Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium — Part 6: Conclusions

John W.M. Jagt

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The palaeobiology of echinoderms occurring in the Meerssen and Geulhem members is discussed and changes in diversity across the K/T boundary are documented. Using literature data on the ecology of extant faunas, the various echinoderm groups are considered. Naturally, such data can only be applied with due caution to fossil forms, whose skeletal morphology is often incompletely known. This holds especially true for asteroids, ophiuroids, and crinoids, which, upon death, rapidly disintegrate into jumbles of dissociated ossicles. Bioturbation, scavenging, and current winnowing all contribute to blurring the picture still further. However, data on extant forms do allow a preliminary subdivision of fossil species into various ecological groups, which are discussed herein. Combining recently published data on K/T boundary sections in Jylland and Sjælland (Denmark) with the picture drawn here for the Maastricht area results in the following best constrained scenario. The demise of the highly diverse latest Maastrichtian echinoderm faunas, typical of shallow-water settings with local palaeorelief and associated unconsolidated bottoms, was rapid, suggestive of a catastrophic event (e.g. increased storm activity as a result of an asteroid impact). Following is the possible equivalent of the 'dead zone' of the Danish sections, capped by the Vroenhoven hardground at the base of the Geulhem Member. At present, due to the lack of bulk samples from the Geulhemmerberg sections, the range of echinoderms between the Berg en Terblijt and Vroenhoven horizons (= section IVf-7 of the Meerssen Member) cannot be fully tested. The earliest Danian echinoderms (e.g. bourgueticrinid crinoids and goniasterid asteroids) occur in fossil hash levels resting on top of the Vroenhoven Horizon, suggesting some time-averaging to have occurred. The immigration of these elements into the study area thus seems to have been rapid. Plotted on a recently published palaeogeographical map of the K/T boundary interval in Denmark, data for the Maastricht area enable a 'K/T boundary sea' to be extended to well south of the Ringkøbing-Fyn High, a structural high. However, the absence of such typical elements as representatives of the echinoid genus *Echinocorys* and isocrinid crinoids from the lower Geulhem Member demonstrates that echinoderm settlement was strongly influenced by local conditions, depth and/or energy related. In short, echinoderm distribution across the K/T boundary in the Maastrichtian type area would indicate rapid extinction of (sub)tropical shallow-water communities, and a subsequent recovery phase characterised by (?rapid) immigration from the north/northwest, linked with an earliest Danian (post-Cerithium Kalk) transgressive pulse. Faunal links with the Danish/North Atlantic region seem to have persisted until the Middle Danian, but by that time local conditions appear to have returned to the pre-K/T boundary development of palaeorelief in the area.

Contents

Introduction

In recent years, a renewed interest in the (bio)stratigraphy and palaeontology of Upper Cretaceous and Lower Palaeogene strata exposed in the type area of the Maastrichtian Stage has become apparent. The discovery in the autumn of 1992 of the Geulhemmerberg K/T boundary sections (Brinkhuis & Smit, 1996) triggered various studies in the type area. Amongst these are a preliminary strontium isotopic analysis of the upper Gulpen, Maastricht and lower Houthem formations (Vonhof & Smit, 1996), a sequence-stratigraphic interpretation of the section exposed at the ENCI-Maastricht BV quarry based on palynomorph (dinoflagellate) distribution (Schiøler et al., 1997), as well as a study of the calcareous nannoplankton content of the type Maastrichtian and of the K/T boundary sequence in the area (Mai, 1999; see also Mai et al., 1997a-b). For the lower part of the Upper Cretaceous sequence, and for the Zeven Wegen, Beutenaken, and Vijlen members (Gulpen Formation) in particular, ecozonations based mainly on bioclasts, ostracods and benthic foraminifera, have been refined (see Jagt, 1999a), as have interregional correlations, especially with the NW German white chalk standard section. All this means that we now have the stratigraphic detail needed for a proper evaluation of particular groups of fossils, with regard to the K/T boundary.

The reasons for choosing echinoderms (i.e., starfish, sea lilies, sea urchins, and brittle stars) are threefold. Firstly, echinoderm fossils range throughout the entire section exposed, and are particularly common at some levels (most importantly, across the K/T boundary). Secondly, they are well preserved and generally highly diverse, and thirdly, although mostly occurring as dissociated ossicles, their morphology is such that familial, generic and specific assignment is possible, allowing broadbrush interpretations of their palaeobiology. In addition, in recent years amateur and professional palaeontologists have assembled important collections of echinoderms from all levels exposed in the area between Maastricht, Liège, and Aachen (see Jagt, 1999a for details). These include numerous new records, which show echinoderm diversity to have been unexpectedly high, especially for crinoids, ophiuroids, and asteroids from the lower Gulpen Formation. It was therefore decided to revise all Late Cretaceous and Early Palaeogene echinoderms (with the exception of holothuroids) and deal with the various groups in separate papers. For a discussion of distribution patterns across the K/T boundary in the Maastrichtian type area, those species occurring in the Meerssen Member (late Late Maastrichtian) and Geulhem Member (Early-Middle Danian) would then be singled out, emphasising palaeobiological aspects of these faunas.

Remains of holothuroids are extremely rare in the study area, having so far been recorded only from the lower Gulpen Formation (Zeleznik, 1985), and the middle/upper Maastricht Formation (Jagt, unpubl.). These echinoderms generally have a low fossilisation potential, and with the exception of a few chance finds of more or less complete individuals (see e.g., Smith & Gallemí, 1992), their skeletons are reduced to microscopic spicules. However, as recent studies have shown (Gilliland, 1992a-b; Reich, 1995), even these spicules provide much information. In the near future, spot samples from the various lithostratigraphic units in the study area will be taken to assess holothuroid diversity.

In the present paper, the palaeobiology of echinoderms occurring in the Meerssen and Geulhem members is discussed here, in order to document changes in diversity across the K/T boundary. Echinoids in particular are an important and diverse benthic component in pre- and post-K/T boundary strata. Moreover, as Smith (1995) pointed out, the relationship between skeletal structure, habitat and mode of life is comparatively well understood, making echinoids excellent palaeoenvironmental indicators. As far as possible, Smith's palaeobiological data for more or less coeval echinoid faunas from the Oman Mountains (United Arab Emirates, Sultanate of Oman), are here adopted for material from the Meerssen Member, as well as for that from the overlying Geulhem Member. Other echinoderm groups have virtually been neglected in previous studies, and this in part explains the unexpected diversity noted. It was therefore decided to have brief introductions to the discussion of the various echinoderm groups, using literature data on extant faunas. Naturally, such data can only be applied with due caution to fossil forms, whose skeletal morphology is often incompletely known. This holds especially true for asteroids, ophiuroids, and crinoids, which, upon death, rapidly disintegrate into jumbles of dissociated ossicles. However, data on extant forms do allow a preliminary subdivision of fossil species into various ecological groups, which will be discussed below. It is these ecological groups, combined with data on other macrofossil groups below and above the K/T boundary, which feature prominently in the discussion on patterns of extinction and origination across this boundary.

The K/T boundary in the Maastrichtian type area

To date, the Geulhemmerberg section (Geulhem-Berg en Terblijt) together with the nearby Ankerpoort-Curfs quarry, represent the most complete and best developed K/T boundary section in the area. A special volume of 'Geologie en Mijnbouw' (Brinkhuis & Smit, 1996), entirely devoted to these sections, contains a number of papers on litho- and biostratigraphic aspects to which reference is here made.

Although typically latest Maastrichtian tegulated inoceramid bivalves (e.g., the genus *Tenuipteria*), baculitid (and ?scaphitid) ammonites, as well as micrasterid and labrotaxid echinoids are known to occur in some abundance in section IVf-7 of the Meerssen Member (see Jagt, 1999a for details), i.e. that part of the section between the Berg en Terblijt (base) and Vroenhoven (top) horizons, palynological and nannofossil as well as sedimentological evidence suggests that the K/T boundary should be equated with the Berg en Terblijt Horizon (see Brinkhuis & Smit, 1996). The Geulhemmerberg section correlates well with the sequence exposed at the Ankerpoort-Curfs quarry, but represents an even more expanded earliest Palaeocene succession, capped by the Vroenhoven Horizon. The latter could well represent the equivalent of the top of the Cerithium Kalk (= base of Early Palaeocene Bryozoan Limestone) in Danish sections (e.g., Højerup and Korsnæb at Stevns Klint, Sjælland), and in the Clayton Formation and at the base of the Littig Member of the United States Gulf Coastal

Plain (see Brinkhuis et al., 1995). With the Geulhemmerberg section having been documented in detail now, there is a need for a reappraisal of the former Albertkanaal sections near Vroenhoven-Riemst. Various authors (e.g., Meijer, 1959; van Harten, 1972) recorded from the top of the Meerssen Member a similarly developed palaeorelief as represented by the Berg en Terblijt Horizon at Geulhemmerberg. The top Meerssen Member/base Geulhem Member there corresponds to the original definition of the Vroenhoven Horizon (see e.g. W.M. Felder, 1975a, b; Jagt et al., 1996); it seems that section IVf-7 as defined at the Ankerpoort-Curfs quarry is absent.

The study by Herngreen et al. (1998) at the Ankerpoort-Curfs quarry focused on benthic foraminifers, palynomorphs, and calcareous nannoplankton. Their results suggest an Early Danian age for strata directly resting upon the Berg en Terblijt Horizon. On palynological evidence, the section studied represents relatively marginal marine (?inner neritic) conditions, with most hardgrounds marking periods of sea level lowstand. From the latest Maastrichtian into the earliest (Early) Danian a 'second-order' deepening trend was inferred by Herngreen et al. (1998), with the Berg en Terblijt Horizon falling within Haq et al.'s (1988) third-order cycle TA1.1, and characterised by first occurrences of the dinoflagellate markers *Senoniasphaera inornata* (Drugg) Stover & Evitt, 1978 and *Lanternosphaeridium reinhardtii* Moshkovitz & Habib, 1993, and an

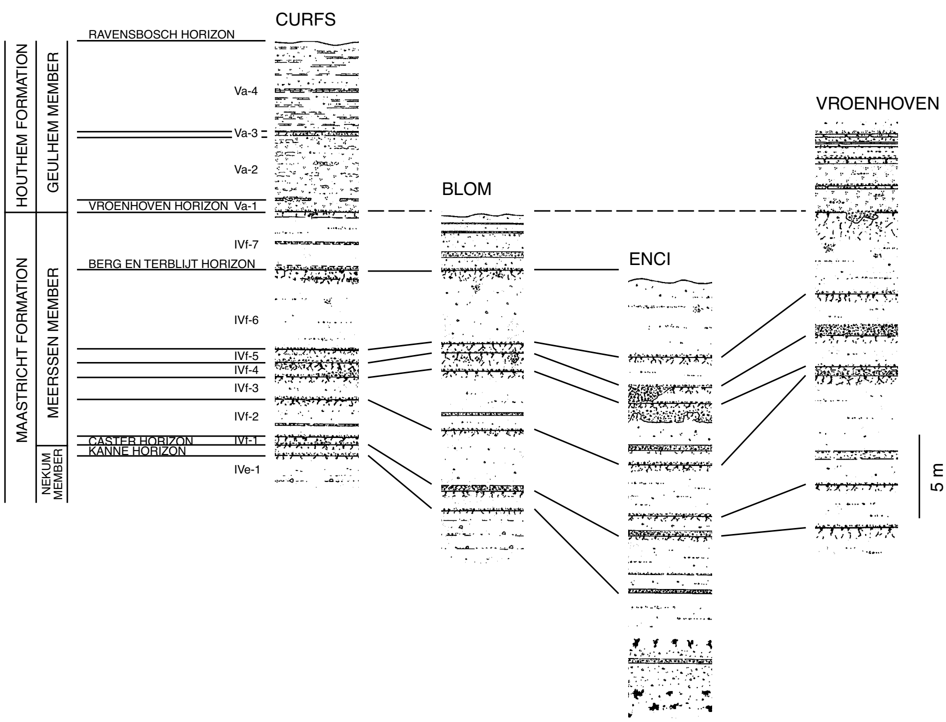


Fig. 1. Correlation between sections exposed at the Ankerpoort-Curfs, Blom, and ENCI-Maastricht BV quarries, and the former Albertkanaal outcrops (Vroenhoven-Riemst, Kesselt), on which echinoderm distribution patterns (Figs. 3-6) in the Meerssen and Geulhem members (Maastricht and Houthem formations, respectively) are based.

influx of bryophyte spores (see also Brinkhuis & Schiøler, 1996). Amongst benthic foraminifers, *Pararotalia tuberculifera* (Reuss, 1862) predominates, but neither their relative numbers nor species diversity across the Berg en Terblijt Horizon suggest a major change to have taken place across the K/T boundary in the studied sections. The same holds true for sporomorphs, with *Jarzenipollis trina* (Stanley, 1965) Kedves, 1980, as a good marker for the Early Palaeocene, and changes in sporomorph assemblages indicating a cooler latest Maastrichtian. Analyses of calcareous nannoplankton show the assemblages above the Vroenhoven Horizon, originally considered to equate with the K/T boundary, to be of definite (later) Early Danian age.

Illustrated in Fig. 1 is a correlation between the four main sections exposing the top of the Maastricht Formation (Meerssen Member) and the base of the Houthem Formation (Geulhem Member), based on lithological features as well as on coleoid and ammonoid cephalopod distribution. Other macrofaunal elements (e.g., rudistid and inoceramid bivalves, and scleractinian corals) have also been taken into consideration. Note that the Berg en Terblijt Horizon (sensu W.M. Felder & Bosch, in press), defined at the Ankerpoort-Curfs quarry, and corresponding to the K/T boundary there, is not developed at the ENCI-Maastricht BV quarry, nor at the temporary Albertkanaal sections (Vroenhoven-Riemst). Current macropalaeontological data and lithological features (W.M. Felder, pers. comm.) suggest that at least 1 m (possibly even more) of the Meerssen Member is missing at the ENCI-Maastricht BV quarry, and that the Vroenhoven Horizon of the Albertkanaal section equates with a hiatus comprising the uppermost Meerssen Member (part of IVf-6, and IVf-7). Echinoderm distribution in Figs. 3-8 is plotted on a combined section, being based mainly on sample series from the Blom quarry (Berg en Terblijt) and the temporary Albertkanaal sections. Reference is made to Jagt (1999a) for a discussion of chronostratigraphic age assignments for the Meerssen and Geulhem members.

Echinoderm distribution across the K/T boundary

With the exception of echinoids, previous studies of echinoderm faunas from the Maastrichtian type area have considered a limited number of species only. The present study shows that diversity was grossly underestimated, particularly with regard to ophiuroids and asteroids. In addition, with few exceptions, material described here is stratigraphically well documented, allowing the ranges of the various species to be determined in some detail. However, a number of problems remain:

1) Although the uppermost Maastricht Formation and lowermost Geulhem Formation are best developed at the Ankerpoort-Curfs and Blom quarries, accessibility of these strata has generally been poor, particularly at the former locality (see e.g., Herngreen et al., 1998, fig. 4). Only rarely were these sections (units IVf-6 and -7) well enough exposed to allow large samples to be taken for macrofaunal analysis. For the present study, material contained in the Kuypers and van Birgelen collections was used, in addition to a few smaller samples collected by myself. It is mainly on these two collections that data on echinoderm diversity of the latest Maastrichtian are based.With the exception of concentrations of macrofossil remains in pockets in the upper part of section IVf-6, most echinoderm material at the base of sections IVf-7 and Va-1/Va-2 is poorly preserved. Only few specimens may be identified to species,

most ossicles being heavily abraded, highly fragmentary and recrystallised in these fossil hash layers of variable thickness. Echinoids are an exception, since these can generally be assigned to species (or genus) even on small, poorly preserved fragments. At the Blom quarry, the best preserved material comes from crustacean burrows in the indurated uppermost part of section IVf-6.

2) With the exception of a limited number of small samples from the top of section IVf-6 and a few hash layers from the lower part of section IVf-7, the Geulhemmerberg section has not been analysed in detail for echinoderms. Collection possibilities there are limited, and bearing the required large sample size for the present study in mind, this explains why this section is still comparatively poorly known. Moreover, it appears that potentially interesting levels occur in portions of the underground workings that cannot be directly linked to the main sampling locality (see Brinkhuis & Smit, 1996 for details), because of lithologic differences. However, the few samples that are available have yielded echinoderm assemblages closely comparable to the ones from the Blom quarry.

3) Although correlation up to the middle (IVf-4/-5) of the Meerssen Member between the various sections (see Fig. 1) is relatively straightforward, being based on the demise of scleractinian corals and rudistid bivalves, coupled with the first appearance datum of the coleoid cephalopod *Belemnella (Neobelemnella)* gr. *kazimiroviensis* (top section IVf-3/base IVf-4), there still are problems correlating the ENCI-Maastricht BV, Blom, and Ankerpoort-Curfs sections. On numerous occasions, the lenticular structure of the various subunits of the Meerssen and Geulhem members, and the discontinuous nature of the hardgrounds and omission surfaces have been stressed. Even within a single quarry (e.g. ENCI-Maastricht BV, Ankerpoort-Curfs), correlation between the various levels is still incomplete. For the present paper, the Ankerpoort-Curfs and Blom quarries are considered for a combined section of the upper Meerssen Member (the ENCI-Maastricht BV quarry being complementary), the Ankerpoort-Curfs quarry/temporary Albertkanaal sections at Vroenhoven/Riemst for the lower Geulhem Member, and the temporary Albertkanaal sections at Kesselt for the upper Geulhem Member.

