides parallel
- morphotype 2: elongate clavate, sides straight as well as divergent
- morphotype 3: elongate clavate, sides divergent

but forming concavity; gradual taper from neck to head; head longer than neck. Maximum width of spine distally.

- morphotype 4: short clavate with elongate head; head and neck approximately of equal length.
- morphotype 5: very short clavate, neck thin, passing abruptly into globose head; lacking 'crown'.
- morphotype 6: as type 5, but with shorter or longer 'crown'.

To these main types may be added the following:

- morphotype 3a: elongate clavate to semiglobose.
- morphotype 3b: elongate clavate, maximum width *c* at mid-length.

Morphotypes

	II	III	IV	V
<i>T. abildgaardi</i>	2.4	12.0	22.4	63.2
"overlap" forms	2.9	50.5	41.9	4.8
<i>T. oedumi</i>	3.6	76.8	19.6	0

Table 3. Morphotype analysis of three tylocidarid populations of the Korsnæb section, Stevns Klint (see text for details).

Test morphology — The terminology used in the descriptions of the test follows that used by Moore *et al.* (1952), Fell (1966), and Smith (1984). Below, reference is made to test characters which ideally should have been treated statistically using bivariate analysis. Due to the limited material collected thus far I have refrained from this, but obviously future work, based on an adequately large material, should include a proper statistical analysis of all test characters suited for such an analysis. The differences between the species described below may not be as pronounced as descriptions and Table 4 would appear to indicate. It still remains to be determined whether or not the differences between *T. oedumi*, 'overlap forms' and *T. abildgaardi* are in fact related, at least in part, to size differences.

Classification — This follows Smith & Wright (1989).

Order	Cidaroida Claus, 1880
Family	Cidaridae Gray, 1825
Subfamily	Psychocidarinae Ikeda, 1936
Genus and subgenus	<i>Tylocidaridaris</i> Pomel, 1883

Type species — *Cidaridaris clavigera* Mantell, 1822.

Tylocidaridaris (*Tylocidaridaris*) oedumi Brännich Nielsen, 1938

Pl. 1, Figs 17-33; Pl. 2

- 1759 clavicularae echinorum Abildgaard, p. 15, pl. 3, fig. 4a (Pb).
- 1923 *Tylocidaridaris vexillifera* Schlüt. ? — Jessen & Ødum, pp. 22, 23, pl. 2, fig. 3.
- 1926 *Tylocidaridaris vexillifera* Schlüter forma gamma Ødum, p. 160, pl. 1, fig. 3a-d.
- 1928 *Tylocidaridaris vexillifera* Schlüt. var. *Abildgaardii* Ravn, p. 35, pl. 4, figs 27, 29 (non 26, 28, 30, ?31, 32-35).
- 1938 *Tylocidaridaris Ødumi* Brännich Nielsen, p. 126.
- 1944 *Tylocidaridaris oedumi* — Andersen, fig. 231.
- 1953 *Tylocidaridaris clavigera Ødumi* (Brännich Nielsen) — Wind, tab. 2.
- 1954 *Tylocidaridaris clavigera Ødumi* (Brännich Nielsen), 1937 — Wind, p. 481, pl. 13, figs 1-10, 59-63.
- 1959 *Tylocidaridaris ødumi* Brännich Nielsen — Brotzen, p. 38, pl. 38, figs 15-19, 24-30; text-fig. 12a-e.
- 1960 *Tylocidaridaris ødumi* — Rosenkrantz & Wienberg Rasmussen, p. 6, figs 1, 7.
- 1966 *Tylocidaridaris ødumi* — Wienberg Rasmussen, p. 61 (fig).

Type — Brännich Nielsen (1938) failed to designate a type specimen. Brotzen (1959, p. 41) proposed to designate 'holotype' the spine illustrated by Ødum (1926, pl. 1, fig. 3b). This specimen is herein selected as lectotype.

Locus typicus — Barmer 1 (Jylland, Denmark).

Stratum typicum — early Early Danian, oedumi Zone.

Diagnosis (amended) — Test: small to medium-sized (maximum height *c* 16 mm); only a single complete test has so far been collected (P. Gravesen Coll., no. 3350, from Stevns Klint, north of Kulsti Rende, see Pl. 2, Figs 1-3), height 12.5 mm, ambital diameter 25.1 mm. Adapically there are 8-13 ambulacral plates per interambulacral plate, the number of tubercles in a scrobicular ring amounting to 12-17. Adradial and admedian parts of interambulacral much reduced. Adradial parts of interambulacral either without or with just a single row of irregularly spaced miliary tubercles; admedian parts of the same interambulacral with 1-3 such rows.

Spines: typically long, rather narrowly clavate, gradually tapering from narrow neck to wider head. Fully-grown spines attaining maximum length of 28-30 mm, referable to morphotype 3 as defined above (Fig. 6), most probably originating from ambital and adapical test regions. Some spines belong to morphotypes 2 and 4. Distal parts of spines with small, rounded to slightly acute mamillae, which become gradually smaller towards the base and are absent in proximalmost part above the collar.

An analysis of 138 complete spines from the second bryozoan limestone bed between flint bands F2 and F3 of the Korsnæb section resulted in the following picture: morphotype 2 - 3.6 %, morphotype 3 - 76.8 %, and morphotype 4 - 19.6 %. (compare Fig. 6 and Table 3).

Comparisons — *Tylocidaris (T.) oedumi* is distinguished from the Late Maastrichtian *T. (Oedematocidaris) baltica* (Schlüter, 1892) on the following test features (compare Salah & Schmid, 1982; Smith & Wright, 1989): in the former, adapically there are 8-13 ambulacral plates per interambulacral and 12-17 scrobicular tubercles per ring as compared to 13-18 (-20) and 18-20, respectively, in the latter species. Adradially, adapical interambulacrals in *T. oedumi* show either a single row of irregularly spaced miliary tubercles or none at all, while in *T. baltica* there are 1-2; in the former species there are 1-2 rows of miliary tubercles in admedian parts of interambulacrals, whereas in the latter there are 2-4 (Table 4). Aboral primary spines of *T. baltica* are typically glandiform and stout, while those of *T. oedumi* are much more narrowly clavate. Adoral primary spines of the former species are not so easily distinguished from those of the latter.

T. oedumi may be distinguished from *T. abildgaardii* (late Early Danian) as follows: adapically the former species has more (8-13 vs 4-11) ambulacrals per interambulacral plate; 12-17 scrobicular tubercles in a ring vs 10-15 in the latter species. Adradial parts of interambulacrals in *T. oedumi* are reduced to such an extent that they show but a single row of miliary tubercles or none at all; in *T. abildgaardii* a similar reduction is seen. In *T. oedumi* the admedian parts of interambulacrals bear 1-3 rows of miliary tubercles, while in *T. abildgaardii* this number varies between 0-2. The spines of these species are clearly different: typical *oedumi* spines are clavate and belong to morphotype 3; those of *abildgaardii* generally are referable to types 4 and 5, and only rarely to type 3 (or 2). Type 3 spines of *abildgaardii* are herein referred to as 'oedumoid spines'; they are difficult to distinguish from true *oedumi* spines.

Geographical and stratigraphical distribution — *T. oedumi* is widely distributed in the earliest Danian bryozoan limestone facies of Skåne (SW Sweden) and Denmark. Records from the Late Maastrichtian of Denmark and northern Germany (Voigt, 1954; Wind 1954) probably refer to *T. (O.) baltica*.

Discussion — Brünnich Nielsen (1909, p. 143) was the first to realise that *T. vexillifera* as described by Schlüter (1892) in fact comprised various types of

Early and Late Danian age. Later, Ødum (1926) distinguished three formae: f. alpha (= *T. abildgaardii* Ravn, 1928), f. beta (= *T. vexillifera* s. str.) and f. gamma (= *T. oedumi* Brünnich Nielsen, 1938). Ravn (1928, p. 35, pl. 4) erected a new var. *Abildgaardii* to encompass Ødum's f. gamma and f. alpha. In 1938 (paper misdated 1937) Brünnich Nielsen considered Ødum's f. gamma to represent a separate species for which he suggested the name *T. Ødumi*, currently correctly spelt *oedumi*. Wind (1953, 1954) referred *T. oedumi* to *T. clavifera* as a subspecies, but failed to justify this action. Brotzen (1959) presented the most detailed description of spines of *T. oedumi* so far.

Species	Numer of sec. tubercles in adradial parts	Number of sec. tubercles in admedian parts
<i>T. abildgaardii</i> (loose finds)	mostly 0 (0-1)	0-2
<i>T. abildgaardii</i> (in situ)	mostly 0 (0-1)	0-2
"overlap forms" (in situ)	0-1	0-2
<i>T. oedumi</i> (loose finds)	0-1	1-3
<i>T. oedumi</i> (in situ)	0-1	1-2
<i>T. baltica</i>	mostly 2	2-4

Table 4. Number of miliary tubercles in adradial and admedian zones of interambulacral plates in *T. abildgaardii*, 'overlap' forms, *T. oedumi* and *T. baltica*, all from Stevns Klint (Korsnæb section and other localities).

All previous work has concentrated on the range of variation displayed by spines of this species. Here, for the first time also test characters are included in the diagnosis.

Tylocidaris (Tylocidaris) abildgaardii Ravn, 1928

Pl. 3, Figs 1-14; Pl. 4, Figs 1-4

- 1759 clavicularae echinorum Abildgaard, p. 15, pl. 3, fig. 4f.
 1926 *Tylocidaris vexillifera* Schlüter forma alpha Ødum, p. 160, pl. 1, fig. 1a-h.
 1928 *Tylocidaris vexillifera* Schlüt. var. *Abildgaardii* Ravn, p. 35, pl. 4, figs 26, 28, 30, ?31, 32-35 (non 27, 29).
 1938 *Tylocidaris Abildgaardii* Ravn — Brünnich Nielsen, p. 126.
 1944 *Tylocidaris abildgaardii* — Andersen, p. 299, fig. 231.
 1953 *Tylocidaris pomifer* (Boll) — Wind, table 2.

- 1954 *Tylocidaris pomifer pomifer* (Boll, 1846) — Wind, p. 483, pl. 13, figs 11-24.
 1959 *Tylocidaris abildgaardi* Ravn — Brotzen, p. 41, figs 11, 14a-f; pl. 1, figs 1-14; pl. 2, fig. 1.

Type — Ravn (1928) failed to designate a type specimen. Brotzen's (1959) proposal to designate the spine illustrated by Ødum (1926, pl. 1, fig. 1a) 'holotype' is invalid. Ravn (1928, pl. 4, fig. 35) figured a near-complete test with four associated spines, clearly demonstrating their conspecificity. In view of this, this specimen is here designated lectotype (Geological Museum Copenhagen collections, no. MMH 2543).

Locus typicus — Stevns Klint, Denmark.

Stratum typicum — late Early Danian, abildgaardi Zone.

Diagnosis — Test: small, largest height 8.6 mm. A specimen with a height of 7.3 mm has an ambital diameter of just 14.9 mm. Adapically there are 4-11 ambulacral plates per interambulacral, and number of tubercles per scrobicular ring amounts to 10-15. Adradial parts of interambulacrals are reduced to such an extent that well-developed miliary tubercles rarely occur; when present, they are arranged in a single irregular row. Admedian parts of interambulacrals are extremely reduced and very narrow, bearing between 0 and 2 rows of miliary tubercles.

Spines: almost 65 % of spines assigned to this species have a very distinctive appearance with an extremely narrow neck and an almost completely globose to slightly elongate head. The range of variation displayed by a typical population from the basal abildgaardi Zone at Korsnæb (section between co-ordinates KO +200 and KO +222.40, and KO +185/F7½ and 1 m below this, n = 125) is as follows: morphotype 5 - 63.2 %, type 4 - 22.4 %, type 3 - 12.0 %, and type 2 - 2.4 %. Whereas type 5 spines are so typical that they are easily identified, type 2 and 3 spines cannot be easily distinguished from typical spines of *T. oedumi*. *In situ* finds within the abildgaardi Zone and co-occurrence of such spines with 'normal' spines of *T. abildgaardi* (see Pl. 3) clearly show that these fall within the range of variation of the present species. Typical spines are very short, attaining a maximum length of *c* 14-15 mm; 'oedumoid spines' may be considerably longer (up to *c* 20 mm).

Comparisons — Adapically, there are 4-11 ambulacral plates per interambulacral and 10-15 tubercles per scrobicular ring. Corresponding figures for *T. oedumi* are 8-13 and 12-17, respectively. Adradial parts of interambulacral plates are extremely

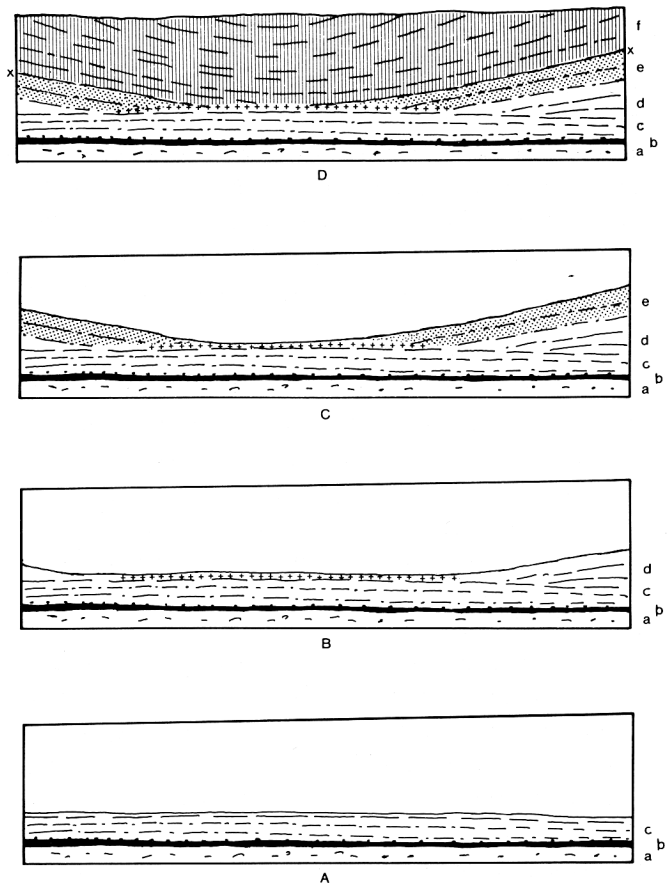


Fig. 7. Reconstruction of development of a trough structure with hardground formation. Abbreviations are as follows: f - Early Danian bryozoan limestones (abildgaardi Zone); x - upper abildgaardi/lower 'overlap zone' boundary; e - 'overlap zone'; d - bryozoan limestones of upper oedumi Zone, forming typical bioherms at this level; c - bryozoan limestones of lower oedumi Zone, in horizontal position ('pre-biohermal phase'); b - K/T boundary strata, with indurated Late Maastrichtian white chalk, Fish Clay and earliest Danian Cerithium Limestone; a - Late Maastrichtian white chalk.

The sequence of events is as follows:

A - the first Early Danian bryozoan limestones (lower oedumi Zone) are in horizontal position here and at most other localities along Stevns Klint; representing the 'pre-biohermal phase' prior to the onset of true build-up of mounds; B - overlying are lower oedumi Zone bioherms, leaving current-swept troughs between them; non-deposition in troughs resulting in hardground formation; C - bioherm growth continues; transition of oedumi type forms to 'overlap' forms. Note that the 'overlap zone' is very thin in or even absent from the trough; D - eventually a thick series of bryozoan limestones (abildgaardi Zone) fill in the troughs.

reduced with 0-1 row of miliary tubercles. Admedian parts are similarly reduced with 0 to 2 rows of miliary tubercles (1-3 in *T. oedumi*) (see Table 4).
Geographical and stratigraphical distribution — This spe-

cies is extremely common in bryozoan limestone facies of Skåne (SW Sweden) and Denmark.

Discussion — Brotzen (1959) presented the hitherto most detailed description of the spines of the present species. He was of the opinion that *T. abildgaardi* co-occurred with *T. oedumi* in his zone of *T. ödumi*. As demonstrated herein, these species do not co-occur and occupy different stratigraphical levels. It was probably the 'oedumoid spines' that misled Brotzen in this respect.

'*Overlap forms*': Although both spines and test material are available from the 'overlap zone' at the Korsnæb section, I have refrained from erecting a new species for this material. A morphotype analysis of such spines (n = 105) indicates the intermediate position they occupy between typical *T. oedumi* and *T. abildgaardi*: morphotype 3 - 50.5 %, type 4 - 41.9 %, type 5 - 4.8 %, and type 2 - 2.9 % (compare Table 3). Test remains collected so far comprise half a test and four test segments, which allow the following characterisation: Test small (maximum height *c* 9 mm); adapically with 6-10 ambulacral plates per interambulacral. Both adradial and admedian parts of interambulacrals are much reduced; adradial parts with 0-1 row of miliary tubercles, admedian parts with 0-2 rows. Scrobicular ring with 11-13 tubercles.

Test characters thus appear to be intermediate between *T. oedumi* and *T. abildgaardi*, but the limited material does not allow additional observations.

Tylocidaris (Tylocidaris) aff. rosenkrantzi
 Brotzen, 1959
 Pl. 4, Figs 5-11

Discussion — A number of peculiar spines found at Karlstrup most probably fall within the range of variation of *T. (T.) rosenkrantzi* Brotzen, 1959. They must obviously have belonged to a fairly large-sized species; they were almost exclusively found loose on scree at the foot of the northern quarry face. Fully-grown specimens are between 26 and 28 mm in length; they generally are clavate with a more or less well-developed 'crown' with papillae often arranged in rows, resembling small ridges. All spines bear prominent tubercles, which extend to rather low on the neck. The specimen illustrated in Pl. 4, Fig. 6 is reminiscent of the type of *T. rosenkrantzi* (Brotzen, 1959, pl. 2, fig. 22). Plate 4, Fig. 11 illustrates an exceptional specimen collected in 1922 by the late Alfred Rosenkrantz and Christian Poulsen at 'Solröd. Ny Brud v. Kagstrup' (= Solröd, new quarry at

Kagstrup, the older name for Karlstrup). These spines clearly originate from a single individual; they bear strongly protruding ridges that form an impressive 'crown'. The smallest spine carries only ridges; this specimen corresponds nicely with many of the smaller spines of *T. rosenkrantzi* illustrated by Brotzen (1959, pl. 2). These Karlstrup specimens are here held to belong to a taxon which is either conspecific with or closely related to *T. rosenkrantzi*, a species in which the spines show a wide range of variation (Brotzen, 1959, p. 45).

The spines under discussion bear a certain resemblance to those of *T. vexilifera* s. str., but the angle between the neck and the basal part of the head is *c* 45° in *T. aff. rosenkrantzi*, while in *T. vexilifera* this transition is more abrupt and often amounts to 80-90°. In the latter species the head is wide and in some spines its width may equal or surpass 50 % of total spine length. From *T. bruennichi* (late Middle Danian), *T. aff. rosenkrantzi* is primarily distinguished by the size of the massive spines with broad heads.