4) The upper Geulhem Member, characterised by highly typical echinoderm faunas (and rich echinoid assemblages, see below), was exposed for a brief period along the Albertkanaal near Kesselt (Limburg, Belgium). Unfortunately, detailed lithostratigraphic logs have never been measured at that locality, and sampling was more or less haphazard, in view of rapidly progressing excavation at the site. This means that this part of the section cannot at present be tied in with the lower part of the Geulhem Member, but on the strength of the occurrence of a well-developed hardground at the base(?) of this upper part, associated with the first representatives of the echinoid *Tylocidaris* gr. *bruennichi*, it is tentatively correlated with the base of section Va-3 at the Ankerpoort-Curfs quarry (see Fig. 1), and the remainder with section Va-4, as recognised at the Ankerpoort-Curfs quarry. This hardground appears to represent an intraformational hiatus (see also Verbeek, 1986), of unknown extent. More importantly, the Kesselt section is not represented at the Ankerpoort-Curfs quarry, where the Ravensbosch Horizon represents an erosional surface on which strata of earliest Oligocene age rest. The Kesselt section might actually correlate with (part of) the Bunde Member and/or Geleen Member (Houthem Formation), both units based on

borehole cores for which no macrofaunal data are available.

5) With the exception of the majority of echinoid taxa, the firmness of specific taxonomic assignment varies. In particular, this holds true for ophiuroids and asteroids. The papers in the current series present an updated alpha-taxonomic framework, on which future phylogenetic analyses could be based. However, for most of the species recognised we need to know more about population structure and faunal migrations, on a supra-regional bases, so that ancestor-descendant relationships may be established. Only in this way will it be possible to consider monophyletic groups for cladistic analyses. Taxonomic turnovers throughout the sequence studied appear closely related to facies changes, with new forms entering the area.

Without exaggeration, the K/T boundary is the best studied time slice in pre-Quaternary earth history. The plethora of papers that have appeared since 1980 is sheer endless. MacLeod et al. (1997) have recently presented an overview of the various biota at the K/T boundary. For echinoderms they noted that:

1) A preliminary survey of holothuroids shows that no distinctive spicule morphologies were lost at the boundary.

2) Little is known about Late Cretaceous asteroids and ophiuroids, since articulated remains are rare, and dissociated ossicles have rarely been considered. Rasmussen (1950) and Gale (1987a-b) did note changes at species level across the K/T boundary, but all Late Cretaceous asteroid and ophiuroid genera continued into the Early Palaeocene.

3) The majority of (benthic) crinoid genera appear to range into the Palaeocene (Rasmussen, 1961), with a severe decline in diversity at the end of the Danian, with bourgueticrinids, holopodids, and isocrinids disappearing from shelf environments; the drop in comatulid diversity at the end of the Maastrichtian noted by Jagt (1995) probably being a local sampling problem associated with a facies change.

4) Echinoids, which have the best fossil record by far of all echinoderms, have been virtually neglected in K/T boundary faunal analyses. Van der Ham's (1988) study of echinoids from the Geulhem Member shows an equally high diversity as in the underlying Meerssen Member (26 and 27 species, respectively), but with only six species in common, implying a major facies change at the very least. A comparable picture emerges from Jeffery's (1997) study of K/T boundary sections in Kazakhstan. Hit by extinction especially were stomopneustids, cassiduloids, and holasteroids, with highest extinction rates in shallow-water carbonate-platform faunas.

MacLeod et al. (1997) concluded that K/T boundary perturbations obviously affected echinoderms, but that the paucity of phylogenetically standardised taxonomic studies, in combination with sampling biases and facies changes occurring at this time, to a large extent complicated any direct interpretation of the fossil record. These authors noted that the present pattern of echinoderm distribution across the K/T boundary points to habitat loss, and the drowning of carbonate platforms specifically, as playing a major role in restructuring latest Cretaceous echinoderm faunas. However, this cannot explain all extinctions, and the concomitant demise of such different groups as planktotrophic (roveacrinid) crinoids and specialised deposit-feeding holasteroid echinoids, suggest that more factors must have been involved in determining the fate of echinoderms across the K/T boundary.

Based on the systematic framework of the various groups (see Jagt, 1999b, 2000 a,

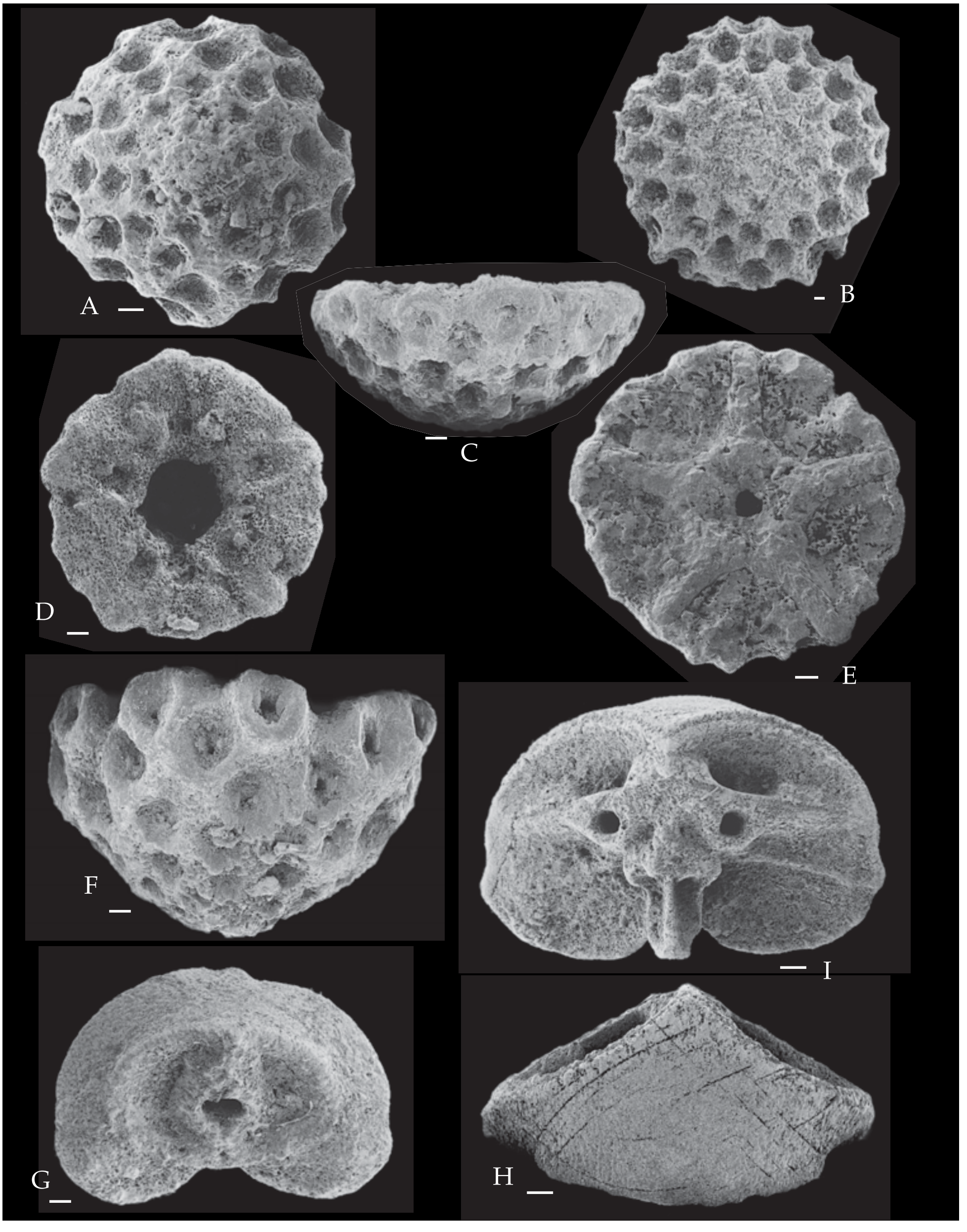


Fig. 2. *Hertha* gr. *mystica* von Hagenow, 1840? All specimens from the upper Geulhem Member (Houthem Formation) of the temporary Albertkanaal sections (Vroenhoven-Riemst/Kesselt); A: NHMM 1996010; dorsal view of centrodorsal; B: NHMM MB 432.OO/1; dorsal view of centrodorsal; C-D: NHMM MB 432.OO/2; lateral and ventral views of centrodorsal; E: NHMM MB 432.OO/3; ventral view of centrodorsal, preserving basals; F: NHMM MB 432.OO/4, lateral view of centrodorsal; G: NHMM MB 432.OO/5, proximal view of axillary primibrach (IBr2, synarthry); H-I: NHMM 1996012, lateral and distal view of axillary primibrach (IBr2). Scale bar equals 1 mm, except for B, where it corresponds to 100 µm.

b; Kutscher & Jagt, 2000), an attempt is made below to reconstruct the life habits of the various species, and determine from the pattern that emerges which mechanism(s) may be held responsible for the faunal turnover at the K/T boundary in the Maastrichtian type area. As noted above, there is of course a certain risk in trying to establish preferred modes of life of extinct organisms, of which generally only a portion is represented in the fossil record.

For all groups, a variety of literature sources have been consulted. The overview of crinoid, ophiuroid, echinoid, and asteroid ecology is used below to reconstruct the life habits of the fossil species considered here.

Crinoids (Fig. 3; Tables 2, 6)

Basic morphology and food

Basically, crinoids are passive suspension feeders, which do not generate their own filtration current, but rely on extrinsic water movement (Lawrence, 1987; Roux, 1987; Messing, 1997; Baumiller, 1997). However, recent observations have suggested that they are not entirely passive, and that most (if not all) species are rheophilic ('current loving'), adapting their arms so as to make best use of prevailing and changing flow patterns and velocities. Food particles are caught by tube feet, and there is little variation in the size of particles caught. Variations in diet are thought to result from place and time of feeding. Modification of tube feet is constrained, which means that only changes in arm and pinnule number and length are possible; this directly affects the filtering efficiency. Food capture seems to be non-selective, with particle size varying between 20 and 150 mm. Baumiller (1997) noted direct interception (see LaBarbera, 1984), rather than sieving, as the dominant mode of capture by the tube feet, and stressed the importance of feeding posture and orientation. D.L. Meyer (1982) analysed gut samples, and documented variation in prey items, noting that species do selectively feed to some extent, with sympatric species not removing the same fraction of particles from the available spectrum, hinted at in earlier studies (D.L. Meyer & Macurda, 1980).

Crinoid larvae, after having escaped the egg membrane, remain in the plankton for a matter of hours, or days, before settling on an adhesive disc (Hyman, 1955). Comatulids pass through a so-called pentacrinule stage, which lasts up to several months, after which the stem is severed and a free mode of life is adopted.

Attachment is either by a terminal disc, a radix or cirri; a permanent attachment, directly to a substrate, is found only in cyrtocrinids (e.g., holopodids). Bourgueticrinids increase the surface area of their attachment by division of branched roots. Donovan (1996) noted that Recent bourgueticrinines are a good model for interpreting the function of the stem as well as radix growth.

Crinoid arms are responsible for locomotion. Articulations are either muscular or ligamentary, the former being commoner. Syzygies and cryptosyzygies have short ligamentary fibres, and are specially developed to increase mobility, in all directions, while synarthries have differential flexibility in two directions only. All comatulids, except comasterids, can swim but over short distances only. Most are active crawlers.

The degree of development of crinoid arms is primarily linked with feeding effectiveness. Each pinnule used in food gathering has groups of three tube feet, but capture of food is passive. Isocrinids and comatulids tend to have more complete pinnulation than most bourgueticrinids and cyrtocrinids. Food particles impact the mucus produced by the primary tube feet and are transferred directly to the ambulacral groove. The spacing and length of tube feet affects the filtering efficiency. Important evolutionary developments include pinnule specialisation, in which the primitive condition of the ambulacral groove (as seen in isocrinids) changed in comatulids to proximal oral pinnules (for protection and tactile use), adjacent genital pinnules (containing gonads), and distal pinnules used for feeding.

Arms (five in number, primitive condition) may increase in number by branching, so that ratio ambulacral area (= food-gathering ability)/body volume increases as well. The number of arms appears related to food supply, with multi-armed species occurring in (sub)tropical settings, while others are known from deep, cold-water environments. In extant forms, there is interspecific variability in arm number, and this could be environmentally induced, leading to phenotypic plasticity. However, the relation between arm number and feeding effectiveness has not been studied in detail yet.

For maximum effectiveness, long tube feet, pinnules and arms should all be at right angles to the direction of water movement. In unidirectional flow, arms are aligned into a filtration fan, with food grooves of pinnules and arms invariably down current. Arm autotomy may be an effective defensive strategy (see Oji & Okamoto, 1994b; Donovan & Lewis, 1997).

In stalked forms (isocrinids, bourgueticrinids), the length of the stalk (or column) determines how far the crown is elevated above the substrate. Short-stalked forms are affected by turbulence near the surface of the substrate, while long-stalked species are affected by laminar flow. In this way a certain stratification, or tiering, is possible. Stalked species, of which some 95 species are currently known, are restricted to depths lower than 60-100 m (D.L. Meyer, 1997; Améziane & Roux, 1997). Roux (1987) considered the absence of stalked crinoids from shallower depths directly due to their functional morphology, rather than to competition with stalkless forms (comatulids), or to teleost predation. Isocrinids may relocate, with cirri on nodals providing anchorage, and temporary attachment to substrates (Roux, 1987; Messing et al., 1988), with calcite callosities forming on the distal articulum nodals (see Jagt, 1999b, pl. 2, fig. 8; pl. 7, figs. 1-2, 5). In actively relocating, crawling isocrinids, movement depends on the antagonistic operation of arm muscles (on the ambulacral side of the transverse fulcral ridge of brachial articulations), in opposition to the elasticity of connective tissue ligaments (on the adambulacral side). Active contractility has recently been suggested to occur in ligaments devoid of muscle cells. There is at least one species of isocrinid, *Metacrinus fossilis* Rasmussen, 1979 (Late Eocene, Seymour Island, Antarctica), which lost the column in the adult stage (D.L. Meyer & Oji, 1993), and thus became comparable to comatulids. In stalks, the stiffness in ligaments may be altered (MCT - mutable collagenous tissues; CCT - catch connective tissues; see Baumiller, 1997). The occurrence of MCT allows autotomy, through irreversible disintegration. Baumiller & Ausich (1996) noted that skeletal morphology is generally a poor guide to stalk flexibility, and that mutable collagenous tissue is the key.

Column loss means a decrease in allocation of resources to the stalk, and thus provides a greater potential for feeding effectiveness, because of increased locomotion.

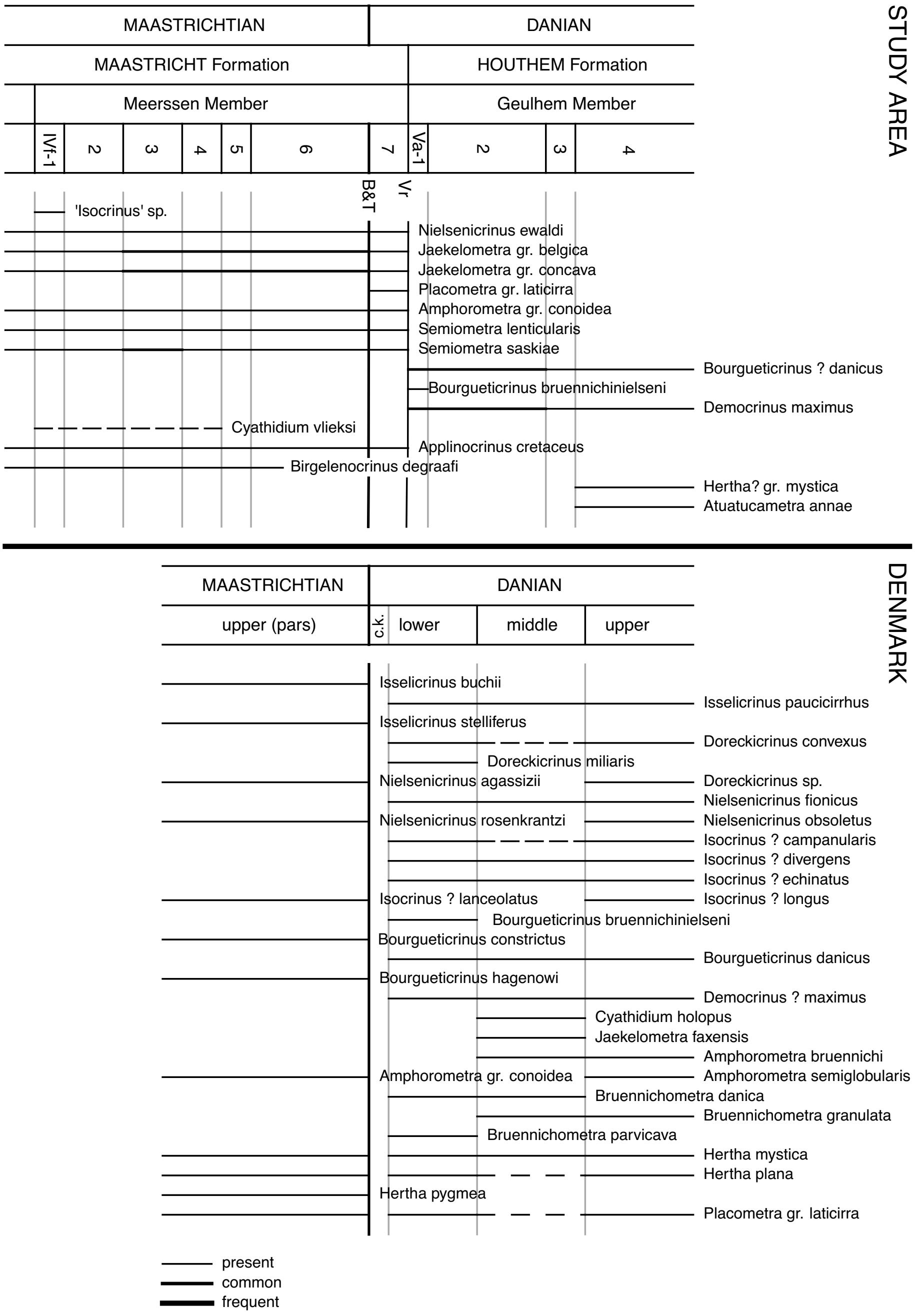


Fig. 3. Crinoid distribution across the K/T boundary in the type area of the Maastrichtian, compared to literature data for the uppermost Maastrichtian and Lower to Upper Danian of Denmark (Rasmussen, 1961; Kjaer, 1993). Abbreviations: Vr = Vroenhoven Horizon; B&T = Berg en Terblijt Horizon; C.K. = Cerithium Kalk.

Stalkless forms (comatulids) can change position, feed wherever food is available, and move to elevated, exposed positions, where they function as stalked crinoids. In addition, they are able to escape from adverse physical conditions and predators, which is considered as one of the factors determining their evolutionary success (D.L. Meyer & Macurda, 1977).

A distinction should be made between high-energy rheophilics (comatulids in uni- or bidirectional wave surges), and low-energy rheophilics (comatulids cryptic, and comatulids/isocrinids in deeper water, low to moderate-energy settings). Current velocity and turbulence are important in crinoid distribution. Roux (1987, p. 4) suggested that turbulence is presumably the most important parameter restricting stalked crinoids to low-energy environments, since some isocrinid species have been shown to be tolerant to relatively high current velocities. Stalked forms, generally less mobile than comatulids, are not adapted to shallow-water environments with bidirectional tidal currents and wave turbulence.

Predation

Predation on living comatulids is mostly sublethal, being the result of grazing by non-specialist fishes, with (semi)cryptic species suffering less (D.L. Meyer, 1985; J.A. Schneider, 1988a), but asteroids and crabs have also been suggested (Mladenov, 1983; D.L. Meyer & Ausich, 1983). Possible defence mechanisms include diurnal seclusion, protection of the visceral mass by spine-like oral pinnules, and crawling/swimming (see e.g., D.L. Meyer et al., 1984). The need for protection of the tegmen in comatulids is demonstrated by modifications of proximal pinnules into stiff, large, spine-bearing oral combs; their importance is underscored by rapid regeneration after damage.

D.L. Meyer (1985) suggested that predation should be considered as a potentially significant selective factor during earlier phases of crinoid evolution. Oji (1996) presented data confirming the view that predation pressure on isocrinids is generally stronger in shallow-water settings, as for comatulids, and noted that there were at least four records of isocrinids in shallow-water settings since the mid-Cretaceous, all in the southern hemisphere (e.g. Eagle & Hayward, 1993; D.L. Meyer & Oji, 1993).

Taphonomy

D.L. Meyer (1997) noted that, although in general the degree of articulation might provide a useful estimate of burial rate and/or degree of transport, field and laboratory studies had shown that disarticulation and/or degradation can occur without significant transport, that crowns and stalks are characterised by differential rates of disarticulation, and that arm autotomy may result from changes in temperature and salinity. Stalks preferentially break down into noditaxes, but it remains to be determined whether this is the result of slow connective ligament, of tight stereom intergrowth, or of early cementation. To account for the bias towards columnal fragments in isocrinid assemblages, both fossil and Recent, Oji & Amemiya (1998) presented experimental evidence showing that stalks can survive for over a year, after removal of the crown.

In modern settings, concentrations of comatulid skeletal material reflect the distribution of living populations. Following death, comatulids disarticulate rapidly within a few days, into jumbles of dissociated ossicles. Ossicle counts vary, but D.L. Meyer &

Meyer (1986) estimated the Recent *Himerometra robustipinna* to have as many as 267,000 skeletal elements, the great majority of them being pinnulars. Pinnulars may be lost by winnowing, and dorsal cups could be removed by predators. Comatulids are fragile organisms, explaining why more or less completely preserved specimens are extremely rare (Simms, 1988d), and why their fossil record is generally poor.

A: Isocrinids

Only two species of isocrinines are known from the Meerssen Member (Fig. 3, Table 2), '*Isocrinus*' sp., and *Nielsenicrinus ewaldi* (see Jagt, 1999b). Both are (extremely) rare in comparison with comatulids (see below), and represent the only stalked forms. A few pluricolumnals (some preserving zygocirrals), and isolated proximal brachials are known, and these are generally well preserved, suggesting these remains to be (par)autochthonous.

Oji (1985) distinguished two groups of isocrinids, one with synarthrial proximal brachial articulations (his 'old group'), the other with cryptosyzygial ones, his 'new group'. *Nielsenicrinus ewaldi* belongs to the latter group, and '*Isocrinus*' sp. is assumed to have belonged here as well, although the type of proximal brachial articulation in that form is still unknown. In assuming the cryptosyzygy to be a specialised articulation for autotomy, Oji (1985) confirmed earlier studies in considering forms with this type of brachial articulation to have been better adapted to cope with (active) predation. The Late Mesozoic teleost fish radiation has been suggested as a factor in the retreat of isocrinids to deeper water settings, but not other groups of stalked crinoids (J.A. Schneider, 1988b, 1989). Apparently, isocrinids were able to survive in (very) shallow-water settings during deposition of the Meerssen Member, so that to Oji's (1996) list of at least four records of isocrinids such settings since the mid-Cretaceous, the Maastricht record may be added. The anomalous occurrence of isocrinids (*Metacrinus fossilis*) in shallow-water, Upper Eocene strata of Antarctica should also be noted. D.L. Meyer & Oji (1993) contributed this occurrence to a combination of reduced predation pressure, a presumed stalkless mode of life, and favourable temperature regime in Antarctic surface waters prior to the onset of cooling during the latest Eocene.

From the Palaeocene (Geulhem Member), no isocrinids are known to date, but it should be pointed out that Rasmussen (1965) recorded the cainocrinid *Nielsenicrinus obsoletus* (Brünnich Nielsen, 1913) from Palaeocene strata in the Belgian Campine area (colliery boreholes?), (north)west of Maastricht. Unfortunately, Rasmussen did not indicate on which collection(s) he based his observation. If correctly assigned stratigraphically, this record could mean that equivalents of the Geulhem Member in the Belgian Campine were deposited at greater depths and/or in less turbulent settings, and/or that these strata extended into the Late Danian, since that is the level from which *N. obsoletus* is recorded in Denmark (Rasmussen, 1961; Kjaer, 1993).

At the temporary Albertkanaal sections (Vroenhoven-Riemst) and the Ankerpoort-Curfs quarry, strata of Early/Middle Danian age have not yielded any isocrinids, despite the fact that isocrinids are common in correlative strata in Denmark and southern Sweden. Rasmussen (1961) and Kjaer (1993) recorded at least six species, *Nielsenicrinus fionicus* (Brünnich Nielsen, 1913), *Isselicrinus paucicirrhus* (Brünnich Nielsen, 1913), *Doreckicrinus miliaris* (Brünnich Nielsen, 1913), *D.*? sp. 1, *Isocrinus*?

echinatus Rasmussen, 1961, and *I.*? *divergens* (Brünnich Nielsen, 1913), occurring at various levels, and extending into the Late Danian. The absence of isocrinids from the Geulhem Member, and their common occurrence in Denmark, is probably not depth related. Bromley (1979) considered the bryozoan limestone to have been deposited under the influence of a predominantly unidirectional flow, below normal wave base, at depths between 80 and 150 m. The depth distribution of Recent stalked crinoids seems to be controlled by variations both in crinoid hydrodynamic vulnerability and in the abundance of food which reaches the sea floor (trophic vulnerability; see Roux, 1987; Améziane & Roux, 1997). The fact that bourgueticrinids are common in the (lower) Geulhem Member suggests that crinoid diversity here may have been influenced by aspects of hydrodynamics, with bourgueticrinids being restricted to a boundary layer of turbulent flow, in which their flexible stem with synarthrial joints allowed differential movement.

It is difficult to explain the co-occurrence of at least four isocrinid species at some localities exposing Lower Danian strata in Denmark. All undoubtedly represent sister taxa of (Late) Maastrichtian forms occurring in the same area, but their exact relationships need to be determined yet. This distribution pattern appears to conflict with Roux's (1987) observation that (extant) stalked crinoids seem to be characterised by slower evolutionary rates and a limited dispersal ability, implying slow recolonisation after tectonic events or sea level changes had destroyed previous shallow-water niches.

In Recent settings, two depth levels with relatively high crinoid diversities are noted. Between 200 and 600 m, isocrinids predominate, and between 1,500 and 3,000 bathycrinids (= bourgueticrinids) and hyocrinids are the dominant forms. From the fossil record, it appears that bourgueticrinids predominantly occurred in much shallower settings, even at depths less than 50 m.

In lower portions of the Upper Cretaceous sequence in the Maastrichtian type area (Benzenrade, Zeven Wegen, Beutenaken, and Vijlen members), isocrinids are fairly common. The distinction between coarsely ornamented forms with short noditaxes and low internodals (e.g., *Nielsenicrinus carinatus*), and those with little or no ornament, tall internodals and long noditaxes (e.g., *Isselicrinus buchii*) is comparable to the situation described by Mitchell & Langner (1995) for the Albian of northeast England. Forms with short noditaxes and low internodals with ornamented latera would represent a functional adaptation for living in shallow, turbulent water, with the stem providing increased anchorage, while those with long noditaxes, high internodals and unornamented latera would have favoured calmer, deeper settings.

Lastly, in the Kunrade-Benzenrade area, isocrinids abound as dissociated columnals, mostly of small size (Table 1). Correlations with the Maastricht area suggest the Kunrade Limestone facies to correspond to the Lanaye Member up to the base of the Emael Member (see Jagt, 1999b). On peaks in crinoid distribution, Jagt (1988) correlated the Benzenrade motorway RW 76 section with the Lanaye Member, but whether this can be upheld is doubtful. Bourgueticrinids dominate in the Lanaye Member, while the Kunrade forms are predominantly small-sized isocrinids. The Kunrade Limestone formation is a shallow-water deposit with increased terrigenous influx (riverine input), which makes the occurrence of isocrinids in such high-energy settings even more puzzling. It should be noted that the isocrinid material appears size

Table 1. Echinoderm fauna from the Kunrade Limestone facies (Maastricht Formation), as exposed in the Kunrade-Benzenrade area.

Crinoidea
'*Isocrinus*' sp.
Nielsenicrinus ewaldi
Jaekelometra gr. *belgica*
Jaekelometra gr. *concava*
Amphorometra gr. *conoidea*
Semiometra cf. *saskiae*
Hertha gr. *pygmea*
Cyathidium vlieksi
Applinocrinus cretaceus
Birgelenocrinus degraafi

Ophiuroidea
Trichaster? *ornatus*
Ophiocten? *yvonnae*
Felderophiura vanderhami
Stegophiura? *hagenowi* (?)
Ophiolepis? *linea*
Ophiomusium lux

Echinoidea
Temnocidaris (T.) sp. 2
Temnocidaris (Stereocidaris) sp. 1
Centrostephanus? sp. (? spp.)
Orthopsis miliaris
Salenia (Pleurosalenia) bonissenti
Salenia (P.) maestrichtensis
Codiopsis disculus
Phymosoma gr. *granulosum*
Gauthieria maeandrina
Gauthieria pseudoradiata
Trochalosoma? *corneti*
Micropsidia? sp.
Echinogalerus muelleri
Echinogalerus transversus
Echinogalerus vetschauensis
Nucleopygus coravium
Nucleopygus scrobiculatus
Cardiaster granulosus
Hemipneustes striatoradiatus
Diplodetus duponti
Hemiaster gr. *aquisgranensis*
Hemiaster prunella
Leymeriaster maestrichtensis
Linthia? sp.

Asteroidea
benthopectinid sp. 1 (? spp.)
Metopaster lisannae (var.)
Chomataster acules
goniasterid? sp. 4

selected, and is mostly (heavily) worn, which could either mean transport over a certain distance, or continued reworking at these localities.

B: Comatulids

From the Meerssen Member, diverse comatulid faunules are known at a number of localities (ENCI-Maastricht BV, Blom, and Ankerpoort-'t Rooth quarries), comprising the atelecrinids *Jaekelometra* gr. *belgica*, *J.* gr. *concava* (including forma *meijeri*), the pterocomid *Placometra* gr. *laticirra*, the conometrid *Amphorometra* gr. *conoidea*, and the notocrinids *Semiometra lenticularis*, and *S. saskiae*, all of which range up to (the equivalent of) section IVf-7 at the Blom quarry. The fact that various ontogenetic stages are known (particularly of *Jaekelometra*, *Semiometra*, and *Amphorometra*), and that faunules also comprise numerous dissociated cup plates, proximal brachials, and cirrals (see Jagt, 1999b, pls 15-23) indicates that these assemblages may be considered autochthonous. In section IVf-7, however, generally only centrodorsals are found. Depositional features suggest current winnowing to have removed all other, lighter brachial, pinnular, and cirral ossicles, rather than cropping of these elements by predators to explain this bias.

The co-occurrence of several comatulid genera in the (upper) Meerssen Member points to favourable conditions, with ample opportunities to exploit the palaeorelief (perching), and the presence of cavities for more cryptic species.

To date, the Geulhem Member has yielded only two species of comatulid, and both are restricted to the upper part, being known only from the temporary Albertkanaal sections at Kesselt, viz. the pterocomid *Atuatucametra annae*, and the antedonid *Hertha* gr. *mystica*? (Fig. 2). Both forms are of small size, and both are comparatively rare. Associated proximal brachials suggest these occurrences to be autochthonous. The palaeorelief (see also Echinoids) represented by the part of the Geulhem Member that yielded these comatulids is broadly comparable to that of the Meerssen Member. From the lower Geulhem Member only bourgueticrinids are known to date.

Although a few species of comatulid display a wide range of variation (see Jagt, 1999b), indicated by the frequent use of open nomenclature (gr.), species distinction is generally straightforward (with the exception of some juvenile and abraded specimens), and is based on centrodorsals.

Extant comatulids show an extraordinary morphological plasticity, which presents major taxonomic difficulties and suggests that diversification continues (Messing, 1997). Some 540 nominal species in 142 genera have been described, but if due consideration is given to variation the number could decrease to c. 470. A revision of Recent taxa has only just begun (see e.g. Messing, 1998a-b). It will undoubtedly greatly reduce the number of taxa considered valid, but the reverse may also be true; currently accepted species may hide undescribed taxa. Messing (1997) noted that comatulid higher-order systematics was still unresolved, and that phylogenetic analyses had not yet been carried out.

As Birkeland (1989) noted, comatulid diversity probably reflects both larval dispersal and nutrient availability. These stalkless crinoids are probably able to make good use of increased productivity from upwelling or from terrestrial runoff, both resulting in conditions favourable for passive suspension feeding. The occurrence of diverse comatulid faunules, in which generally one of the forms predominates, in the Meerssen Member probably reflects such a shallow-water, (sub)tropical setting with riverine input. The occurrence of (locally numerous) quartz pebbles, of millimetre to centimetre size, at these levels suggests a high-energy setting, and considerable terrestrial runoff.

Within the Meerssen Member, comatulid distribution is highly irregular, and probably reflects former seafloor topography (palaeorelief), as well as differences in benthic flow regime associated with small-scale topographic irregularities. Such conditions were documented for much deeper, Recent settings in Little Bahama Bank east of Florida (Llewellyn & Messing, 1993). These authors noted that crinoidal skeletal material showed considerable fidelity with respect to living assemblages. D.L. Meyer & Meyer (1986) reached a similar conclusion for Lizard Island (Great Barrier Reef).