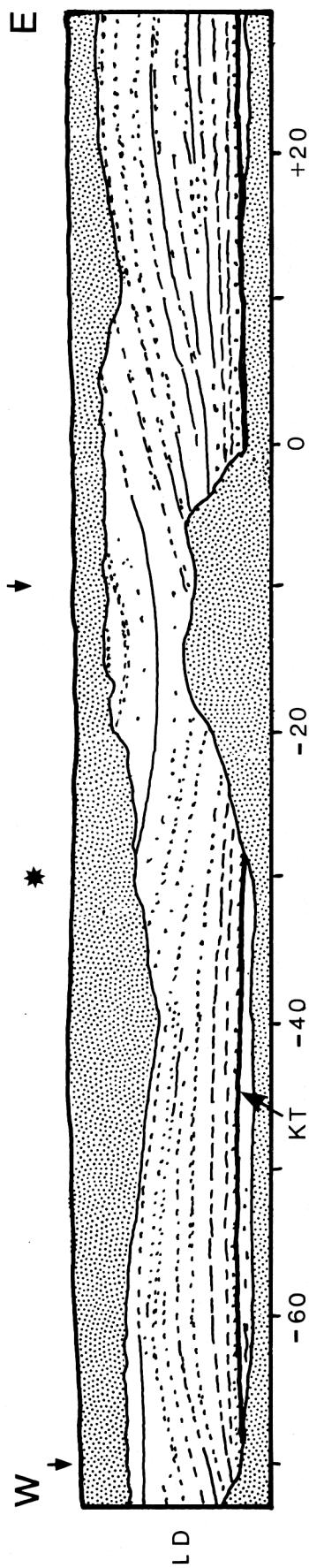
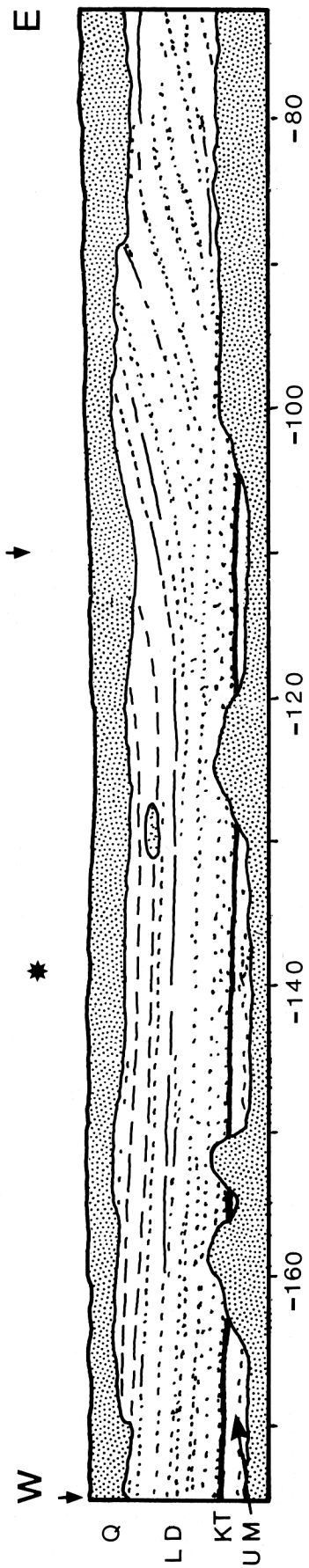
Geographical and stratigraphical distribution — Typical *T. rosenkrantzi* are of early Middle Danian age and occur at Limhamn (Sweden).

Tylocidaris (Tylocidaris) ravni Brotzen, 1959

Discussion — To this species I refer spines that originate from the upper abildgaardi Zone of Stevns Klint and from the early Middle Danian of Limhamn, and resemble those of *T. abildgaardi*, but have a diminutive or small crown. The stratigraphical range of *T. ravni* (if accepted as a separate species) probably extends from the latest Early Danian (upper abildgaardi Zone) to the early Middle Danian (rosenkrantzi Zone). In my opinion, this species forms an evolutionary link between *T. abildgaardi* and *T. bruennichi*. For a detailed discussion the reader is referred to Brotzen (1959).

Tylocidaris (Tylocidaris) windi Brotzen,
 1959

Discussion — I consider this to be an ill-defined species. Spines illustrated by Brotzen (1959, pl. 1, figs 20-23) do not show enough distinctive features upon which a separate species could be based. The type specimen (pl. 1, fig. 23) is indistinguishable from the minutely 'crowned' forms occurring in the upper abildgaardi Zone at Stevns Klint, and are perhaps better referred to *T. ravni*. Brotzen's (1959, p. 47) indication that *T. windi* occurred 'in all beds



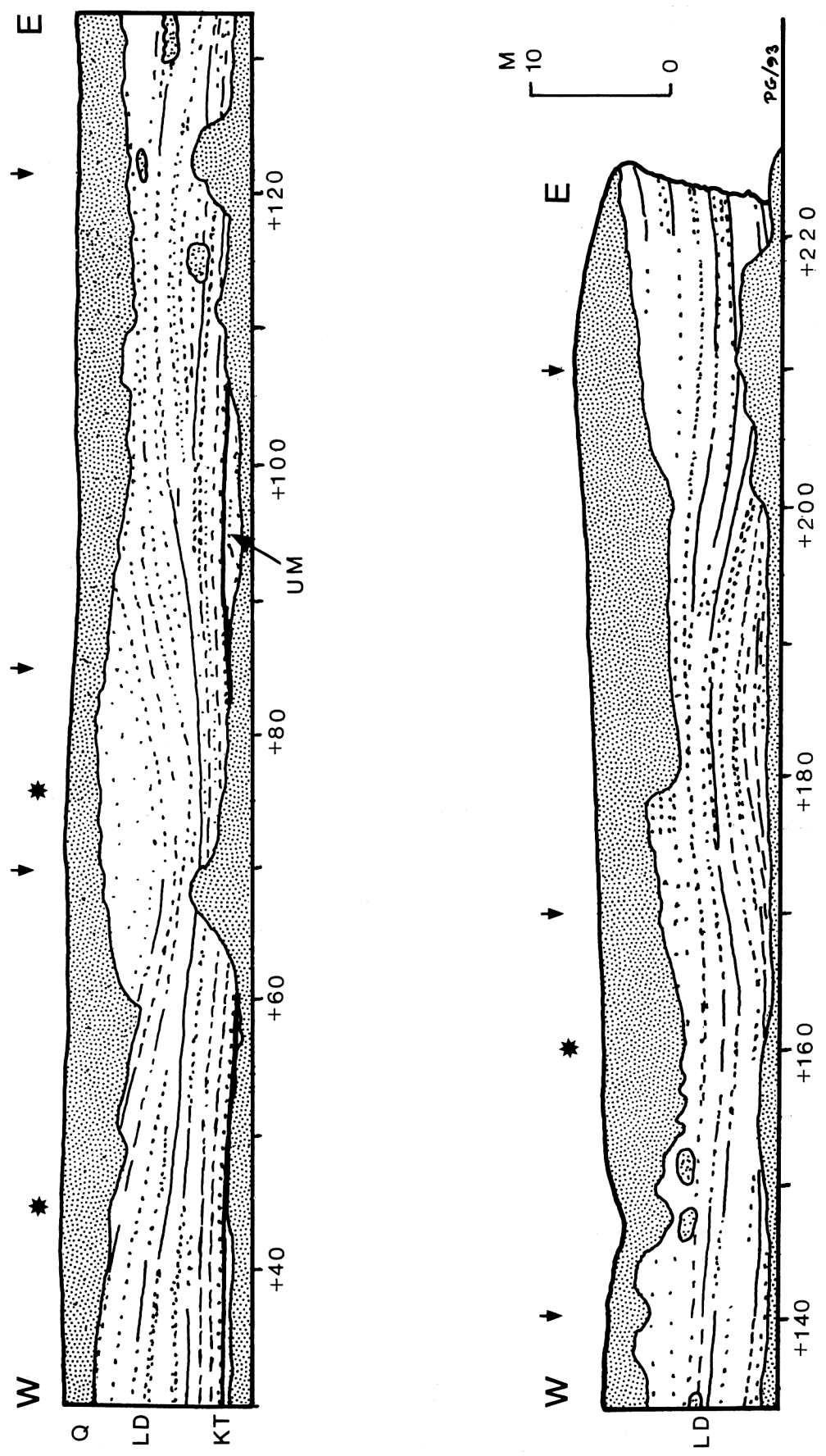


Fig. 8a, b. The Korsnæb section, Stevns Klint, showing latest Maastrichtian white chalk (UM), K/T boundary strata (KT) and Early Danian bryozoan limestones (LD). Some of the more prominent flint bands are indicated. Q - Quaternary till. Numbers on horizontal axis correspond to part of co-ordinate system. Arrows indicate boundaries of the sections described in the text (first measured 1987, redrawn 1993). Asterisks mark positions of detailed sections shown here in Figs 11-15.

of the Lower Danian at Limhamn' cannot be corroborated by the present study.

CONCLUSIONS

In the Late Maastrichtian white chalk facies at Korsnæb spines of *T. (Oedematocidaris) baltica* are fairly common. The earliest Danian Cerithium Limestone has so far yielded no tylocidarids. Although details of some parts of the Korsnæb section are in need of clarification, the picture of the distribution pattern of species of *Tylocidaris* within the Early Danian bryozoan limestones of this section is now fairly clear:

- throughout the entire section the lowermost beds of the Bryozoan Limestone exclusively yield *T. oedumi*, mostly spines, but locally also fragmentary tests.

- the highest levels to which *T. oedumi* can be traced with certainty are:

- | | |
|-------------------|--|
| section KO - 150: | base of flint KO -150/F3 |
| section KO - 30: | top of flint KO -30/F3 |
| section KO + 25: | top of flint KO +25/F4 |
| section KO +100: | limestone directly overlying top of flint KO +100/F4 |
| section KO +130: | limestone directly overlying top of flint KO +130/F4 |
| section KO +150: | limestone directly overlying top of flint KO +150/F2 |
| section KO +185: | limestone directly overlying top of flint KO +185/F2 |

- overlying the oedumi Zone is the 'overlap zone', the base of which is generally difficult to define because of a combination of an apparent rarity of *Tylocidaris* spines at this level, unfavourable conditions for collecting (salt crusts etc.) and last but not least, the gradual character of the change from *T. oedumi* to 'overlap forms'. The lowermost levels at which the 'overlap forms' has so far been documented are:

- | | |
|------------------|--|
| section KO - 90: | base of flint KO -90/F5 ^{1/2} |
| section KO - 30: | top of flint KO -30/F3 |
| section KO + 25: | top of flint KO +25/F5 |
| section KO +150: | base of flint KO +150/F3 |
| section KO +185: | base of flint KO +185/F5 |

The topmost levels of this zone documented so far being:

- | | |
|------------------|-------------------------|
| section KO - 90: | base of flint KO -90/F6 |
| section KO - 30: | base of flint KO -30/F4 |
| section KO + 25: | base of flint KO +25/F6 |

section KO +150: between flints KO +150/F3 and /F4

section KO +185: base of flint KO +185/F6

- the base of the abildgaardi Zone generally is easily distinguished by a truly mass occurrence of spines (about two thirds belonging to the easily recognised morphotype 5) and of fairly common test fragments (mostly segments) of this species. It has so far been documented at the following levels (** indicate places where the top of the 'overlap zone' and the base of the abildgaardi Zone are situated at the base/top of the same flint band):

- | | |
|-------------------|---------------------------|
| section KO - 150: | base of flint KO -150/F5 |
| section KO - 90: | top of flint KO -90/F7 |
| section KO - 30: | top of flint KO -30/F4 |
| section KO + 25: | top of flint KO +25/F6** |
| section KO +185: | top of flint KO +185/F6** |
| section KO +200: | top of flint KO +220/F1 |

- the abildgaardi Zone extends over the entire upper part of the section exposed, up to the erosive contact between the Early Danian Bryozoan Limestone and the overlying Pleistocene glacial till.