Whether or not there was competition between the various comatulid species, or niche differentiation, in the Meerssen Member cannot be determined. In many Recent settings, various species may coexist with no signs of competition (D.L. Meyer & Ausich, 1983). However, at most localities studied one form predominates, and this is mostly *Jaekelometra* gr. *concava*. The isocrinid *Nielsenicrinus ewaldi* found associated probably attached to boulders, or palaeorelief, by its cirri but in less turbulent niches.

Comatulid diversity in the uppermost Meerssen Member (Fig. 3) strongly contrasts with their absence in the overlying lower Geulhem Member. However, it should also be noted that in earliest Palaeocene strata in Denmark comatulids are rare as well (Kjaer, 1993). Comatulid faunules comparable to the ones characterising the Meerssen Member, both in composition and diversity (see Fig. 3), are known from the Middle and Upper Danian of Denmark (Rasmussen, 1961), representing at least eight species in five genera [*Jaekelometra faxensis* (Brünnich Nielsen, 1913), *Amphorometra bruennichi* (Rosenkrantz, 1945), *A. semiglobularis* (Brünnich Nielsen, 1913), *Bruennichometra danica* (Brünnich Nielsen, 1913), *B. granulata* (Brünnich Nielsen, 1913), *Hertha mystica* von Hagenow, 1840, *H. plana* (Brünnich Nielsen, 1913), and *Placometra laticirra* (Carpenter, 1880)]. Estimated depth ranges for the Middle Danian coral mounds of Fakse (Sjælland, Denmark) differ considerably. Bernecker & Weidlich (1990) assumed the Fakse strata to represent aphotic, azooxanthellate coral mounds, in water depths of between 200 and 300 m, while Collins & Jakobsen (1994), citing other literature sources, noted maximum depths of 80 m. Rasmussen (1973) also indicated that deposition must have occurred within the photic zone.

C: Bourgueticrinids

The Meerssen Member has not yielded any bourgueticrinid (Fig. 3). In fact, it appears that bourgueticrinids disappear from the area coinciding with the onset of deposition of the Emael Member, only to return in the Geulhem Member, from which three morphotypes are known (*Bourgueticrinus bruennichinielseni*, *B. danicus*, and *Democrinus*? *maximus*; see Jagt, 1999b).

If there is limited current activity, the bourgueticrinid column is stiff. On rough substrates, moderate to strong currents result in a boundary layer with turbulent flow, making a highly flexible stem with synarthrial joints necessary (Roux, 1987), allowing differential movements. This may explain why only bourgueticrinids are known from the (lower) Geulhem Member, and no isocrinids (see above). Other (adult) stalked crinoids occur in laminar flow, either for the most part or entirely so. The occurrence of synarthrial articula in the columns of juvenile isocrinids reflects this habit.

In a food-rich environment a lower filtration capacity is feasible, implying either a reduction in arm length or in the number of brachial divisions. Both morphotypes (if *B. bruennichinielseni* is included in *B. danicus*, see below) have axillary IBrr2, i.e. ten arms. There are no indications for further arm divisions. This contrasts markedly with the Late Maastrichtian *Dunnicrinus aequalis*, which invariably has five arms, albeit of considerable length.

The occurrence of relatively numerous articulated individuals of *D. aequalis* in the lower Gronsveld Member (Maastricht Formation) at the ENCI-Maastricht BV quarry (Jagt et al., 1998) is the only example recorded to date from the study area, for which population density can be analysed. Being the result of sudden burial (obrution) by storm activity or by submarine gliding, rather than reflecting an increase in drag which would have resulted in collapse of crowns (i.e. surpass tolerance threshold; see Roux, 1987), these populations compare well in structure and scope with other crinoid lagerstätten (see e.g. Taylor, 1983; C.A. Meyer, 1990). It may even prove possible to determine the spatial distribution of these crinoids, since radicular cirri are so extensive that dislodging of stalks may be ruled out. Baumiller (1997) noted that for conspecific crinoids with stalks of subequal length, tiering is generally not an option, and that inference by upstream neighbours could have a detrimental effect on a downstream individual's ability to feed. An analysis of the spatial distribution of the extant isocrinid *Endoxocrinus parrae* led to the introduction of the Interference Avoidance Hypothesis (Baumiller, 1997). The ENCI occurrence might provide clues to determine whether or not bourgueticrinids behaved similarly.

In comparing isocrinids with other Late Cretaceous crinoids, Oji (1985) noted, based on the 'bathycrinine' *D. mississippiensis* Moore, 1967, that this group of stalked crinoids persisted in shallow-water environments longer than isocrinids did. This is confirmed by *D. aequalis* at the ENCI-Maastricht BV, but the observation has to be modified to account for the isocrinids from the Meerssen Member (see above).

Kjaer & Thomsen (1999) showed that, following the perturbations at the K/T boundary, bourgueticrinids differed markedly in distribution from other invertebrate taxa, by showing an increase in the lowermost Palaeocene. Accompanied with this is a heterochronic change in which the proximale is lost by paedomorphosis (neoteny), implying that stem growth could continue representing an adaptation for longer columns. What caused these crinoids to grow longer columns is difficult to determine, but Kjaer & Thomsen (1999) suggested that longer stems could mean a potentially higher feeding level, i.e. be the result of increased competition in a depleted environment. However, bottom conditions could also hold the key. Lowermost Danian deposits are richer in clay, suggesting the occurrence of muddier bottom waters, in which longer-stemmed crinoids could have had a selective advantage. Kjaer & Thomsen (1999) included in their concept of *B. danicus* morphologies previously referred to as *B. bruennichinielseni* (see Jagt, 1999b) characterised by shorter proximalia, and taller basals. Representatives of this type are a minor element only in 'populations' from the lower Geulhem Member, and reflect different stages of development.

Of note also in these Early Palaeocene bourgueticrinids is the character of columnal articulation of the *Conocrinus* type (Roux, 1987), with a deep bilobate areolar depressions and a rather weak fulcral ridge with secondary crenularium. This would reflect a process towards higher flexibility of the articulations, and a reduction of material needed to build the skeleton, in environments poor in carbonate and food (Roux, 1987). *Bourgueticrinus danicus* continues the lineage of *B. constrictus* (of Early/Late Maastrichtian age) into the Palaeocene, and although the latter species is also known from the study area (Vijlen and Lixhe 1 members, Gulpen Formation), the occurrence of *B. danicus* in the lower Geulhem Member must represent a migration event from the north (northeast). From the Lanaye (? Lixhe 2/3) Member to the base of the Emael Member, the only bourgueticrinid in the study area is *D. aequalis*, and this is unrelated to the *constrictus/danicus* lineage. Of note is a possible Late Campanian precursor, referred to as *Bourgueticrinus* sp. 1 (aff. *baculatus* Klikushin, 1982) in Jagt (1999b, pl. 31, figs. ?1, 4, 8, 10; pl. 32, fig. 10), occurring in the Zeven Wegen Member.

The fact that bourgueticrinine faunules from the lower (lowermost) Geulhem Member contain all morphologies recognised from the lowermost Danian of Denmark, suggests this migration event to be a comparatively rapid one.

Heterochrony has been shown (Simms, 1988a-c, 1990a) to be of fundamental importance to the development of post-Palaeozoic crinoids. The difference in the degree and polarity of heterochrony appears sufficient to account for all articulate crinoid morphotypes, and both paedomorphosis and peramorphosis have been documented. The occurrence of synarthrial articulations in juvenile isocrinids, and their absence in millericrinids, lends support to previous hypotheses concerning a neotenous derivation of bourgueticrinids from an isocrinid rather than a millericrinid ancestor (Simms, 1989a). Roux (1987) disagreed with such a scenario.

D: Holopodids and roveacrinids

Representatives of these crinoid groups are only known from the Cretaceous. *Cyathidium vlieksi*, originally based on material from the Kunrade Limestone facies, is also known from the tuffaceous chalk facies west of the River Maas, but there it is stratigraphically poorly constrained. Like the Palaeocene *C. holopus*, this form may be assumed to have been restricted to a sheltered environment, either in hardground cavities, or in crustacean burrows that characterise such an environment. The absence of *Cyathidium* from the upper Geulhem Member is puzzling, since the depositional environment of that part of the sequence (see also Echinoids) would have been favourable for this species.

The saccocomid *Applinocrinus cretaceus* and the roveacrinid *Birgelenocrinus degraafi* both extend to high in the Meerssen Member, but only the former appears to have ranged to the very top of the unit. Manni et al. (1997) considered the stemless saccocomids (i.e. the genus *Saccocoma* in particular) to be benthic opportunists in mud-dominated facies. These authors agreed in many respects with Milsom's (1994) view, but rather than have arms outspread on the sea floor in a collecting bowl, they assumed a flower-like construction of the crown, with proximal arm segments tightly held together, and only distal portions used in food collection. So far, no conclusive evidence of the presence of brachials in *Applinocrinus* has been put forward. This type of crinoid is also assumed to have been benthic, with a set of covering plates representing highly modified brachials(?).

Whether roveacrinids were benthic or nektonic is still a matter of debate, the problem being that these crinoids are mostly found as dissociated ossicles only. Finds of more or less articulated material are extremely rare (see e.g. Scott et al., 1977), and skeletal morphology and ontogeny still poorly known (H.L. Schneider, 1987, 1989a). Milsom (1999) presented evidence of two roveacrinid lifestyles: benthic with the ability to swim, and nektonic. Benthic forms are characterised by flanges and spines occurring on the dorsal cup and proximal brachials, and limited arm mobility. Nektonic forms have an enlarged dorsal cavity, extreme arm mobility, are almost devoid of ornament, and show evidence of skeletal lightening. With roveacrinids feeding via a mucus net, there exists a critical hydrodynamic balance between arm length and stability. Nektonic forms appear to have sacrificed large feeding nets in favour of increased stability (Milsom, 1999). *Birgelenocrinus degraafi* shows evidence of skeletal lightening, has highly modified brachials, and a dorsal cup with little or no ornament, and thus would belong to the nektonic forms. Being directly dependent on suspended material in the (upper) water column, this crinoid type may be expected to have been influenced primarily by a food chain collapse postulated for the latest Cretaceous.

In general, following major environmental crises, there are new areas for colonisation by opportunistic taxa (r strategy), which are geographically widely distributed, have a highly variable morphology, as well as a wide ecological tolerance, being characterised by a low level of specialisation. *Bourgueticrinus danicus* and *Democrinus*? *maximus* would fit this category. Near the end of the radiation occur taxa which are mostly specialised to ecological niches (K strategy), are highly vulnerable to new crises, and have a high degree of differentiation, and are relatively restricted (revealing a trend towards endemism), and low variability of morphological characters. The comatulids of the upper Geulhem Member and of the Middle/Upper Danian of Denmark would belong here.

Ophiuroids (Fig. 4; Tables 3, 7)

Basic morphology and food

Ophiuroids (brittle stars and basket stars) show a wide range of body plans, including smooth as well as extremely spiny forms, and basket stars with numerous branching arms. In size, discs range from a few to 65 millimetres, and arms may be over a metre in length. In contrast to most asteroids, arms and disc in brittle stars are invariably well demarcated, and covered by series of ossicles of various types (plates, shields, scale, spines, and granules). Arms are heavily calcified, and are used in feeding and locomotion. Emerging from beneath arm joint are minute, finger-like tube feet that lack suckers. Some extant ophiuroids are known to use tube feet for locomotion, but most species move by muscular exertions of pairs of arms flexing and extending to push the disc ahead, with minimal involvement of tube feet. A few species can swim. Adhesion by tube feet also allows many species to climb smooth vertical surfaces and catch and manipulate food particles.

Within the disc are a large stomach, a series of gonads, and sack-like bursae. The

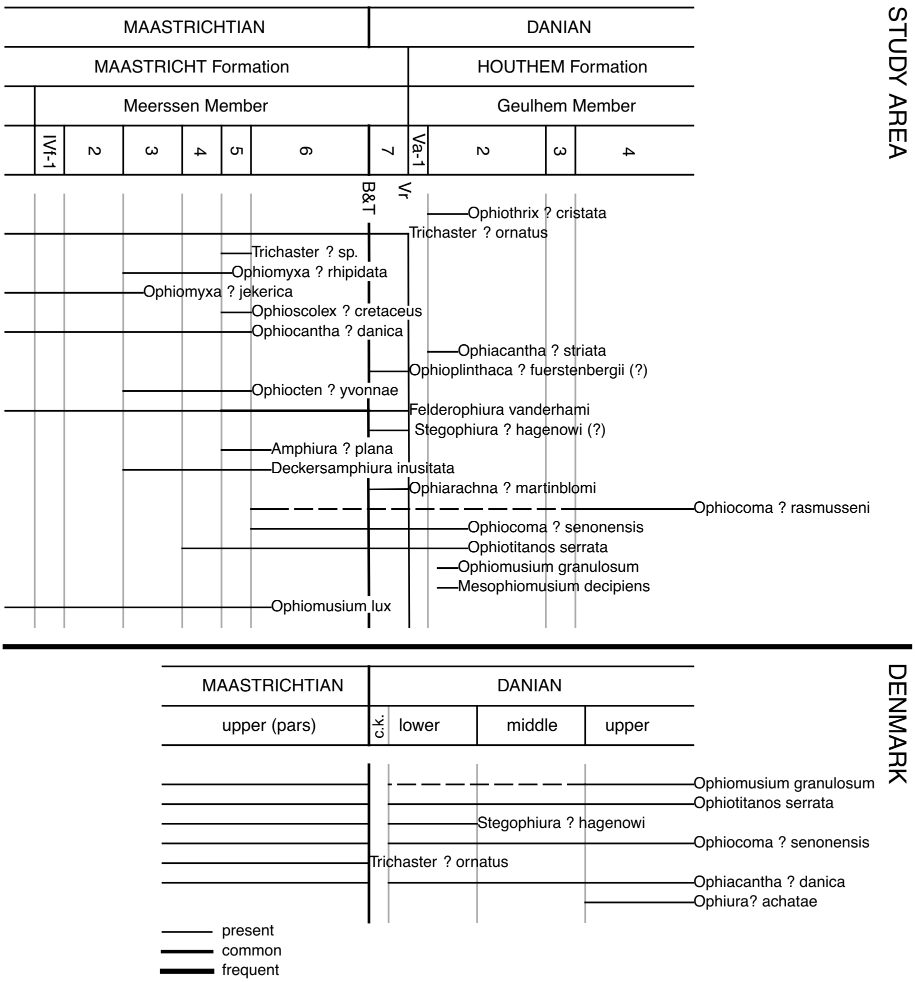


Fig. 4. Ophiuroid distribution across the K/T boundary in the type area of the Maastrichtian, compared to literature data for the uppermost Maastrichtian and Lower to Upper Danian of Denmark (Rasmussen, 1950, 1952, 1972). Abbreviations: Vr = Vroenhoven Horizon; B&T = Berg en Terblijt Horizon; C.K. = Cerithium Kalk.

latter open besides the arm base into slits, supported by genital shields, and are used in respiration and reproduction. The reproductive organs comprise clusters of gamete-lined tubules housed within the disc. When spawning, brittle stars assume a push-up posture, with discs raised off the bottom while pumping gametes from bursal slits. This happens at night, when predation is reduced or less effective. Larvae develop for a few days to over a month, then complete metamorphosis during which they continue to swim around, and transform into juvenile brittle star. Some species have large, yolk-rich eggs and nonfeeding barrel-shaped larvae, which metamorphose in less than a week, while others produce thousands of tiny eggs which develop into more elaborate, long-lived larvae. A minority of ophiuroids are hermaphroditic, either sequentially or simultaneously. All of these brood their young, i.e. they are held in the bursae until they reach a certain size. Yet another group can reproduce asexually by fission, i.e. splitting across the disc.

In many forms, above arm base paired radial shields are seen. Conspicuous features of the oral side of the disc include five oral shields, one (or more) of which may be enlarged and perforate.

Arms comprise a series of flexible joints, consisting of vertebrae linked by muscles and connective tissues, lateral arm plates bearing a variable number of spines, as well as dorsal and ventral arm plates. Arm spines may either be erect or appressed, stout or inconspicuous. Some spines may be modified into anchorage hooks, as in some ophiothricids and amphiurids (but poorly developed), and in ophiomyxids (numerous and well developed). Together with associated arm hooks and tentacle scales, arm spines serve in feeding and defence. New arm joints are added at the inner edge of terminal plate (arm tip), and as the disc grows, new plates and scales are added between older ones, and the disc tends to encroach on the proximal arm joints. Almost every brittle star species is able to a degree of vertical bending or coiling of the arms.

Highly modified arm ossicles form five triangular jaws that frame the centrally placed mouth. Attached to the jaws are oral papillae, dental papillae, and teeth, in a characteristic arrangement, diagnostic of higher-level groups.

In reefal habitats (e.g. the Caribbean), coral-associated brittle stars may reach densities of 20-40 individuals per square metre. Burrowing species in soft sediment, however, may be 10-100 times more numerous. Hendler et al. (1995, p. 90) recorded over 44 species on a single cay on the Belize Barrier Reef.