From this emerges the following picture:

1 - the oedumi Zone is confined to the lowermost beds of the Bryozoan Limestone, the beds at first being horizontal, and showing a slight tendency towards biohermal formation in the topmost parts.
2 - the 'overlap zone' occurs only in the cores and on the flanks of the biohermal mounds between KO -80 and KO -30, KO +5 and KO +50, thinning out here in an easterly direction but remaining connected to the next maximum in the double biohermal structure occurring between KO +90 and KO +200. This 'overlap zone' is absent from the large trough between KO -25 and KO +5 and from the giant trough structure in the western part of the Korsnæb section (west of KO -85). This latter trough is characterised by an impressive multiple sequence of intensely bioturbated horizons, hardgrounds and incipient hardgrounds, all with numerous *Thalassinoides* burrows.

PHYLOGENY

Data available to date allow the following reconstruction of tylocidarid evolution in the Danish and Swedish Danian:

In the earliest Early Danian (Cerithium Limestone) rare representatives of *T. aff. oedumi* occur (so far only at Karlstrup). In the overlying oedumi Zone

the index species is the sole representative of the genus. Apparently gradually this species is subject to change leading to 'overlap forms' demonstrating a morphological variation in their primary spines ranging from true *oedumi* type spines via intermediate types to spines characteristic of *T. abildgaardi* (morphotype 5 spines). In places where the 'overlap zone' is thin, one might at first be tempted to interpret the development of 'overlap forms' as an example of the mechanism of punctuated equilibrium (*sensu* Eldredge & Gould, 1972), but the fact that the 'overlap zone' is actually thick in the cores and on the flanks of well-developed bryozoan mounds (in places reaching thicknesses identical to that of the *oedumi* Zone, see Fig. 9a, b), is in my view best explained as being the result of straightforward evolutionary change over a reasonably long time span. The change from *T. oedumi* to the 'overlap forms' is apparently gradual and thus the actual boundary between the two zones may often be difficult to draw. The boundary between the 'overlap zone' and the *abildgaardi* Zone, on the other hand, is mostly easily defined by the sudden mass occurrence of typical *abildgaardi* spines (morphotype 5).

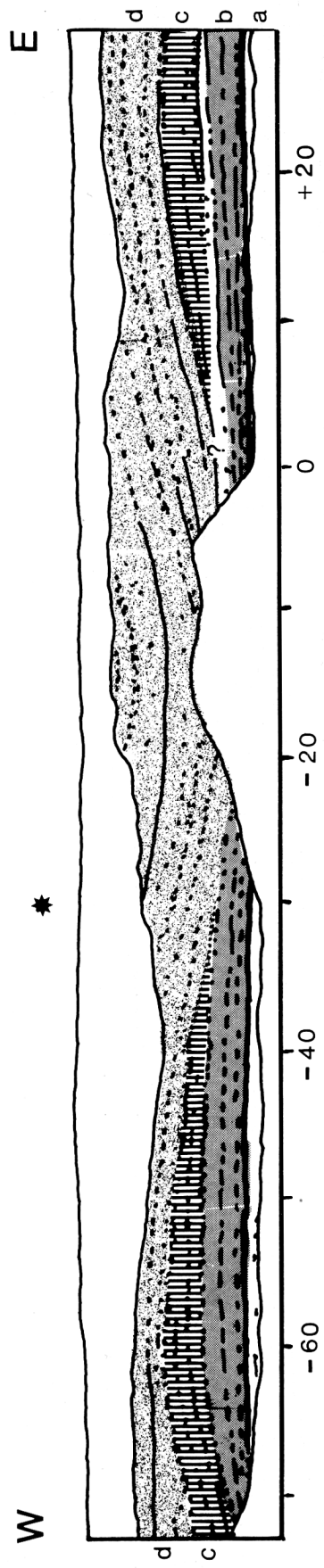
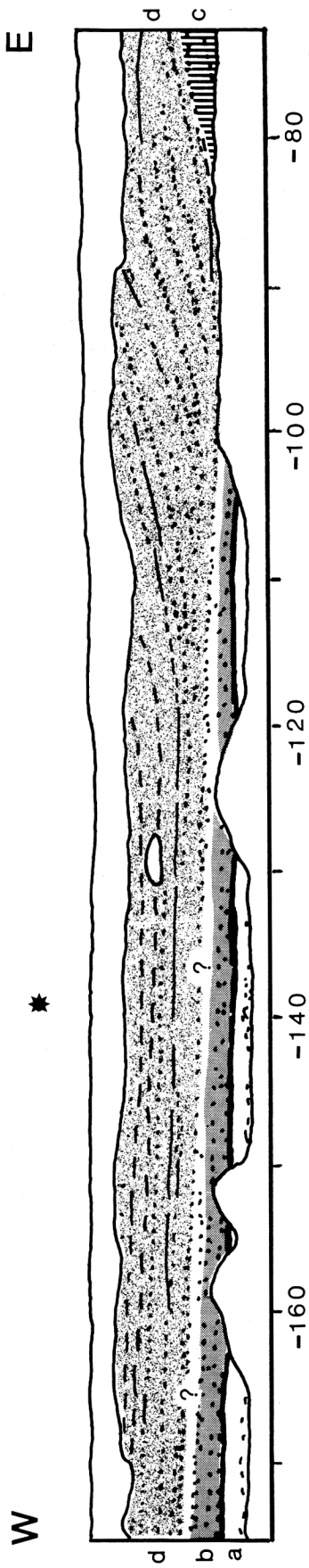
At present, it is difficult to determine whether the picture of a sudden change at the boundary 'overlap zone'/*abildgaardi* Zone that emerges, is real, *i.e.* a result of a truly heightened evolutionary turnover, or that the growth of bryozoan mounds slowed down so as to give the false impression of such a turnover. Alternatively, the change from *T. oedumi* via 'overlap forms' to *T. abildgaardi* might be explained by the entry of an immigrant tylocidarid species in the Dano-Swedish basin which interbred with *T. oedumi* to form a new population.

Following the firm establishment of *T. abildgaardi* a long time elapsed during which there were no changes. Not until the boundary between the Early and Middle Danian was reached did *T. abildgaardi* exhibit evolutionary changes; it gradually started developing diminutive 'crowns' and by doing so changed into *T. ravni sensu* Brotzen. A continuation of this process led to *T. bruennichi* (late Middle Danian). What exactly happened at the Middle/Late Danian transition remains unresolved. For Limhamn, Brotzen (1959) postulated a gradual change from *T. bruennichi* into *T. vexilifera*. In the NE corner of Fakse quarry (Sjælland) these species co-occur (personal observations), but it remains to be determined whether this is a gradual evolutionary change or an abrupt replacement. As an alternative to a

bruennichi-vexilifera lineage there exists a possible transition of *T. rosenkrantzi* (early Middle Danian) into *T. vexilifera*. I follow Brotzen (1959) in assuming *T. rosenkrantzi* to have evolved from *T. oedumi* during the late Early Danian (*abildgaardi* Zone times). This probably took place in the near-coastal areas of the Dano-Swedish Danian basin which, unfortunately, are not preserved (see palaeogeographical maps in Thomsen, 1989), or possibly even further afield, in an adjacent basin. This evolutionary link cannot be documented in the late Early Danian of the central parts of the Dano-Swedish basin as now preserved. As *T. rosenkrantzi* first appears in the early Middle Danian, its presence is typically confined the easternmost parts of the Dano-Swedish basin (SW Skåne, eastern Sjælland).

In the Early Danian of the Dano-Swedish area, Brotzen (1959) distinguished a 'zone of *Tylocidaris oedumi*' yielding both *T. windi* and *T. abildgaardi*. This calls for comment: as mentioned above, I have been unable to find any spines that could be referred to *T. windi* in the *oedumi* Zone either at Karlstrup or at Korsnæb and have serious doubts about the status of this 'species'. Nor have I ever found *T. abildgaardi* in the *oedumi* Zone, which may be explained as follows: when collecting at Limhamn, Brotzen mistook 'oedumoid' spines belonging to *T. abildgaardi* (see above) for genuine *T. oedumi* spines in the *abildgaardi* Zone there. Consequently, he assumed both species to co-occur in this zone. The present study shows this conclusion to be incorrect; these species define separate zones and only in the 'overlap zone' of the Korsnæb section does an intermediate population occur.

As mentioned above, the occurrence of a *rosenkrantzi* Zone has so far not been recorded from Denmark, where only the *bruennichi* Zone represents the Middle Danian. The *rosenkrantzi* Zone probably is a zone with but local distribution being apparently restricted to the Limhamn area; elsewhere in Skåne, *e.g.* at Skanör and Trelleborg this zone is missing, which may be explained either by non-deposition or penecontemporaneous erosion (Brotzen, 1959, p. 24). In this light, spines herein referred to as *T. aff. rosenkrantzi* and spines possibly belonging to *T. ravni* collected at Karlstrup are of prime importance in providing evidence not only for the occurrence of Middle Danian strata at Karlstrup (highest levels at northern quarry face), but also for the presence of the early Middle Danian *rosenkrantzi* Zone in Denmark, not previously recorded.