Ophiuroids are notorious for self mutilation, or autotomy. This helps an animal survive predator attacks. Some forms even cast off their disc, with stomach, gonads, and other tissues, but are able to regenerate the broken arms completely and regrow the disc and associated viscera fairly rapidly. Other defences include distastefulness, luminescence, speedy escape, shadow response (see e.g., Hendler, 1984b), and stop-motion reflex triggered by passing predators.

Vertebral structure is either zygospondyline (ball and socket, allowing arm twisting), with arms mostly moving laterally and functioning for active locomotion, or streptospondyline (hourglass shape articulation), allowing the arms to coil vertically. During locomotion, the disc becomes elevated. Amphiurids use their tube feet to burrow vertically, while shallow-water ophiuroids move their arms in a swimming motion when released into the water column, but they have not been observed to swim in the field.

Amongst ophiuroids, there are two major feeding types. One is primarily predatory and carrion-feeding (macrophagous) and includes foraging carnivores, with short arm spines and tube feet. The second type includes microphagous, often sedentary feeders on substrate particles or on particles from the water column, with long spines and tube feet. Microphagous deposit-feeding involves only the tube feet; for instance, burrowing amphiurids sweep the sediment surface with mucus-lined tube feet. Microphagous suspension-feeding implies the use of arm spines and tube feet, with the ambulacral surface facing the current, unlike crinoids. Medeiros-Bergen

(1996) recently provided examples of differences in stereom microstructure in teeth of microphagous and macrophagous ophiuroids, and theoretically, this could also be applied to fossil brittle stars, provided their oral frame is well exposed and well enough preserved. That author showed species of asteronychids, ophiacanthids, ophiodermatids, ophiolepidids, and ophiomyxids to be microphagous feeders, and species of amphiurids, ophionereidids, ophiocomids, and ophiothricids to be macrophagous. However, Medeiros-Bergen (1996) noted that tooth type appears to be a homoplastic characteristic between ophiuroid families, implying a functional convergence of tooth stereom microstructure in feeding.

Digestive efficiency in ophiuroids is probably low (Lawrence, 1987), and regional specialisation limited. However, the selection of food is important in ophiuroids since they lack an anus. Despite this, individuals may be both generalists and specialists (Lawrence, 1987). Feeding habits are remarkably diverse. Some forms obtain nutrients by the uptake of dissolved compounds through the skin, but generally particulate food is conveyed to the mouth by the tube feet and muscular arms. Some forms may coil their arms quickly (arm-loop), and capture small active organisms, occasionally even fish. Many forms bend their arms in broad loops to transport larger chunks to the mouth. By using the tube feet, food can also be collected from the sediment surface, from the water column, or from the hooked, or sticky, mucus-lined arm spines.

The tube feet are capable of sensing extremely dilute concentrations of chemicals such as amino acids and vitamins. Most forms remain concealed during the day, hiding from diurnal predators. It is assumed that nerves beneath microscopic transparent nodules in the skeletal plates are photosensitive; some forms are known to change colour. This adjustment allows them to detect crevices in sunlight or moonlight. However, in most species colours are fixed, but occasionally pigmentation changes with growth.

Ophiuroid body plan may often correspond more closely to substrate type than to phylogenetic affinity or distribution. For instance, amphiurids have soft discs and long arms for burrowing into soft sediment, while some burrowing, unrelated ophiocomids appear very similar. Epizoic forms on soft coral and sponges have hooked spines used for clinging.

Predation

In Recent settings, hermit crabs, mantis shrimp, sea stars, other ophiuroids, and fish have been cited as predators. For European seas, Sköld & Rosenberg (1996) recorded the highest incidence of damaged arms in infaunal suspension- and deposit-feeding ophiuroids (amphiurids), and suggested selective cropping of arms by demersal fish.

However, not only predation, also physical changes induced by storms may lead to sublethal damage in ophiuroid arms (compare Aronson, 1993). Aronson & Harms (1985) measured predation pressure as a determinant of ophiuroid abundance in shallow marine communities in the Caribbean, while Aronson (1992) noted that the Mesozoic decline of brittle star beds documented in the fossil record, was associated with the diversification of predators adapted to eat skeletonised prey, including teleost fish, neoselachian sharks, and decapod crustaceans. That author used the frequency of sublethal damage to ophiuroids as a predation index. In general, predation pressure was hypothesised to have been low on ancient ophiuroid populations, but this increased after the Jurassic (Aronson, 1987, 1989a-b, 1991). In short, predators appear to have eliminated populations of epifaunal suspension feeders from shallow, soft-substrate marine environments beginning in the Mesozoic. However, Aronson et al. (1997) documented an ecological anomaly for the Upper Eocene of Antarctica, where both dense ophiuroid beds and isocrinid crinoids occur in shallow-water settings, with low predation intensity. These authors suggested changes in temperature and productivity to account for this return to a Palaeozoic type of community structure.

In general, dense populations of suspension-feeding echinoderms can only exist if predation pressure is low (Fujita, 1992), if rates of sediment resuspension are low, and flux of particulate organic matter is high.

Preliminary data on ophiuroid palaeoecology were presented by Jagt (1999c); these are here complemented. However, it should be noted that inferring the modes of life of fossil ophiuroids cannot be but in general terms (compare also C.A. Meyer, 1984). Only rarely are more or less complete specimens found, showing all features of disc plating, oral frame structure, arm structure, and arm spines. Such occurrences are examples of obrution through storms (compare C.A. Meyer, 1988). Dense aggregations may be considered to represent pioneer communities of opportunistic species in unstable environments, while a limited diversity may be seen as an expression of biotopes subject to important changes in physical and/or chemical conditions.

A: Euryalida

In euryalids, thick skin (naked or with closely set granules) covers disc and arms, and the calcareous body armature is reduced. Occasionally, forms may have distinct disc scales. Ventral and dorsal arm plates are lacking or rudimentary at best, and are also covered by thick skin, while lateral arm plates are small and confined to the lower (= ventral) side of the arms. Euryalids possess unique hook-like arm spines, and have the ability to throw their arms into tight vertical coils (Hendler & Miller, 1984).

Euryalids are mostly found attached to corals and other coelenterates. The coiling of arms is made possible by the streptospondyline type of vertebra, in which the articulation is characterised by hourglass-shaped articulatory pegs. Like crinoids, they depend on a current flow for feeding, the oral side facing the current.

Gorgonocephalids are associated with hard and soft corals and columns of stalked crinoids, are slow moving and may be more active at night, clinging to gorgonians, etc., digesting copepods and other planktonic material, which is caught by smooth, pointed tube feet. *Astrophyton muricatum* is a nocturnal suspension feeder (Hendler, 1982b; Hendler et al., 1995), feeding mostly on copepods.

Astronychids have long and slender, unbranched arms with a thick skin cover. Fujita & Ohta (1988) observed extant *Asteronyx loveni* clinging to gorgonians and pennatulids, and with stomach contents comprising crustacean fragments, polychaetes, sediment particles and flocculent material. Simple-armed *Asteroporpa annulata* may be a good analogue for species of *Trichaster* recognised in the present study from the Meerssen Member. Hendler & Miller (1984) reported individuals of that species perched on scleractinians at night and during the day, mostly in a suspension-feeding posture during the night. Its diet consisted mostly of pelagic organisms, mainly copepods, and other prey. Despite its heavy armour, predation appears to be fairly high (20% of specimens examined).

Kutscher & Jagt (2000) reassigned *Asteronyx*? *ornatus* to the genus *Trichaster*, a euryalid with moderately large discs and stout, simple or branched arms. In addition to *Trichaster*? *ornatus*, these authors recognised another, undescribed form (*T*.? sp.). Most conspicuous in these are the coarse granules on the lateral surfaces of vertebrae, which represent the attachment sites of small platelets once embedded in the thick skin. *Trichaster*? sp. may ultimately prove to represent either the juvenile stage of *T*.? *ornatus*, or alternatively, a distinct morphotype. Vertebrae of this type, the only remains of this form known to date, range throughout the Late Cretaceous sequence, but have not yet been recognised in samples of Early Palaeocene age. This form may have clung to bryozoans, octocorals, and/or (large) scleractinian corals.

B: Ophiomyxina

Thick, naked skin covers both arms and disc, and conceals exceedingly brittle and comparatively poorly developed scales and plates. In general, arm spines are stout and erect. Byrne & Hendler (1988) pointed out that two strata of connective tissue obscured the underlying skeleton in ophiomyxid arms, and noted an inverse relationship between the thickness of the connective tissues and size of the skeletal elements, with these tissues playing a supportive role. These authors also documented a continued decrease in the amount of skeletal material characterising the genera *Ophiomyxa*, *Ophiobyrsa*, and *Ophiogeron*.

Extant *Ophiomyxa flaccida* is found in reef habitats as well as in seagrass beds, but may actually be associated with many substrate types. Stomach contents on record include sponges, algae, and detritus. Arms stiffen when disturbed, and individuals are active at night. Another Recent form, *Ophioscolex glacialis*, lives on muddy bottoms, in Arctic and Boreal waters.

Three forms, all known from the Meerssen Member, but in small numbers of dissociated arm plates only, are placed here. One of these, *Ophiomyxa*? *rhipidata*, has fan-shaped spines, and may have been able to swim over short stretches (? escape from predators). Of *O*.? *jekerica* only the highly distinctive vertebrae are known, while of the third species, *Ophioscolex*? *cretaceus*, the Meerssen Member has yielded a limited number of lateral arm plates. All these forms may have lived in between bryozoan ‘thickets’, or amongst scleractinian corals, probably partially hidden beneath rubble, and emerged only at night to feed.

C: Ophiocanthidae

Ophiacanthid discs have a close-set cover of small scales, with spines, stumps or granules. Arm spines are erect, slender and often long. Forms referred here are often found clinging to corals, other coelenterates and sponges, with arms able to coil ventrally. Most probably, these are rather sluggish detritus feeders.

Fossil species referred to the Ophiacanthidae generally occur only as dissociated ossicles in the study area, although at least one more or less complete specimen with arms attached is known from the basal Gronsveld Member (Jagt et al., 1998; Kutscher & Jagt, 2000). From the Meerssen Member two forms are known, *Ophiacantha*? *danica* and *Ophioplinthaca*? *fuerstenbergii*(?), while from the overlying lower Geulhem Member, a single apparently closely related species, *Ophiacantha*? *striata*, is recorded. The type material of that species is from the Lower Maastrichtian of Rügen (northeast Germany), but the Geulhem material appears to be conspecific, and would thus represent one of the few forms crossing the K/T boundary. As in the case of euryalids, accompanying faunal elements include medium- to large-sized bryozoan colonies, octocorals and sponges, to which these ophiuroids may have clung.

D: Ophiuridae

Discs are mostly scale covered, generally naked, arms often short or of medium length with closely appressed, small and more or less rudimentary spines. Extant *Ophiura* is found on hard (sandy) and soft, muddy bottoms, moving about freely and not buried. These ophiuroids acquire food by placing themselves over it or grabbing it by extending their arms. Items taken include worms, crustaceans, molluscs, other echinoderms, and detritus.

From the Meerssen Member, at least three species are known of these conspicuously plated brittle stars. These include one of the commoner ophiuroids in the type Maastrichtian, *Felderophiura vanderhami*, with highly distinctive dorsal disc plating. A slightly smaller species, *Ophiocten*? *yvonnae*, occurs in almost equal numbers, and is often associated with *F. vanderhami*. Of the third, tentatively assigned to *Stegophiura*? *hagenowi*, only a few isolated arm and disc plates are known so far.

The two first-named forms occur quite commonly at certain levels in the Meerssen Member, and appear to represent former dense aggregations. However, most material has been collected from bulk samples taken from thick fossil hash levels, and a certain amount of man-induced breakage must be expected to have occurred during sample preparation. Only once have specimens of *F. vanderhami* been found on several bedding planes in the upper Meerssen Member (ENCI-Maastricht BV); these may represent individuals smothered by temporary storms. A single specimen (see Kutscher & Jagt, 2000) of *F. vanderhami*, embedded vertically in the fairly coarse-grained sediment, has two arms lodged firmly in the substrate, curved in different directions. The remaining arms, broken off, probably emerged from the substrate. This position either represents a suspension-feeding mode for this species, or alternatively, illustrated escape behaviour after being buried by sediment.

E: Amphiuridae

Amphiurids generally have distinctly scaled, tiny discs, which occasionally bear spines. Arms are mostly very long, slender and flexible with muted colour patterns, and spines short and erect. Most amphiurids live buried at depths of c. 10 cm, with only the tips of arms protruding through mucus-lined channels, catching detritus, but also small animals such as worms and juvenile molluscs. Burrows are ventilated by undulations of the arms. Sometimes many individuals may form webs across the seafloor. Most extant forms live on muddy bottoms, some also under rocks in low water, but, unlike other ophiuroids, they do not move about freely. Regularly, amphiurids cast off the discs voluntarily and gradually regenerate these.

Despite their preferred habitat, amphiurids are rare fossils. The fairly coarse-grained biocalcarenites of the Meerssen and Geulhem members would have provided ample opportunities for amphiurids, but only from the former unit are they known, and in small numbers only. The most distinctive species is *Deckersamphiura inusitata*, in which the disc shows unusually large plates; estimated arm length exceeds disc diameter at least three or four times.

F: Ophiothricidae

Ophiothricid discs usually have well-developed scales, but these are more or less concealed by small spines or thorny stumps. Arms have many, long, erect spines, which are generally distinctly thorny and of a glassy appearance. This family mostly comprises tropical representatives, which live attached to sponges, gorgonians, comatulid crinoids etc., and suspension feed. Raised surfaces (i.e. topographical highs) appear to confer an advantage to suspension-feeding *Ophiothrix* (Aronson & Harms, 1985). Hendler (1984a) noted that the extant *Ophiothrix lineata*, unlike other congeners, was a non-selective deposit feeder, feeding on detrital particles while adhering to a sponge, and cleaning it (mutualistic relationship).

Extant *Ophiothrix fragilis* lives on hard bottoms, in empty shells, amongst serpulids and also under rocks on the shore, hiding itself in small cavities, and known to feed on worms and crustaceans, but also on small shells, other echinoderms, foraminifera and ascidians, occasionally even detritus. This and closely related species occur in shallow waters, close to the shore.

Ophiothricids are amongst the most fragile of ophiuroids, which would explain their scarcity in the fossil record. From the lower Geulhem Member, only dissociated arm ossicles are known of *Ophiothrix*? *cristata*.

G: Ophiocomidae

Ophiocomids comprise relatively large and conspicuously coloured forms, mostly with discs covered in granules which conceal both scales and radial shields. Ventral and dorsal arm plates are well developed, and spines generally are solid and erect. The extant genus *Ophiocoma* is highly typical of littoral settings in tropical seas. The Ophiocomidae is the dominant family of coral-reef ophiuroids (Sloan et al., 1979), and all species are cryptic.

Ophiocomids occur in all reef zones, seagrass beds and mangroves, and are particularly common in rubble (*Ophiocoma echinata*; see Hendler et al., 1995), the stomach contents mostly consisting of sand and pieces of fleshy algae. Arms are raised and curled, probably for suspension feeding.

Hendler & Byrne (1987) reported on a photoreceptor system in the dermis of dorsal arm plates of extant *Ophiocoma wendti*. A closely comparable stereom microstructure characterises the dorsal arm plates of the ophiurid *Stegophiura*? *hagenowi* (see Kutscher & Jagt, 2000).

Although ossicles of Late Cretaceous and Early Palaeogene species referred to this family are not particular stout, they are a common element in ophiuroid faunules. Only disc fragments and fragmentary arms, occasionally preserving spines are known, as well as numerous dissociated ossicles. From the Meerssen Member three species are known to date (*Ophiarachna*? *martinblomi*, *Ophiocoma*? *rasmusseni*, and *O.*? *senonensis*). The two last-named extend upwards into the Geulhem Member, and are amongst the few species crossing the K/T boundary, suggesting similar habitats for ophiocomids.

H: Ophiodermatidae

Stout forms, generally with close-set granules concealing the fine scales of both sides of the disc, and arms appearing smooth, with small and closely appressed spines. For the extant, shallow-water species *Ophioderma appressum*, Hendler et al. (1995) recorded reef and seagrass habitats from the intertidal to the forereef slopes, under coral rubble and in branching and foliose corals. Its diet includes plant material, but it may also scavenge at night on fish faeces. The adhesive tube feet enable this species to handle food, and it is exceedingly quick when pursued.

The stomach contents of extant *O. brevispinum* include small peracarid and brachyuran crustaceans, worms, sponges, debris, and algae (Hendler, 1982a). Many species of Recent ophiodermatids are carnivores.

On account of the stout structure of arms and discs, the ophiodermatid *Ophiotitanos serrata* (previously assigned to the Ophiolepididae) is well represented in ophiuroid faunules of both the Meerssen and Geulhem members. Of note is that these forms generally have much thicker lateral arm plates than material from white chalk facies (Zeven Wegen, Vijlen, and Lixhe members), reflecting adaptations to high-energy environments. *O. serrata* also crosses the K/T boundary in the area.

I: Ophiolepididae

Like members of the foregoing family, ophiolepidids are well known from fossil record, owing to the fact that their discs and arms generally are heavy plated. In species of *Ophiomusium*, the arms are stiff and lack ventral and dorsal arm plates for most of their length. Tentacle pores are restricted to the proximalmost arm joints, and arm spines are generally small and more or less rudimentary.

On account of their solid arm structure, relatively numerous fragmentary arms are known, especially of species referred to the 'lump' genus *Ophiomusium*. This shows a curious distribution pattern within the Maastricht Formation. *Ophiomusium granulosum* (= *O. subcylindricum*) ranges from the base of the Valkenburg Member to the base of the Emael Member, then disappears, only to reappear during deposition of the Geulhem Member, but being quite rare in that unit. In the Nekum and Meerssen members another, apparently unrelated, form occurs, *Ophiomusium lux*, but this is not known to range to the very top of the Meerssen Member. Accompanying *O. granulosum* in the Geulhem Member is an ?ophiolepidid (*Mesophiomusium decipiens*), of which so far only a single arm fragment, and dissociated arm and disc ossicles have been recognised. This form, however, shows tentacle scales over the entire arm length, and thus may have occupied a different niche.

Hendler et al. (1995) recorded extant ophiolepidids from firm shell and sand bottoms or muddy sand, as well as from sandy habitats around reefs, seagrass beds, and mangroves, but also from sediment-filled crevices amongst algae, corals, and sponges.

Although assignment of fossil ophiuroids is occasionally fraught with difficulties, as witnessed by the liberal use of open nomenclature, the Late Cretaceous faunule in particular documents a remarkable diversity. All modes of life known from extant forms appear to be represented; forms clinging to coelenterates and thus occurring well above the substrate, those resting and moving about freely on the sediment surface, and those burying themselves to variable depths within the sediment. A single form, with fan-shaped spines may have been able to swim. Predation traces (i.e., sublethal damage to arms) have been noted in *Ophiacantha*? *danica*, *Felderophiura vanderhami*, *Ophiocten*? *yvonnae*, and *Ophiomusium granulosum*. However, in general such instances are rare, despite the fact that diverse faunas of teleost fish and decapod crustaceans (brachyuran crabs) are known from the same strata.

Of the seven species occurring in the Geulhem Member, four are also known from underlying strata of Maastrichtian age, and these comprise relatively stout, epibenthic forms. However, these Geulhem faunules also include small, fragile forms such as ophiacanthids, and ophiothricids, implying that the occurrence of stouter forms is not taphonomically biased. Of note is the absence of euryalids and amphiurids from the Palaeocene faunules, suggesting that objects to which members of the former could cling were missing, and that bottom conditions were less favourable for the settlement of members of the latter group.

Rasmussen (1979) noted that ophiuroid distribution across the K/T boundary in Denmark did not reveal any significant generic changes, but also pointed out that reference to extant genera of fossil species should not be taken as a strong indication of close relationship.

Echinoids (Fig. 5A-C; Tables 4, 8)

Basic morphology and food

To date, about 900 extant species of echinoid are known, which occur in a bewildering variety of shapes and sizes. The test consists of twenty columns of interlocking plates: five paired columns of radially placed ambulacral plates, alternating with five pairs of interradially placed interambulacrals. The outer test surface shows numerous knobs and tubercles carrying moveable spines and other specialised structures. 'Regular' echinoids are radially symmetrical, and have subspherical or hemispherical tests, with the mouth centrally placed on the ventral side, and the anus opposite the mouth, within a centrally placed apical system of 10 plates, five genitals alternating with five oculars. The genitals have pores (gonopores) for the passage of eggs or sperm during spawning. One genital carries the madreporite of the water vascular system. Oculars have a single tube foot, which actually is the terminal extension of the radial water vessel. During growth, plates are added to the test at the outer edge of the ocular plates, and the varied rates of plate growth between the apical system and mouth determine final test shape. 'Irregular' echinoids are bilaterally symmetrical, with the anus having migrated posteriorly, i.e. no longer within the apical system. Tests are highly variable, from flattened, to heart shaped. In 'regulars', five zones of tube feet run from the anus to the mouth. Numerous thin, extensible tube feet are used for locomotion, sensory perception, and manipulation of nearby objects. In 'irregulars' the tube feet are arranged into petals, and are used for respiration; on the oral surface numerous scattered tube feet aid in locomotion and feeding.

Suckered tube feet characteristically have an internal ring of supportive ossicles. Heart urchins (spatangoids) have penicillate tube feet for grasping sediment particles; these terminate in a radiating fringe of finger-like processes with internal supporting ossicles.

Spines occur in two sizes; primaries on large tubercles, and secondaries on

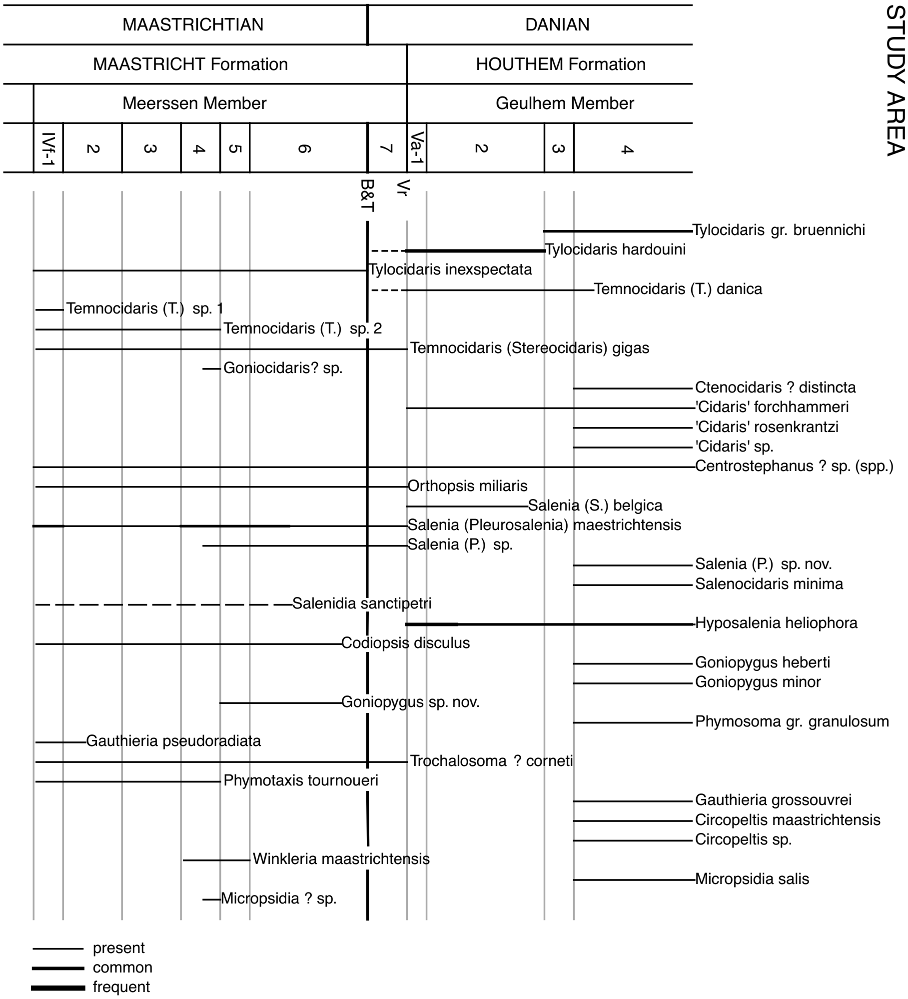


Fig. 5A. Regular echinoid distribution across the K/T boundary in the type area of the Maastrichtian (compare 5B). Abbreviations: Vr = Vroenhoven Horizon, B&T = Berg en Terblijt Horizon.

small(er) tubercles. A muscular collar connects the spine base to the smooth tubercle. Spines may be used for defence (often associated with poison sacs in deep-sea forms), and prevent structural damage (Strathmann, 1981). Some burrowing forms, such as cassiduloids, have numerous small spines shielding the test from surrounding sand and permit oxygenated water to flow around the animal. Mud-dwelling spatangoids use mucus-lined spines as a barrier and have mucus-producing spines concentrated in fascioles, which are visible as bands of minute tubercles on a naked test.

Cidaroids use spines as locomotory appendages; in many other echinoids tube feet play a more substantial role in locomotion. Numerous, pincer-like stalked pedicellariae occur in a variety of shapes and sizes, and have different functions (e.g.,

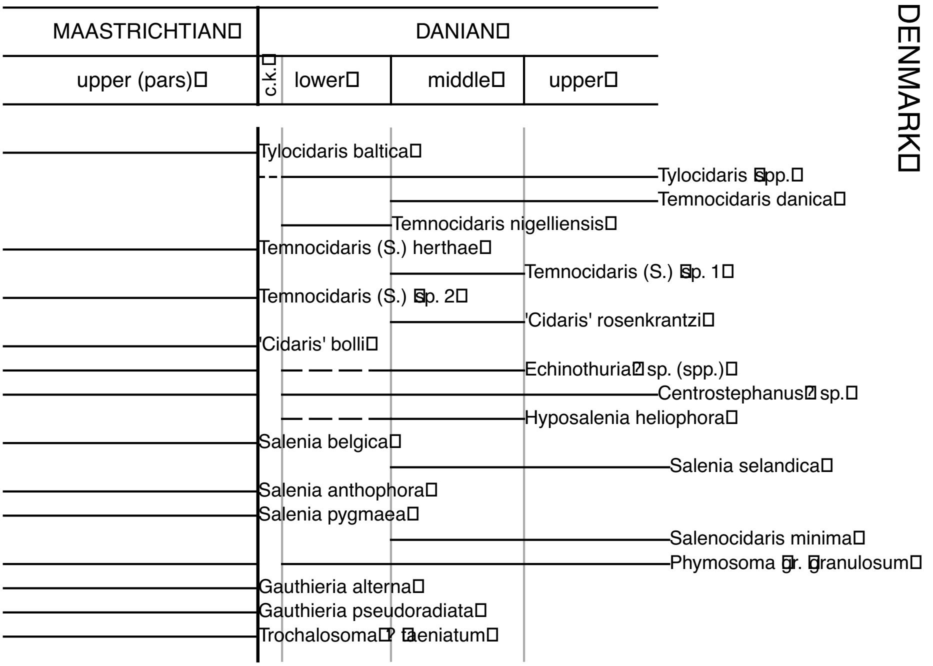


Fig. 5B. Regular echinoid distribution across the K/T boundary for the uppermost Maastrichtian and Lower to Upper Danian of Denmark (Smith & Jeffery, in press). Abbreviation: C.K. = Cerithium Kalk.

removal of debris, to discourage predators and 'fouling' organisms). Globeriferous pedicellariae are active as defensive structures, with claw-like termination, each containing a poison sac. All echinoids, except cidaroids, bear microscopic club-shaped, spine-like structures (sphaeridia) thought to act as organs of equilibrium.

In general, the test cavity is spacious, and contains all major organs, including the digestive tract of a long, tube-like intestine. Regulars have a lantern attached by muscle and connective tissue to the so-called perignathic girdle. The gonad consists of five interradially placed organs suspended within body cavity in regulars; 3 to 5 in irregulars. The genital duct connects each gonad to a genital plate in the apical system. When genital pores are open, this implies sexual maturity.

Regulars and irregulars differ considerably in ecology. Cidarids are omnivorous grazers on encrusting organisms, especially animals; they are usually cryptic, and emerge at night to feed. The long-spined, large diadematids occur in coral, sea grass, mangrove habitats, are herbivorous, but also ingest encrusting animals and even living coral. Irregulars feed on sediment, ploughing through the substrate. Sediment particles are moved to the mouth by tube feet and spines; occasionally small animals and plants are selectively ingested as well. Spatangoids collect particles from the sediment with penicillate tube feet, bound in mucus, and pass these to the mouth by ciliary tracts. Burrowing in soft sediment means that burrows need to be stabilised with mucus. Faeces and excavated particles are removed via a sanitary drain.

Many extant forms have an annual reproductive cycles; in most, fertilisation is

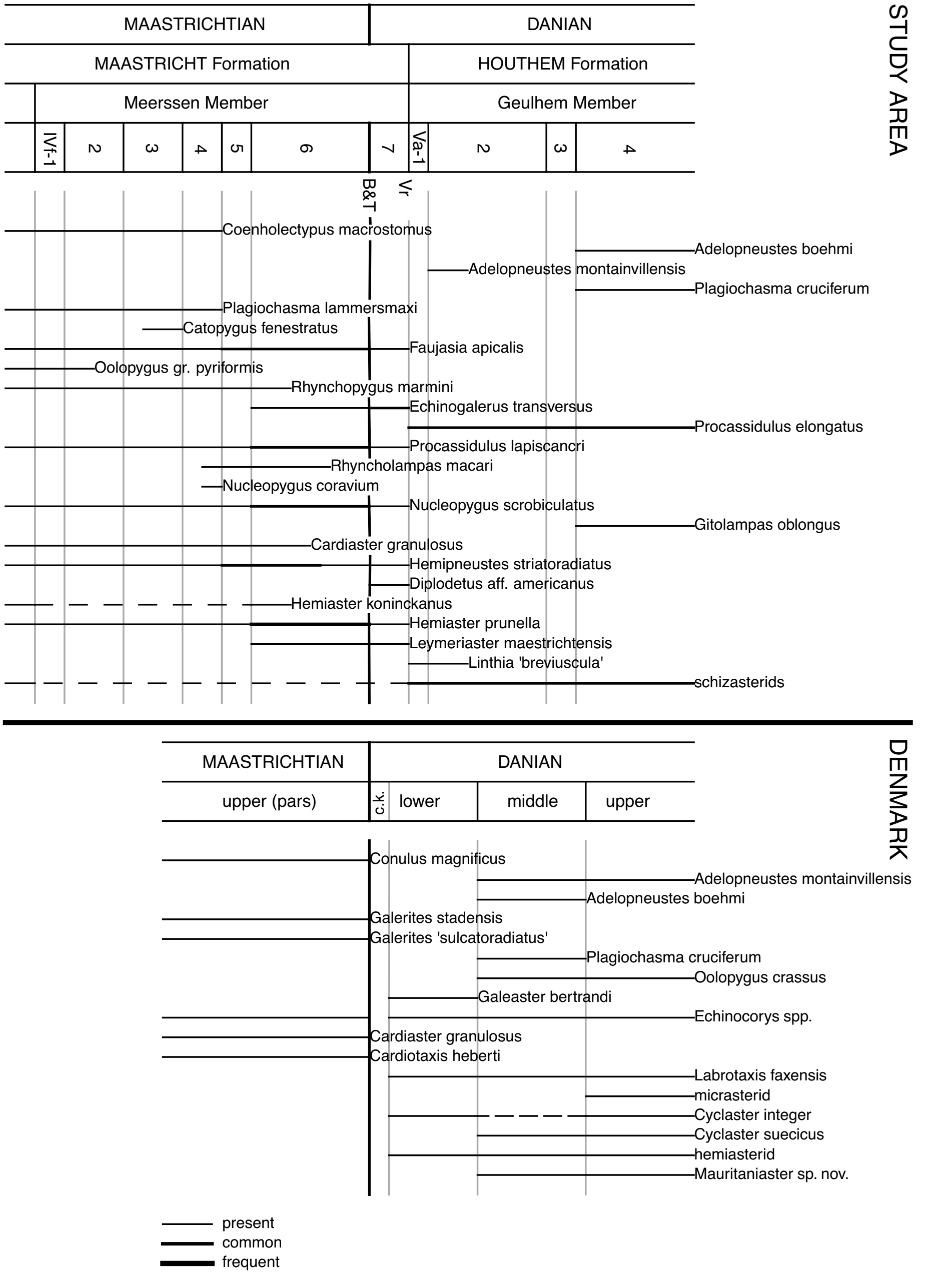


Fig. 5C. Irregular echinoid distribution across the K/T boundary in the type area of the Maastrichtian, compared to literature data for the uppermost Maastrichtian and Lower to Upper Danian of Denmark (Smith & Jeffery, in press). Abbreviations: Vr = Vroenhoven Horizon, B&T = Berg en Terblijt Horizon; C.K. = Cerithium Kalk.

external. In some species, the larval stage is reduced or suppressed, and the young are brooded on or inside a parent. Some brooders have drastic test modifications, such as pouches. Sexual dimorphism is also expressed in the size of the gonopores (see e.g., Néraudeau, 1993).

Predation

The main predators of extant echinoids are crustaceans, fish, and birds. Generally, echinoids have the capacity to heal moderate injuries, e.g. spines, and portions of test.