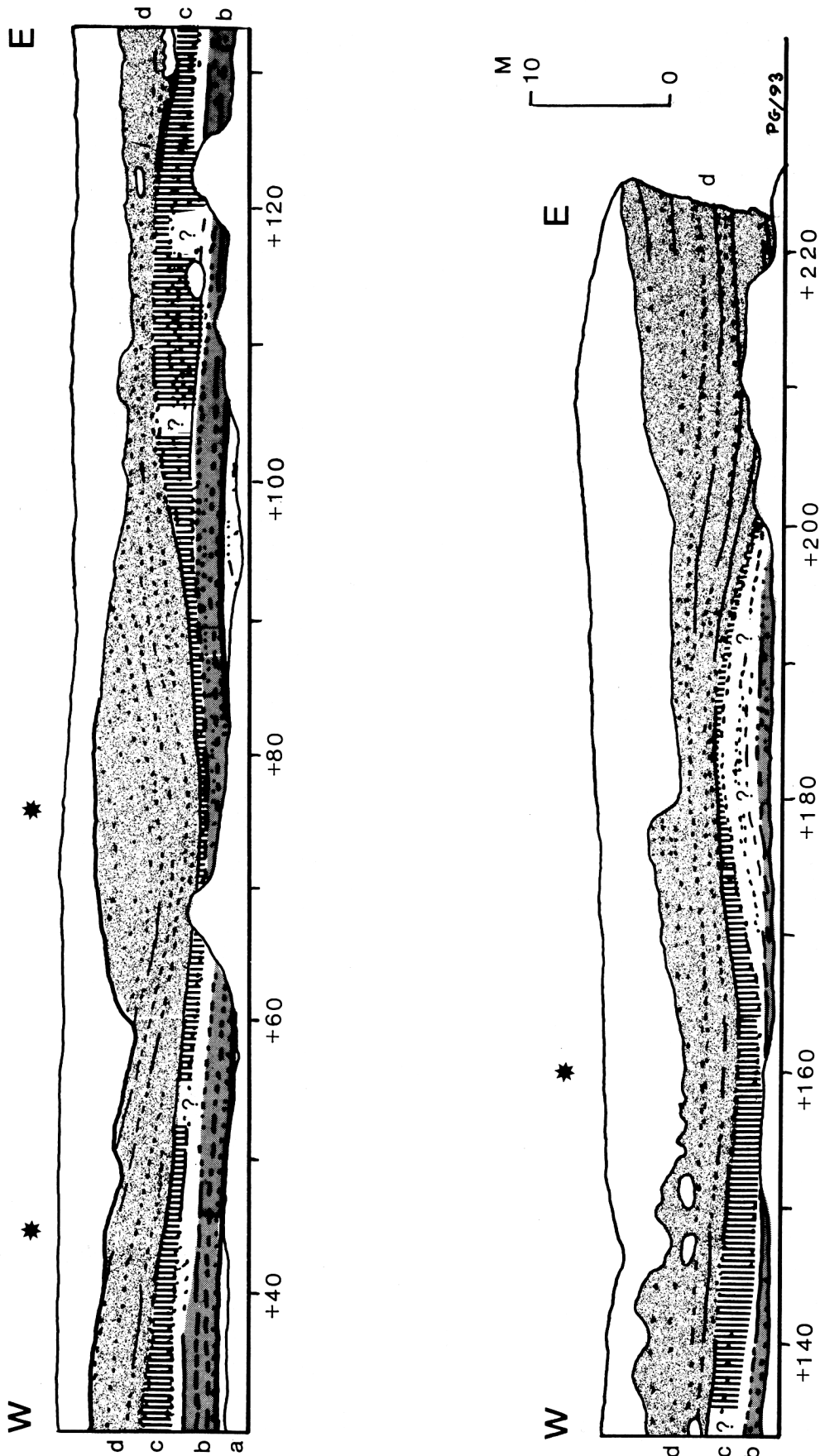
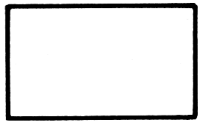
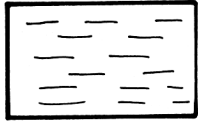


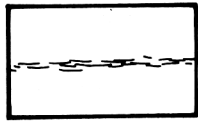
Fig. 9a, b. Tylocidarid distribution in the Late Maastrichtian and Early Danian of the Korsnæb section: a - *Tylocidaris baltica* (Late Maastrichtian); b - *T. oedumi* (early Early Danian); c - 'overlap' forms; d - *T. abildgaardii* (late Early Danian). White areas indicate parts of section where conditions are unknown with certainty (either because of heavy salt crusts or overhanging rocks preventing bed-by-bed collecting). Asterisks mark positions of detailed sections shown here in Figs 11-15.



Late Maastrichtian
white chalk or
Early Danian
bryozoan limestone



Lamination



Marly horizon



Hardground



Hardground with
Thalassinoides
burrows



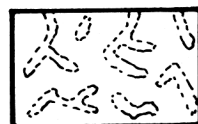
Hardground with
slickensides



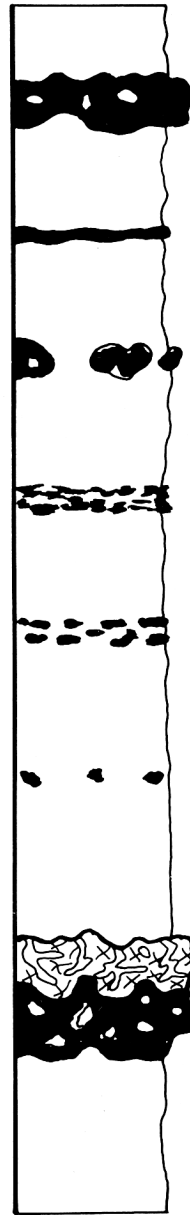
Burrows filled with
greyish marl



Thalassinoides
burrows



Thalassinoides
burrows
(indistinct)



Massive flint

Tabular flint

Flint nodules

Irregular
flint band

'Double flint'

















Small flint
nodules

Hardground (above)
and massive flint
(below)

Fig. 10. Key to Figs 11-15.

Selected macrofossils:

Echinoids

-  *Tylocidarid abildgaardi*
(or 'overlap forms')
 -  *Tylocidarid oedumi*
(or 'overlap forms')
 -  *Tylocidarid baltica*
 -  *Stereocidarid* primary spine
(*S. rosenkrantzi* or
S. danica)
 -  *Stereocidarid* test plate(s)
(*S. rosenkrantzi* or
S. danica)
 -  *Phymosoma* aff. *granulosum*
spine(s)
 -  *Phymosoma* aff. *granulosum*
test fragment
 -  *Phymosoma* aff. *granulosum*
complete test
 -  *Echinocorys sulcata*
(uncrushed)
 -  *Echinocorys sulcata*
(crushed)
 -  *Brissopneustes danicus*
- Other biota
-  *Spondylus danicus*
 -  *Pycnodonte*
 -  *Glomerula* aff.
gordialis
 -  Octocorals
 -  '*Terebratula fallax*
var. *tenuis*'

To sum up, the tylocidarid lineage of the Dano-Swedish Danian is by no means straightforward, and requires two separate evolutionary lineages. I propose the following scheme:

1 - a main evolutionary lineage including representatives of the *T.* aff. *oedumi* (Cerithium Limestone), *T. oedumi*, 'overlap forms', *T. abildgaardi*, *T. ravni*, and *T. bruennichi*. This line may end with the last-named species in the latest Middle Danian;
 2 - a local lineage of *T. oedumi* and *T. rosenkrantzi*, situated outside the preserved parts of the Dano-Swedish Danian sea and leading to *T. rosenkrantzi* entering the easternmost parts of this sea in early Middle Danian times and evolving during the late Middle Danian into *T. vexilifera*. This transition must also have taken place outside the Dano-Swedish Danian as now preserved. At the Middle-Late Danian transition, *T. vexilifera* may then have entered the central parts of the Danian sea to compete with *T. bruennichi* of the main lineage causing that species to become extinct, leaving *T. vexilifera* as the sole representative of the genus for the remainder of the Danian Stage.

PATTERNS OF BRYOZOAN MOUND GROWTH

If the above pattern of tylocidarid distribution in the Korsnæb section is accepted to represent an evolutionary lineage (as here advocated), this pattern has a significant bearing on the interpretation of the formation of biohermal mounds (Fig. 7). At the time of formation a system of alternating mounds and troughs must have existed, and have persisted for a considerable period of time. This assumption is based on the way in which the 'overlap zone' occurs in the bryozoan mounds between KO -80 and KO -30, in that occurring between KO +5 to KO +50 and in the 'double biohermal structure' between KO +90 and KO +200.

Mound growth is assumed to have been so slow as to allow ample time for the change from *T. oedumi* via 'overlap' forms to *T. abildgaardi* to take place, either through evolution or through the entry of a 'foreign' tylocidarid species, that hybridised with *T. oedumi* to form a new species, *T. abildgaardi*. During the same time span there was ample opportunity for hardgrounds to develop in the troughs between the mounds, e.g. in the trough occurring between KO -25 and KO +10 (+15) and in the sequence of hardgrounds and incipient hardgrounds in the large trough structure west of KO -85.