Taphonomy

In a series of papers, Smith (1978b, 1980a-c) demonstrated that stereom microstructure, pore structure and functional morphology of associated tube feet, as well as tubercle structure all provided important clues for palaeobiological reconstructions of fossil echinoid faunas. Numerous other studies have provided examples of the relationship between echinoid test morphology and (litho)facies, of echinoid substrate preference and biofacies distribution, of the relationship between echinoid assemblages and depth of deposition, and between echinoid distribution and relative sea level changes (see e.g., Ernst, 1970; Ernst et al., 1973; Croft & Shaak, 1985; McKinney & Zachos, 1986; Dafni, 1988; Smith, 1978a, 1984, 1988; Carter et al., 1989; Carter, 1990; Carter & Hamza, 1994; Nebelsick, 1992, 1995; Neumann, 1996; Néraudeau & Villier, 1997, and Néraudeau & Moreau, 1989).

The most detailed data on the palaeobiology of Late Cretaceous echinoids are those published by Smith (1988, 1995) and Smith et al. (1995a-b). These are used here to subdivide the various Late Cretaceous and Early Palaeocene echinoids from the Maastrichtian type area into several ecological groups.

A: Regular echinoids

All regular species are epifaunal; however, differences in skeletal morphology allow various ecological groups to be recognised, as follows:

1) Species occurring on (nearshore) hardgrounds, within the zone of active wave surge (0-5 m depth): Included here are *Codiopsis disculus* and *Phymotaxis tournoueri* (both Meerssen Member), and *Circopeltis maastrichtensis* and *C.* sp. (Geulhem Member).

These all have flat oral surfaces, enlarged phyllodes of P3/P4 type pore pairs, and typically dense or modified aboral pore pairs indicative of specialised respiratory tube feet.

In extant forms, a broad/flat base and numerous, large oral tube feet are indicative of rocky surface forms, with additional tube feet providing adhesion in turbulent environments; grazing/rasping rock surface, and feeding on filamentous or fleshy algae.

2) Species occurring on (nearshore) hardgrounds, subtidally within uppermost few metres of water column, but subject to limited wave surge only: Included here are *Goniopygus heberti*, *G. minor* (both Geulhem Member), and *G.* sp. nov. (Meerssen Member).

These species have moderately strong phyllodes, a depressed test profile with a broad, flat oral surface. On the form of the pore pairs, these may have had well-developed aboral respiratory tube feet, showing them to have been adapted to life in shallow, warm waters. However, in view of rather poor phyllode development, these species did probably not occur in fully exposed habitats; they were epifaunal grazers.

3) Shallow-water species (2-10 m), occurring in more protected environments, within wave base, but not subject to strong currents and/or wave surge: Included here are *Orthopsis miliaris*, *Gauthieria pseudoradiata*, *Trochalosoma*? *corneti*, *Winkleria maastrichtensis* (all Meerssen Member), and *Phymosoma* gr. *granulosum*, and *G. grossouvrei* (both Geulhem Member).

All have a depressed test profile, slight phyllode development, in some forms also increased densities of aboral pore pairs, possibly specialised for gaseous exchange. Spines are moderate to long, cylindrical or flattened.

Modern analogues are predominantly grazers, feeding on encrusting or boring algae, or plants. Those lacking phyllodes and with sunken peristomes would have been grazers, the others raspers/browsers. These may be expected to have lived on or close to firm bottoms, i.e. rocky knolls or stabilised substrates.

Also referred here is *Centrostephanus*? sp. (both in Meerssen and Geulhem members), a diadematid with long spines, which probably lived amongst algal thickets in a reef-flat environment.

Cidarids probably belonged here as well, all being clearly shallow-water forms, with globular test profiles, and all lacking phyllodes; pore pairs are either nonconjugate or weakly conjugate; stout spines used to deter predators, as well as in locomotion (*Tylocidaris inexspectata*, *Temnocidaris (T.)* sp. 1, *T. (T.)* sp. 2, *T. (Stereocidaris) gigas*, *T. (S.)* sp. 2, *Goniocidaris*? sp., all Meerssen Member; and *Tylocidaris* gr. *bruennichi*, *T. hardouini*, *Temnocidaris (T.) danica*, *Ctenocidaris*? *distincta*, *Cidaris*? *forchhammeri*, *C.*? *rosenkrantzi*, *C.*? sp., all Geulhem Member). These species were probably confined to the most protected of shallow-water habitats, possibly co-occurring with e.g., *Centrostephanus*. Extant cidarids and diadematids are generalist feeders (omnivores), preferentially grazing on animals and plants, but they may also take up bottom material.

4) Species occurring on protected subtidal (> 10 m), soft-bottom substrates, below active wave base: Included here are *Salenia (Pleurosalenia) maestrichtensis*, *S. (P.)* sp., *Salenidia (Platysalenia?) sanctipetri* (all Meerssen Member), and *Salenia (S.) belgica*, *S. (Pleurosalenia)* sp. nov., *Salenocidaris minima*, and *Hyposalenia heliophora* (all Geulhem Member).

All have a more or less depressed test profile, and lack specialised respiratory tube feet, and may be considered epifaunal generalists, i.e. predominantly herbivorous browsers, cropping algae, and taking loose bottom material. Like cidarids, saleniids have relatively large interambulacral spines, to deter predators. Extant saleniids are generalised omnivores, not specialised for rasping, and take in a variety of food.

Referred here are also *Micropsidia*? sp. (Meerssen Member), and *Thylechinus* sp. nov., and *Micropsidia salis* (both Geulhem Member), which probably had simple, suckerless aboral tube feet, but much smaller, and more numerous spines, and a globular test profile. These may have lived amongst algal strands, feeding on these.

B: Irregular echinoids

5) Infaunal, medium-fine sandgrade burrowers: Included here are *Hemiaster koninckanus*, and *H. prunella* (both Meerssen Member).

Both have globular tests with no real frontal sulcus; pores are poorly differentiated, but adapical funnel-building tube feet may have been present in in amb III, as well as subanally. These species appear to have lived in relatively poorly permeable, rather fine-grained sediment; in such an environment an apical funnel is required, as is an aboral fasciole. The lack of specialisation of the frontal groove suggests that all food particles came from the sediment, and not from sediment/water interface (i.e. selective deposit feeders with penicillate tube feet around mouth to pick up food particles from sediment of burrow floor).

6) Infaunal, medium-fine, sandgrade burrowers, selective deposit feeders: Included here are *Diplodetus* aff. *americanus*, *Leymeriaster maestrichtensis* (both Meerssen Member), and *Linthia*? sp., '*Linthia breviuscula*', and *Paraster sindensis* (all Geulhem Member).

Characterising this, admittedly heterogeneous, group is a slight frontal sulcus; pores in ambulacrum III bore presumably funnel-building tube feet, and enlarged pores near peristome and subanally suggest penicillate tube feet, and funnel-building tube feet, respectively. *Leymeriaster* has a well-developed aboral fasciole, the schizasterids an additional lateroanal fasciole, while *Diplodetus* lacks a fasciole, but dense aboral miliaries would probably have been able to produce a mucous layer. Perhaps all species relied primarily on selective particle feeding, but the sunken ambulacrum suggests part of the diet reached the mouth along that way. All species have well-developed petals, suggesting them to be relatively shallow-water forms.

7) Shallow infaunal/semi-infaunal ploughers in stable, unconsolidated bottoms; selective deposit feeders harvesting sediment at or close to water/sediment interface: Included here are *Hemipneustes striatoradiatus* and *Cardiaster granulosus* (both Meerssen Member).

The former species has a well-developed frontal groove with specialised grill spines and tube feet; sediment entered the groove adapically and was passed down to the mouth via mucous string running down ambulacrum III. There is no protection for the tube feet in the asymmetric petals; the surrounding sediment may be assumed to have been highly permeable, i.e. this species lived only shallowly buried. The peristome is surrounded by a small number of large, distinct isopores showing that the associated tube feet gathered food, and were probably penicillate. Ambulacrum III is sunken; pores are indicative of small, sensory tube feet. Tubercles bordering the groove supported spines for an arch across ambulacrum III.

The second species is comparable, except that is has a much more flattened test, a well-developed marginal fasciole, and enlarged adoral tubercles, lining ambulacrum III and the apical disc. Food was probably acquired mostly through ambulacrum III, despite the fact that phyllode tube feet are found near the peristome.

8) Mobile, highly permeable, unconsolidated, medium-coarse sands; infaunal bulk sediment swallowers: Included here are *Nucleopygus coravium*, *N. scrobiculatus*, *Catopygus fenestratus* (f. *suborbicularis*, f. *subcircularis*), *Rhyncholampas macari*, *Oolopygus* gr. *pyriformis*, *Rhynchopygus marmini*, *Procassidulus lapiscancri* (all Meerssen Member), and *P. elongatus* (Geulhem Member).

All species have more or less well-developed petals, and would have had thin-walled tube feet specialised for gaseous exchange. Adorally, pores crowd in small phyllodes (tube feet small, suckered ?), with moderately well-developed bourrelets (for manipulating sand grains); a medium- to large-sized periproct and an anal sulcus suggest that much faecal material was produced. The bilaterally symmetric arrangement of oral tubercles in most species suggest unidirectional movement. The dense adoral tuberculation is indicative of close-set spine canopy allowing these forms to burrow in medium- to coarse-grained sediments.

Also placed here are *Plagiochasma lammersmaxi*, *Echinogalerus transversus*, and *E.* sp. 1 (all Meerssen Member), and *Gitolampas oblongus*, and *Plagiochasma cruciferum* (both Geulhem Member), but the plagiochasmids differ in having a clearly depressed, large peristome, of an irregular outline, and lacking buccal slits. The size of the periproct in these forms suggest them to have been bulk sediment swallowers.

9) Mobile, permeable unconsolidated sands: selective infaunal deposit feeders: Included here is *Faujasia apicalis* (Meerssen Member).

This has a small peristome, with moderately well-developed phyllodes, slight bourrelet development, and a rather small, posteriorly placed periproct, as well as dense, uniform aboral tuberculation; petals moderately large; this species could probably have burrowed only into permeable sands, so as to ensure a water flow over well-developed petals.

10) Infaunal grazers/detritivores, selective particle feeders, within coarse permeable sands in 0-10 m depths: Included here are *Coenholectypus macrostomus* (Meerssen Member), and *Adelopneustes boehmi*, and *A. montainvillensis* (both Geulhem Member).

These are broad-based tests, with a low ambitus and a low-domed apical surface, for stability in unconsolidated sediment. Peristome large, perignathic girdle, active protrusible lantern. Periproct large (i.e., sediment-rich diet); ambulacral pores uniform, associated tube feet cylindrical and with suckered disc. No concentrations of tube feet near peristome, i.e. dependent on lantern for food gathering. No respiratory tube feet. Apical tuberculation dense, allowing burrowing in sands, but only vertically.

Asteroids (Fig. 6A-B; Tables 5, 9)

Basic morphology and food

Extant asteroids, some 1800 species of which are known to date, range in overall size from 10 mm to more than 1 m. Ancient starfish are much rarer; for these to fossilise they would have to be rapidly buried, and physical reworking (bioturbation) would have to be very limited to absent. Moreover, upon death asteroid bodies commonly collapse, thus distorting ossicular relationships. This explains why fossil asteroids are difficult to study, especially where ambulacral structure is concerned. All this means that the fossil record of star fish is, as Blake (1989, p. 182) put it, '...... unlikely to be representative of original importance.'

Homoeomorphy amongst asteroids is common, suggesting a strong adaptation to environment. With the exception of sphaerasterids, all asteroids have flexible body walls. Shallow-water forms tend to be stoutly constructed for protection, and are small-particle feeders. Blake (1996b) remarked that ambulacrals and adambulacrals

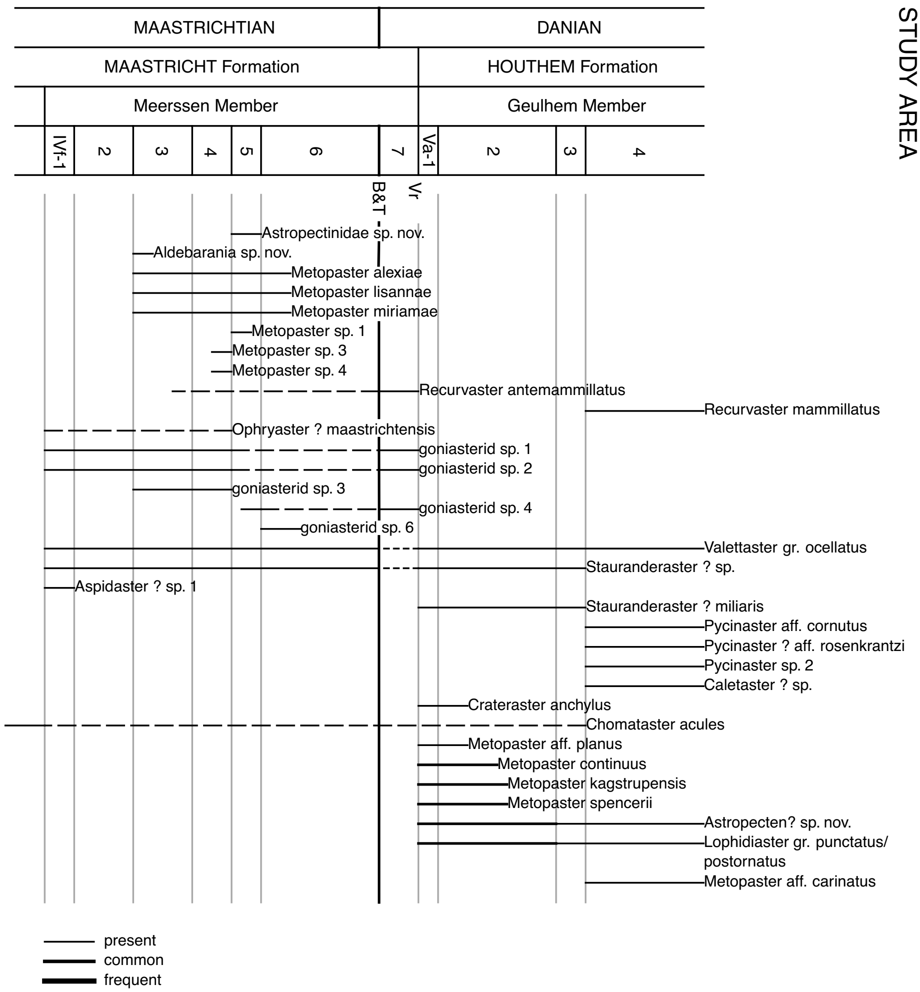


Fig. 6A. Asteroid distribution across the K/T boundary in the type area of the Maastrichtian (compare 6B). Abbreviations: Vr = Vroenhoven Horizon, B&T = Berg en Terblijt Horizon.

have complexly arranged articular structures, and that both provide a fair amount of information on the taxonomic position of the animal involved and on its mode of life, but strangely enough these ossicle types have not been commonly recognised in sediment samples.

The paucity of asteroids in the fossil record could well be primary. Extant species are widely distributed in all seas, but usually are not abundant where they occur. However, there are also important preservational properties to be considered. Ossicles are not fused, and upon death these become rapidly dispersed; subsequent scavenging and predation make matters worse still. There is often also recrystallisation, especially in the coarse-grained sediment types, which tends to obliterate surface details of ossicles.

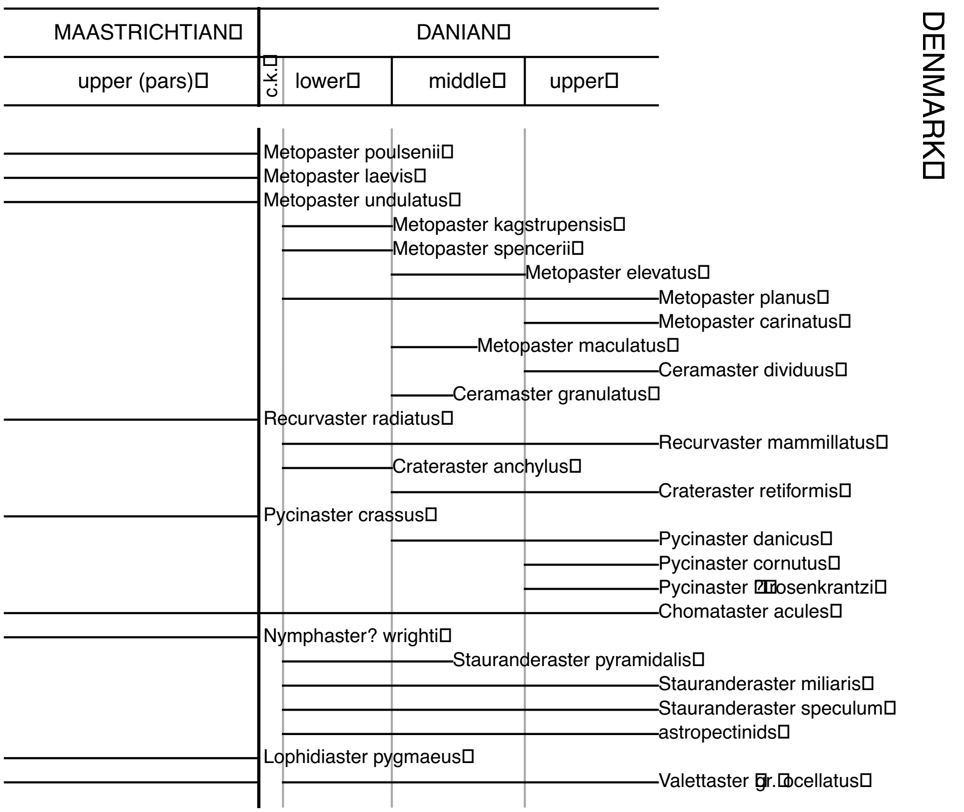


Fig. 6B. Asteroid distribution across the K/T boundary for the uppermost Maastrichtian and Lower to Upper Danian of Denmark (Rasmussen, 1950, 1972). Abbreviation: C.K. = Cerithium Kalk.