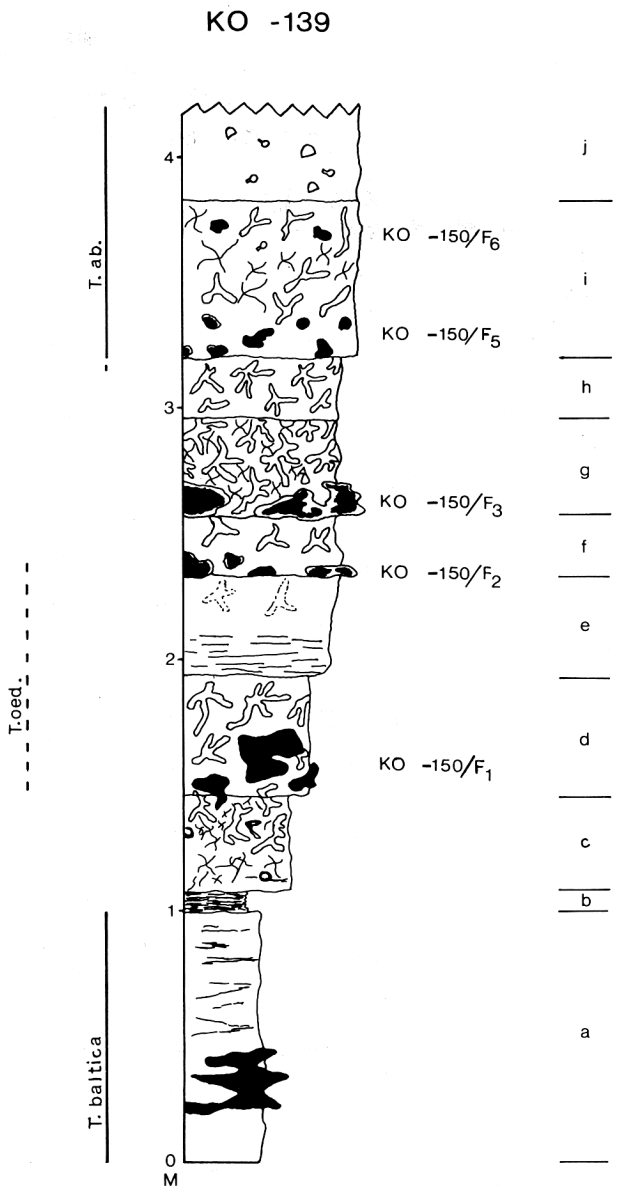


Fig. 11. The Korsnæb section, detailed section at KO -139 (for position see Fig. 8a), showing very large trough structure, the filling up of which apparently took a long time (see text for details). A sequence of multiple hardgrounds or incipient hardgrounds and thorough bioturbation is indicated by numerous *Thalassinoides* burrows. Three tylocidarid zones are represented (measured 1985).

This implies that the considerable time span needed for mound formation equals the time during which the troughs persisted with little or no sedimentation. Hardground development is evidence of such a period of non-deposition. That such hiatuses comprise long periods of time was already pointed out by Bromley (1979a, pp. 28, 29).

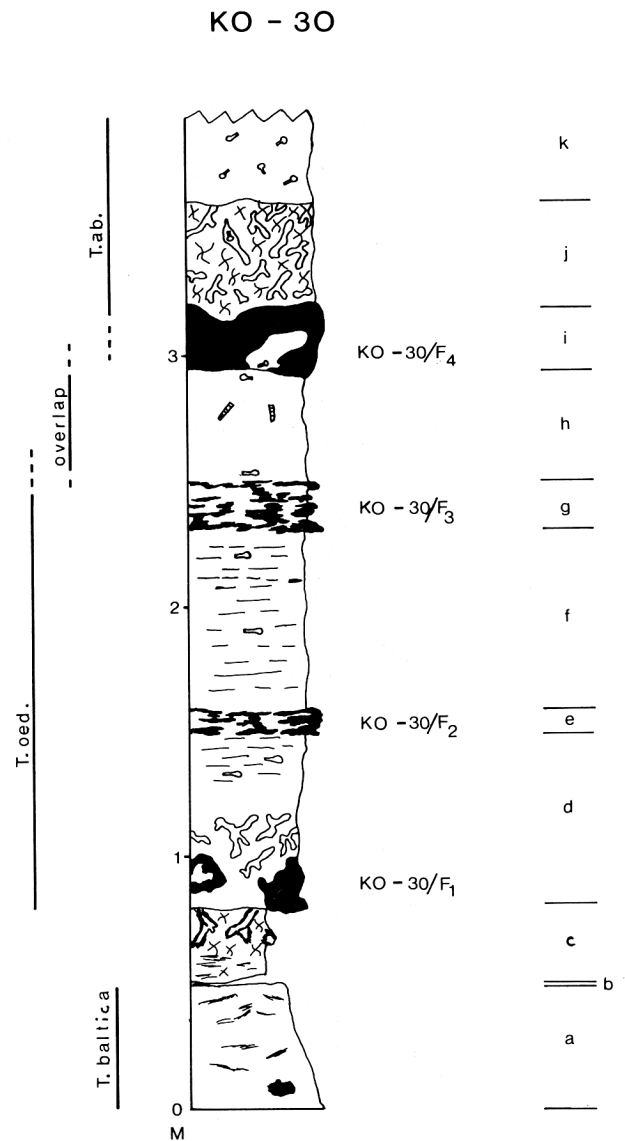


Fig. 12. The Korsnæb section, detailed section at KO -30, eastern flank of bryozoan mound with hardground formation at the 'overlap'/abildgaard Zone boundary, the hardground becoming more prominent in the trough further east and continuing to section KO +15. Note the very thin 'overlap zone' here. Four tylocidarid zones are represented (measured 1985).

In the trough between KO -25 and KO +10 (+15) the bryozoan limestones with *T. oedumi* are capped by a hardground, on top of which rest bryozoan limestones yielding *T. abildgaardii*. Thus, a typical non-deposition sequence in which the hiatus (marked by hardground) equals the sedimentary sequence with a well-developed 'overlap zone' in

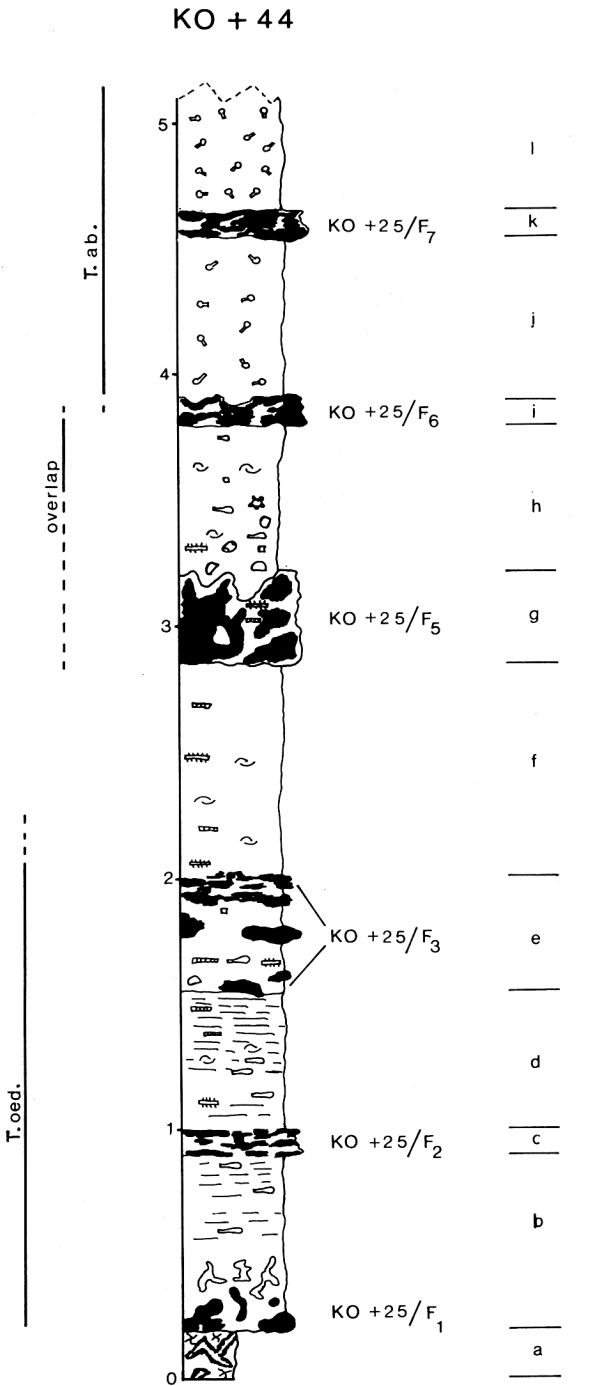


Fig. 13. The Korsnæb section, detailed section at KO +44, showing the eastern flank of a bryozoan mound with thin 'overlap zone'. Three tylocidarid zones are represented (measured 1985).

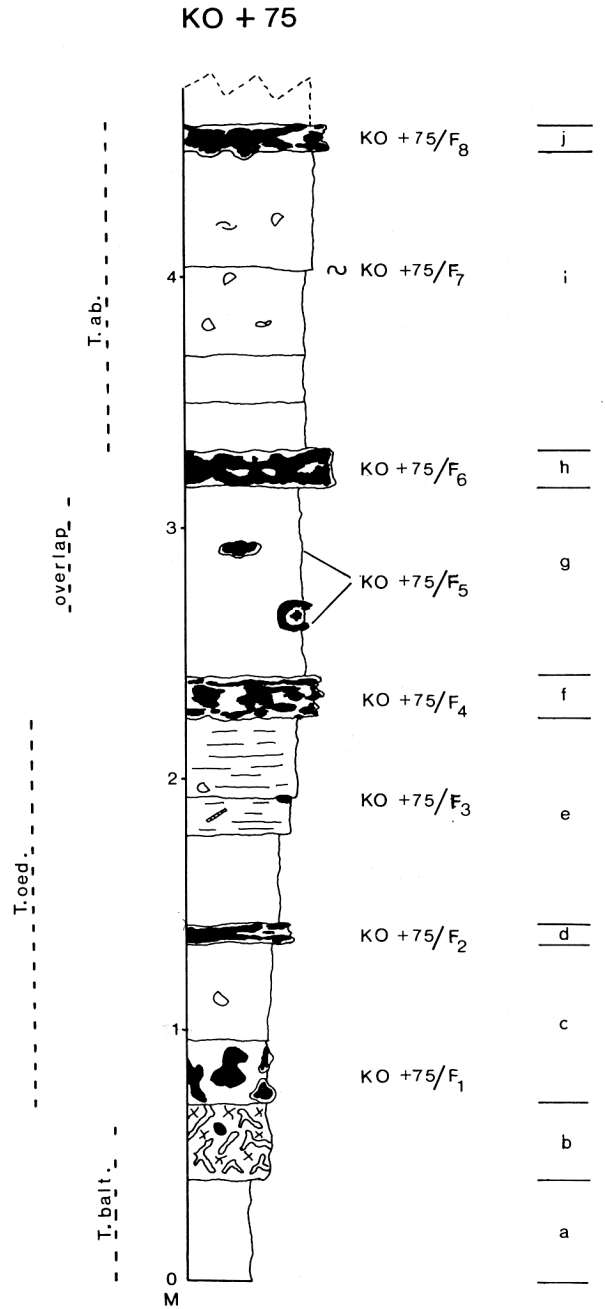


Fig. 14. The Korsnæb section, detailed section at KO +75, showing lower parts of very wide trough. Here there is no hardground at the 'overlap'/abildgaardi Zone boundary; the width of the trough probably lessened the momentum of submarine current here and so allowed a certain deposition to take place during 'overlap' time. Four tylocidarid zones are represented (measured 1985).

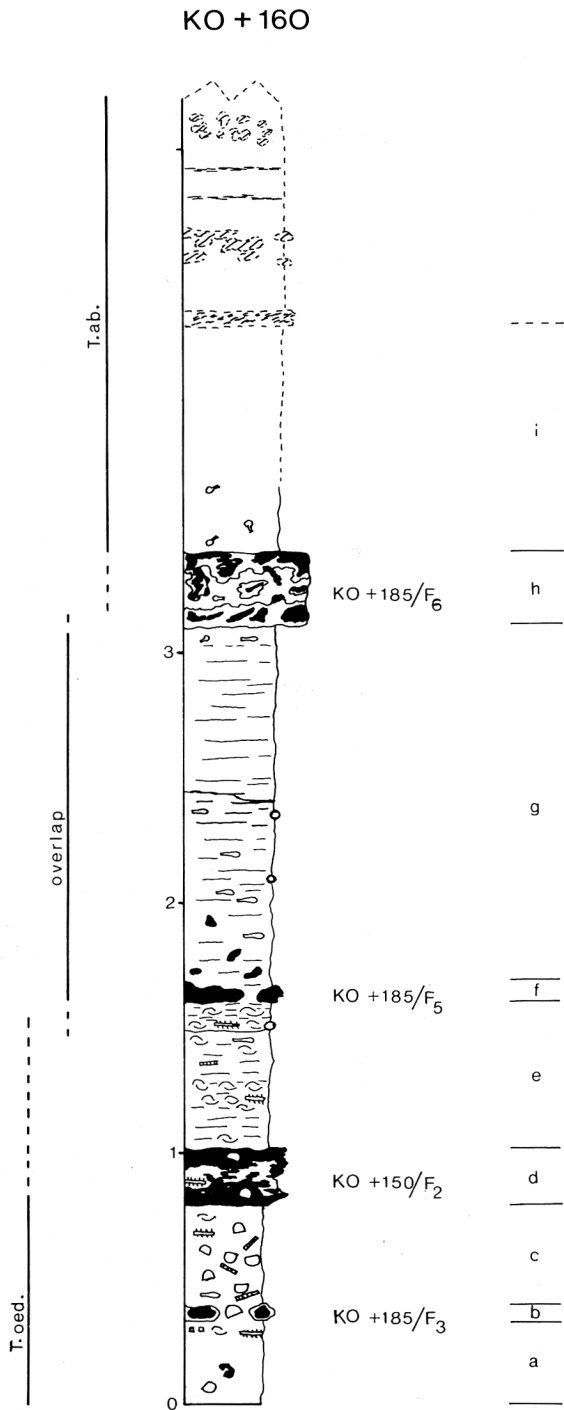


Fig. 15. The Korsnæb section, detailed section at KO +160, showing a very wide trough without hardground formation at 'overlap'/Abildgaard Zone boundary. Three tylocidarid zones are represented.

adjacent mounds is seen. The non-deposition in the troughs may be related to submarine currents which swept away sediment particles that would otherwise have been laid down here. At Karlby Klint in east-

ern Jylland, Thomsen's (1976, 1977a, b) studies of bryozoan mound growth have demonstrated the existence of such currents in the Early Danian sea, coming at Karlby Klint from a southeasterly direction (Thomsen, 1977a, p. 135). For eastern Denmark, at Fakse quarry (only 16 kilometres away from the Korsnæb section) Bernecker & Weidlich (1990, p. 118) demonstrated the existence of a southerly to northerly palaeocurrent during the mid-Danian. Their findings seem to substantiate the existence of a palaeocurrent going from southeast to northwest, or locally from south to north, through the narrow sea across Denmark in the Early and Middle Danian. In my view, the existence of such a current corresponds very well with the pattern of bryozoan mound growth as found at the Korsnæb section and described herein.

ACKNOWLEDGMENTS

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PLATE 1

With the exception of the specimen illustrated in Plate 4, Fig. 11, which is housed in the collections of the Geological Museum at Copenhagen, all other specimens are in the P. Gravesen Collection, currently curated at the Midtsønderjyllands Museum at Gram (Denmark).

- Figs 1, 2. *Tylocidaris* aff. *oedumi*. 'Streaky chalk' (= Cerithium Limestone), Karlstrup quarry, Gravesen Collection, nos 3032, 3033, respectively, x 2.
- Figs 3-16. 3-6 and 8-16 - selected spines illustrating typical *oedumi* and *abildgaardi* type and intermediate forms, x 2; 7 - fragmentary test, x 3. All specimens from the 'overlap zone' as exposed at the Korsnæb section, Stevns Klint. Gravesen Collection, nos 3446 (3), 3236 (4), 3432 (5), 3240 (6), 3394 (7), 3214 (8), 3211 (9), 3441 (10), 3484 (11), 3431 (12), 3393 (13), 3449 (14), 3392 (15) and 3235 (16).
- Figs 17-33. *Tylocidaris oedumi* Brünnich Nielsen, 1938; 17-19, 25, 26 from the stratigraphically oldest *oedumi* populations from the first bryozoan limestone bed at Korsnæb section, x 2. Gravesen Collection, nos 3373 (17), 3378 (18), 3376 (19), 3369 (25) and 3372 (26); 20-24, 27-30 represent the 'second *oedumi* population', from the second bryozoan limestone bed at Korsnæb, being the population used for morphotype analysis (see text), 21 representing a pathological specimen, x 2, Gravesen Collection, nos 3420 (20), 3108 (21), 3187 (22), 3425 (23), 3096 (24), 3129 (27), 3120 (28), 3162 (29) and 3080 (30); 31, 32 from the first bryozoan limestone bed at Korsnæb, x 3, Gravesen Collection, nos 3364 (31) and 3516 (32); 33 from the second bryozoan limestone bed at Korsnæb, x 2, Gravesen Collection, no. 3388.

PLATE 1

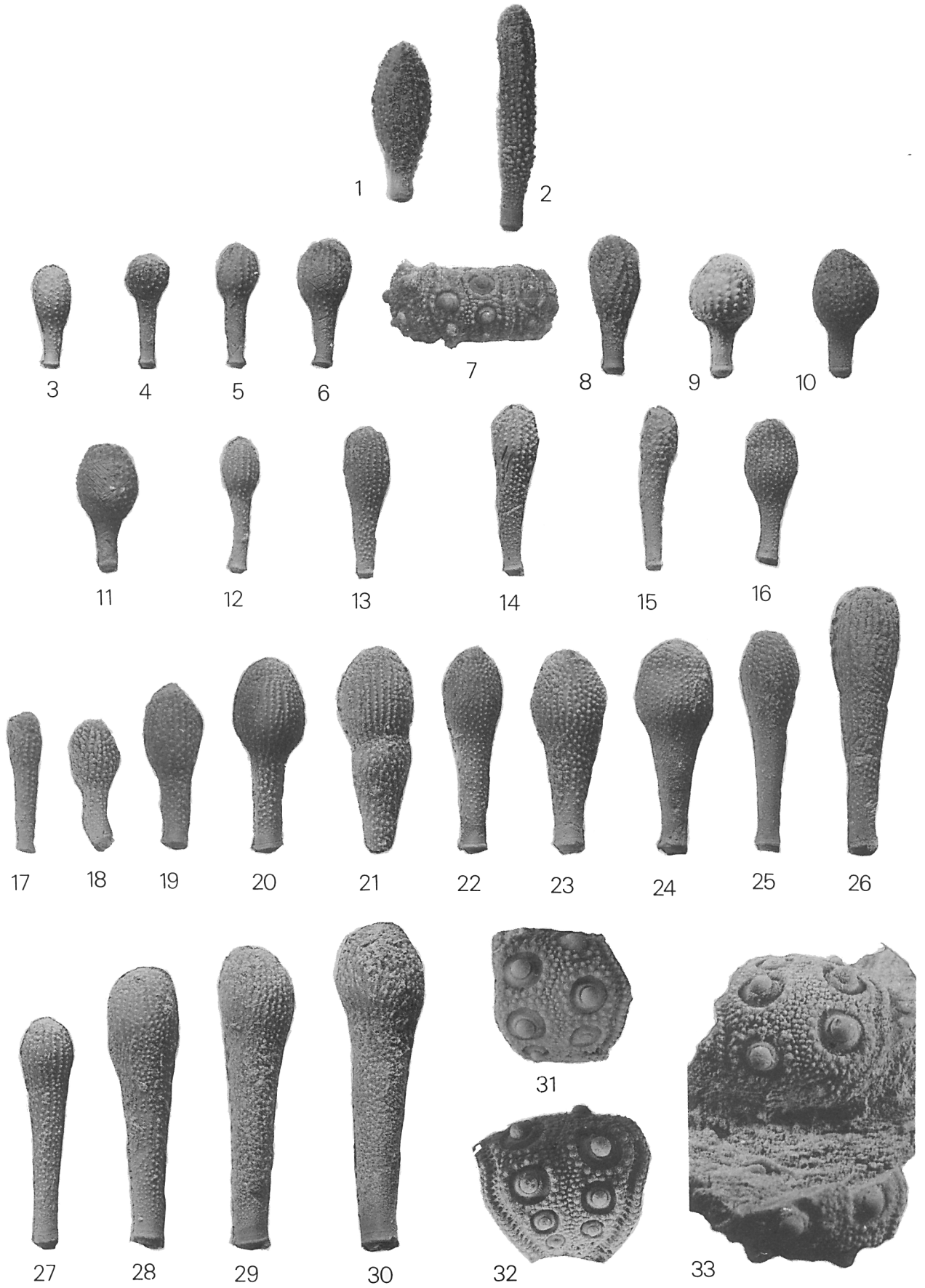
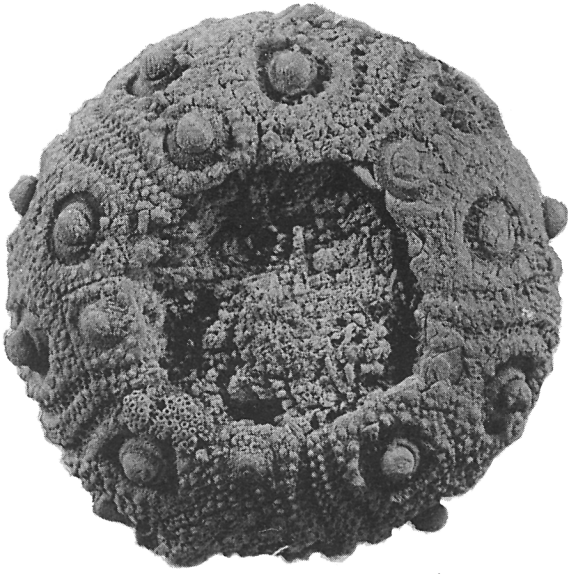


PLATE 2

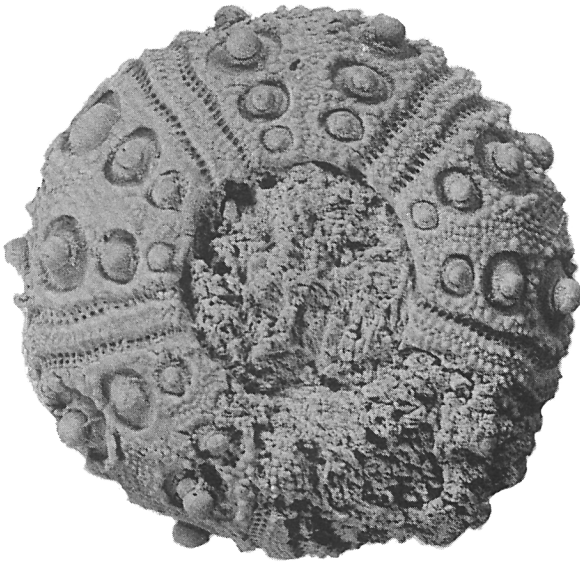
Tylocidaris oedumi Brünnich Nielsen, 1938

- Figs 1-3. The sole complete test known to date, Stevns Klint, north of Kulsti Rende, found loose in scree. P. Gravesen Collection, no. 3350, x 3.
- Figs 4-6. From stratigraphically oldest *oedumi* populations (first bryozoan limestone bed at Korsnæb section). Note spine of *Phymosoma* aff. *granulosum* (Goldfuss, 1829) in 5, and isolated demipyramid and unidentified interambulacral plate in 6. Gravesen Collection, nos 3379 (4), 3380 (5) and 3375 (6), x 2.
- Fig. 7. A crushed test with associated spines, Korsnæb section, found loose in scree. Gravesen Collection, no. 3414, x 2.

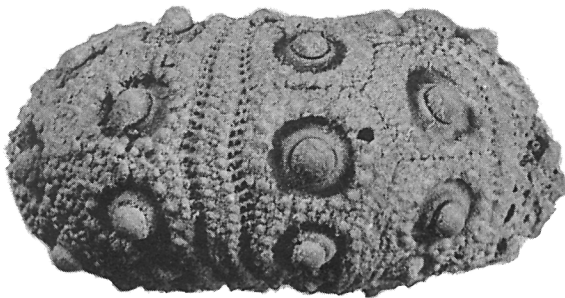
PLATE 2



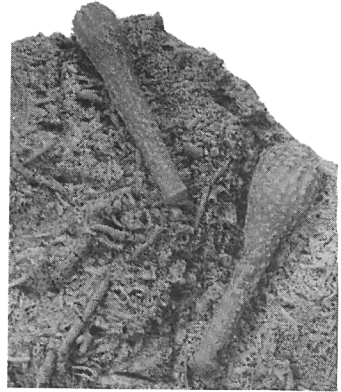
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2



3



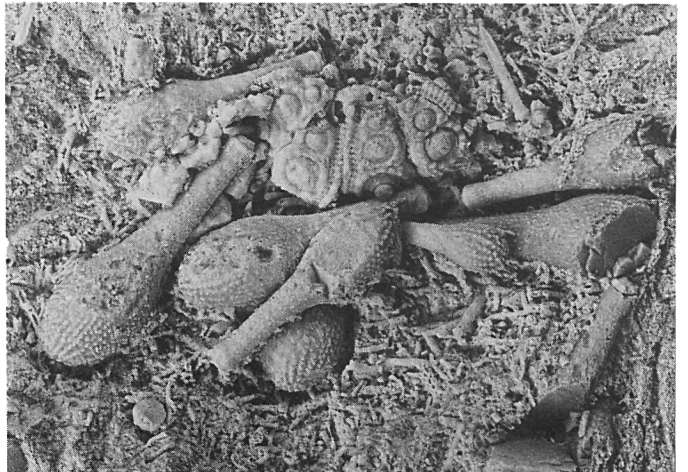
4



5



6



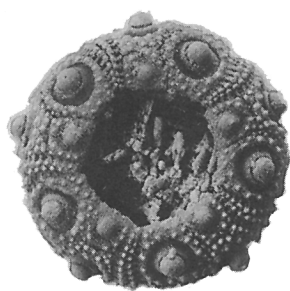
7

PLATE 3

Tylocidaris abildgaardi Ravn, 1928

- Figs 1-3. A complete test, Karlstrup quarry, Gravesen Collection, no. 3354, x 3.
- Fig. 4. Fragment of test of 'reference population' used in morphotype analysis (see text), Korsnæb section. Gravesen Collection, no. 3900, x 5.
- Fig. 5. Fragment of test, *ex situ*, north of Højerup church. Gravesen Collection, no. 3901, x 3.
- Figs 6, 8, 13. Fragments of test with associated spines, all from Stevns Klint; 6 - of 'reference population' used in morphotype analysis (see text); 8 and 13 - from fallen blocks north of Højerup church. Gravesen Collection, nos 3384 (6), 3355 (8) and 3390 (13), x 2.
- Figs 7, 9-11. Spines of the 'reference population' used in morphotype analysis (see text). Note 'oedumoid' spines in 7, 10, 11; 9 illustrates two typical spines. Gravesen Collection, nos 3342 (7), 3313 (9), 3301 (10) and 3335 (11), x 2.
- Fig. 12. A crushed test with associated spines. Korsnæb section, of 'reference population' used for morphotype analysis (see text). Gravesen Collection, no. 3404, x 2.
- Fig. 14. Bedding plane with different spine types, all referred to *T. abildgaardi*, the one in the centre being of the 'oedumoid' type. Stevns Klint, fallen block 400 m north of Højerup church. Gravesen Collection, no. 3351, x 1.

PLATE 3



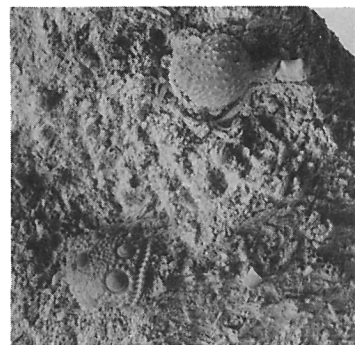
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2



3



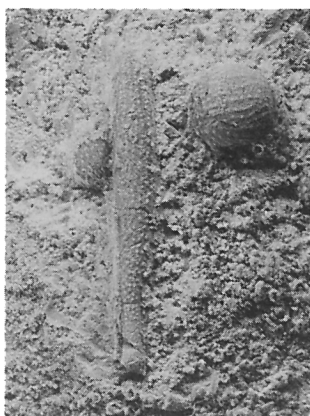
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4



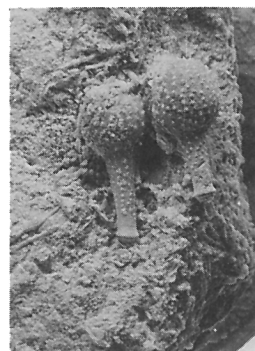
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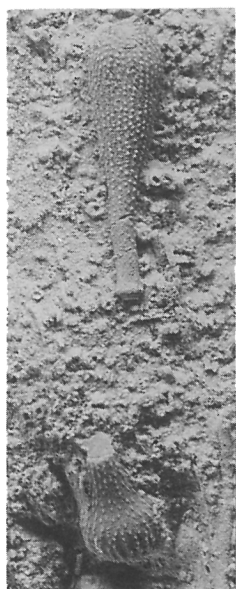
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8



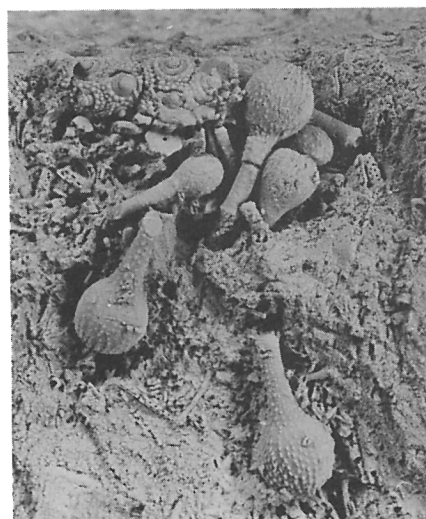
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10



11



12

13



14



PLATE 4

- Figs 1-4. *Tylocidaris abildgaardi* Ravn, 1928, complete tests, 1 and 2 from Højerup, Stevns Klint, 3 and 4 from Karlstrup quarry. Gravesen Collection, nos 3352 and 3367, respectively, x 3.
- Figs 5-11. *Tylocidaris* aff. *rosenkrantzi* Brotzen, 1959; 5-10 from Karlstrup quarry. Gravesen Collection, nos 3902-3905 (5-8), 3005 (9) and 3906 (10), x 2; 11 - specimen collected by Rosenkrantz and Poulsen in 1922, Karlstrup quarry. Geological Museum Copenhagen Collections, no. 1925.191, x 2.

PLATE 4