Papulae in living animals are transparent, retractable evaginations of the body cavity; these provide surface for respiratory gas exchange. Typically, asteroids have an array of spines, tubercles, and granules attached to the underlying skeletal plates, and occasionally spinelet-covered paxillae. The lower surface shows a double series of ambulacral ossicles united by muscles and connective tissue, which form the ambulacral groove. From the central arm furrow project two series of tube feet, suckered or not, one foot between each successive pair of ambulacrals, and a terminal tube foot under the ocular plate, which contains light-sensitive cells. The tube feet can be retracted into the furrow, which may be protected by the moveable spines of the ambulacrals.

Many forms (e.g., goniasterids, astropectinids) have distinct, well-developed marginal ossicles, and additional ossicles arranged in a reticulate, imbricate, or tessellate pattern. Connective tissue and a series of circular and longitudinal muscles allows an asteroid to change the shape of its arms. The centrally placed mouth is surrounded by five, multiplated triangular jaws. The digestive tract is generally well differentiated, with in many species a two-chambered stomach, intestine, rectal ceca, and paired pyloric caeca, secretory-absorptive organs which fill the large body cavity within each arm. Here the gonads also occupy a prominent position.

The general body form is stellate, the number of arms usually five. Some are even near-spherical (some valvatidans, fossil and extant; see e.g. Blake, 1984a) in shape, but multiarmed species are also known, from the fossil record as well (Blake & Guensburg, 1989). The variation in body form is linked with the length and width of the arms; the ratio of interradius length (r) to arm length (R) is highly variable. Since pentagonal (i.e., armless) forms are a minor constituent in asteroid faunas only, free arms appear to be important, in their primary roles of locomotion and feeding. For locomotion, asteroids depend on their tube feet, which are either suckered or not. Suckers allow them to live in high-energy environments, and have a major role in feeding.

Carnivorous species prey on sponges, molluscs, crabs, corals, worms and other echinoderms, and are even known to be cannibalistic. Some forms scavenge on decaying fish and invertebrates. Others are deposit feeders swallowing mud, while suspension feeders take prey and food particles from the water column.

In asteroids, feeding is greatly affected by the absence of arms that are capable of rapid movement or are appropriate for suspension feeding, on account of the skeletal support being within the body wall, rather than internally. Asteroids must move about to obtain food, and an optimal foraging behaviour is an important aspect of their feeding biology. The switch to macroprey meant a major evolutionary step, and bulk sediment ingestion was abandoned entirely.

Astropectinids primarily ingest macroprey, still involving intraoral feeding but now taking food of higher nutritive quality. These asteroids do not need suckered tube feet, since they restrict themselves to feeding on prey associated with particulate substrates. Tube feet are used to push food into the mouth, with some size selection taking place. Food taken from rocky substrates means that suckered tube feet are needed; these also allow position in currents to be maintained.

Another evolutionary step was extraoral feeding by stomach extrusion; this opened up many new food resources. Extraoral feeding occurs in advanced groups (Valvatida, Spinulosida, Forcipulatida), and these species occur in high-energy settings, where paxillosidans generally do not. The advances over intraoral feeding are immense: asteriids are able to feed on large and well-protected prey such as bivalves. Similar behaviour has been documented from an Ordovician species (Blake & Guensburg, 1994). In addition, bacterial films, encrusting organismsm, corals or echinoderms, have become food items. Valvatidans dominate tropical, shallow-water asteroid faunas where predation is high.

Asteroids do not need to move about rapidly, in view of the required type of food and the method of capture.

Predation

Like ophiuroids and crinoids, asteroids can regenerate well and autotomy is protective, as of course are regenerative abilities. Neumann (in press, and references therein) recorded a few examples of predation (tooth marks) on Late Cretaceous goniasterids from northern Germany.

Taphonomy

In view of the fact that asteroid ossicles are loosely bound during life, and upon death become rapidly dispersed, more or less complete individuals are rare, unless these are rapidly buried, and not exhumed during subsequent bioturbation of the sediment, or by scavenging. Gale (1987a) and Breton (1992) noted that normally Late Cretaceous asteroids are known only from isolated ossicles, with the comparatively large and stout marginals well represented. In fact, current classificatory schemes of Late Cretaceous goniasterids rely heavily on marginal ossicle morphology. This is of course practical, since it allows species to be identified even in the field. However, focusing on marginals alone means that other ossicle types, and ambulacrals and adambulacrals in particular, are virtually neglected.

In the northwest European white chalk facies asteroids occur roughly in three modes of preservation:

as more or less completely preserved individuals, with or without granules, spines, and/or pedicellariae;

in skeletal concentrations, with two subtypes: all ossicles represented originate in a single species (either of one or more individuals), or ossicle types can be demonstrated to belong to a suite of species.

The former was interpreted by Gale (1987a) as representing accumulation after spawning, the latter as faecal waste (coprolites) of predators feeding on an array of asteroid taxa.

In the extended Maastrichtian type area, articulated remains of asteroids are extremely rare. Most finds on record to date originate from the white chalk facies represented by the Zeven Wegen and Vijlen members, but the Emael, Nekum, and Meerssen members have now also yielded fragmentary remains as well as superbly preserved astropectinids. Such finds allow the numerous dissociated ossicles to be referred to species with confidence, and naturally generic assignments of these are more reliable. Blake (1989) noted that higher-energy habitats were not conducive to asteroid preservation.

It has become apparent that asteroid diversity throughout the Cretaceous-Palaeocene sequence was fairly high. Of necessity, the taxonomic framework (Jagt, 2000b) is based almost exclusively on marginal ossicles. Assignment to the various families is, with few exceptions, relatively straightforward, which in turn allows some general remarks about the palaeobiology of these asteroids to be made. Although many asteroids are feeding generalists, Blake's (1990b) overview of asteroid life habits, functional morphology, and phylogeny can be applied, with caution, to fossil starfish. After all, 'modern' asteroids (i.e. the Neoasteroidea of Gale, 1987c) diversified early, and all groups are known from the Early Jurassic onwards (Blake, 1984b, 1986, 1987, 1990a, 1993, 1996a).

A: Forcipulatida

The only forcipulatidan family represented in the Late Cretaceous of the study area is the Asteriidae, which are known from the Zeven Wegen and Vijlen members only, and although they do not feature in the K/T boundary discussion they are here briefly discussed.

Asteriids are offensive specialists, typical predators on sessile or slow-moving, armoured macroinvertebrates, epifaunal on hard or particulate substrates; rare in shallow, warmer water. Defence includes 3-element pedicellariae, which are also used to grab food, and body armour. Specialisation allows protective aboral armour, which in turn allows living in higher-energy settings. Asteriids are flexible on account of small discs and numerous relatively small, imbricated ossicles.

Fossil asteriids have been recorded from much shallower settings than extant taxa (Blake, 1990b; Blake & Peterson, 1993; Breton, 1997a). They appear to be well represented in the fossil record, but the small-sized isolated ossicles are highly susceptible to taphonomic alteration (Blake et al., 1996). *Afraster scalariformis* from the Coniacian of Angola was found associated with small ostreid bivalves, which might well represents its prey (Blake et al., 1996).

B: Valvatida

To this order belongs the family Goniasteridae, representatives of which are common in Upper Cretaceous and Lower Palaeocene strata throughout northwest Europe. Valvatidans are defensive, epifaunal specialists with heavily armoured skeletons, occurring over a broad depth range. Food taken varies, but most taxa rely on smaller particles from the substrate or on colonial prey; they are most common in shallow-water, tropical habitats.

All valvatidans use adambulacral and jaw ossicles to protect ambulacral and gut tissues by closing the furrow; many have stout skeletons and thickened dermal tissues. Stout, angular, closely spaced spines as well as abundant granules provide additional protection. The sturdy construction probably prevented valvatidans from becoming predators of larger solitary invertebrates.

The protective trend is strongest in the families Sphaerasteridae and Stauranderasteridae (Blake, 1987). The former, characterised by a semi-rigid dome-shaped skeleton, might represent a polyphyletic group. Hess (1994), in describing the Jurassic *Testudinaster peregrinus*, pointed out that it was still uncertain whether its skeletal buildup was convergence or an indication of true phylogenetic relationship.

Valvatidans account for over 60% of all extant asteroids, and also tend to predominate in Late Cretaceous faunas (Blake & Reid, 1998).

Both in the Meerssen and Geulhem members, valvatidan asteroids form the bulk of the asteroid faunas, in number of species as well as in number of individuals. Typical, short-lived(?) offshoots of the main *Metopaster parkinsoni* lineage, in the former unit are *Metopaster alexiae*, *M. lisannae*, and *M. miriamae*. Many European goniasterids are closely related, and heterochrony has been considered an important evolutionary mechanism (Breton, 1992, 1997b), the most convincing example of which is the peramorphocline *Metopaster parkinsoni—M. loirensis—M. trichilae—M. chilipora—M. hypertelicus* from the Cenomanian to Upper Campanian of France. This cline developed irrespective of substrate conditions, and migrated from the Paris Basin to the Aquitaine Basin during its development. The material of the new species from Maastricht is too limited (e.g., no growth series are available) to allow a similarly detailed analysis of their status.

Associated are a few indeterminate congeners [*Metopaster* sp. 1, *M.* sp. 3, and *M.* sp. 4 (aff. *elegans*)], which will all have had closely similar modes of life. Also known from the Meerssen Member are the comparatively large-sized *Recurvaster antemammillatus*, which may well be the direct ancestor of *R. mammillatus*, and *Ophryaster*? *maas-*

trichtensis, of which so far only to holotype has been recorded. Although this is of note in being one of the very few more or less complete asteroids from the type Maastrichtian, preservation of marginal ornament is poor. However, a preliminary study has shown that it cannot be maintained in the genus *Ophryaster*.

Smaller-sized goniasterids, represented by at least five types, range throughout the entire Maastricht Formation, and are well represented in the Meerssen Member. Unfortunately, of most only a limited material is currently available, which does not allow their taxonomic position to be properly assessed. These include goniasterid sp. 1, goniasterid sp. 2, goniasterid sp. 3, goniasterid sp. 6, and goniasterid? sp. 4. The latter appears close to the genus *Pseudarchaster*, a generalist as far as substrate (muddy bottoms to solid rocks) and diet (sponges, molluscs, crustaceans, sediment, and detritus) are concerned. Blake (1986) noted that this genus is amongst the more widely distributed and ecologically tolerant asteroids.

Of the sphaerasterid *Valettaster* gr. *ocellatus* only isolated aboral ossicles are known. The same goes for the stauranderasterids *Stauranderaster*? sp. and *Aspidaster*? sp. 1.

The Geulhem Member has yielded a total of 18 valvatidan taxa, 2 of which appear to be conspecific with material from the underlying Meerssen Member (*Valettaster* gr. *ocellatus*, and *S*.? sp.), but it should be noted that the range of variation of these two forms is still poorly known. Especially for the former, a wide range of variation has been accepted, since there are no clear-cut boundaries between the various 'types' of aboral ossicle and their ornament (see Jagt, 2000b). The functional morphology of this bizarre asteroid is still poorly understood (cf. Breton, 1985).

Of particular note amongst this assemblage are forms that appear closely related to, if not conspecific with, species described originally from the Danian of Denmark (Brünnich Nielsen, 1943; Rasmussen, 1945, 1950), viz., *Metopaster* aff. *carinatus*, *M. kagstrupensis*, *M*. aff. *planus*, *M. spencerii*, *Recurvaster mammillatus*, *Crateraster anchylus*, *Stauranderaster*? *miliaris*, *Pycinaster* aff. *cornutus*, and *P*.? aff. *rosenkrantzii*. With *M. spencerii*, *M. kagstrupensis*, and *C. anchylus*, the lower Geulhem Member thus includes a number of stratigraphically important taxa. On previous occasions it has been demonstrated that certain asteroid species could well be considered to represent good marker fossils. Representatives of the *Nymphaster studlandensis—alseni—peakei* lineage (Gale, 1989) come to mind, but also forms such as *Metopaster andreae* Gale, 1987a, occurring in the Lower Cenomanian of southern England and Basse-Normandie (France; see Breton & Decombe, 1997). There may be more potential here than previously thought (see also Villain et al., 1997).

Other goniasterids are either long-ranging (*Chomataster acules*, which occurs in various facies types as well), new species (*Metopaster continuus*) which appear to continue particular Late Cretaceous lineages into the Palaeocene, or indeterminate forms of which too limited material is currently available (*Pycinaster* sp. 2, *Metopaster* sp. 2, and *Caletaster*? sp.).

C: Notomyotida

Although not known from the Meerssen or Geulhem members, a limited material from a few levels may be assignable to the Benthopectinidae. Modes of life of this now deep-water family are uncertain, but its representatives appear to live on particulate substrates, being either suspension feeders, scavengers/carnivores, and/or detritus feeders. Marginal ossicles alternate, giving arms flexibility, and soft tissues are reduced. Typical are specialised, longitudinal aboral arm muscles, which Blake (1984b) thought indicated that arms were held in the water column for suspension feeding.

The benthopectinid mode of life exposes them to predators; spines, of considerable length in some species, would provide some protection. Extant forms occur almost entirely beyond shelf depths, but fossil occurrences are from shallow-water settings (Blake, 1984b; Blake & Reid, 1998).

D: Paxillosida

Paxillosidans, and astropectinids in particular, are offensive specialists occurring on soft substrates, living semi-infaunally. Many, if not all, forms have the ability of self-burial; astropectinids are voracious predators, and feed on molluscs, echinoderms and other invertebrates.

Paxillosidans are common on unconsolidated sediments, the deep, parallel, radially directed intermarginal channels (‘fascioles’) allowing an unobstructed waterflow over the body surface, aiding in self burial. The evolution of fascioles might thus be predation driven (Hess & Blake, 1995). Self-burial obviously increases the preservation potential (see e.g., Blake & Sprinkle, 1996). The sturdy skeletal structure of *Astropecten* reflects an adaptation to shallow, turbulent settings. Important in paxillosidans is the internal gut capacity (Blake & Sturgeon, 1995).

With the exception of extant *Astropecten* and *Luidia*, paxillosidans live below most wave activity. In the former, the relatively small discs represent an inferred compromise for shallow, turbulent environments.

Both the Meerssen and Geulhem members have yielded at least two species of astropectinid each, but generic composition is clearly different. From the former unit, astropectinid sp. nov. and *Aldebarania* sp. nov. (?) are known, while in the latter *Astropecten*? sp. nov., and *Lophidiaster*? gr. *punctatus/postornatus* are locally common. Although the Geulhem forms are known to occur as dissociated ossicles only, these are quite numerous, and suggest astropectinid predation to have occurred on shelly faunas in the Early Palaeocene.

Mass extinction or otherwise ?

As outlined above, the correlation between the various sections (see Fig. 1), and the combined section in Figs. 3-6 used to plot echinoderm distribution in the Meerssen and Geulhem members, is more or less preliminary. There are still problems in correlating the upper portion of the Meerssen Member and the lower portion of the Geulhem Member at the various localities. Although clay layers have not yet been recognised at the Blom quarry in that part of the section held to be equivalent to IVf-7 at the Ankerpoort-Curfs quarry, this is here considered to be coeval. Ammonite distribution at the former locality does not contradict this assumption. Moreover, since the Blom section is very close to the main sampling site within the Geulhemmerberg, it is assumed to match that section more closely in lithological detail than it does the Ankerpoort-Curfs section.

In the absence of large enough sample series from section IVf-7 in the Geulhemmerberg underground workings, from where only a few spot samples have been studied, the faunas from the Blom quarry provide the best evidence of latest Maastrichtian echinoderm diversity in the area. Lower in the Meerssen Member, between section IVf-3 and IVf-6 (i.e., between 5 and 8 m below the K/T boundary = Berg en Terblijt Horizon) correlative sections are available at the Ankerpoort-Curfs and ENCI-Maastricht BV quarries. Echinoderm faunules from section IVf-7 were collected, unfortunately rather indiscriminately, from both the crustacean burrows penetrating the hardground capping section IVf-6, as well as from the various fossil hash levels. As it can no longer be determined from samples available for the present study (Kuypers and van Birgelen collections), exactly from what level these originated, they are lumped here. The loss of information, however, appears minimal, also judging from state of preservation of ossicles which is moderate to good.

With these samples at hand, it may be concluded that sampling across the K/T boundary, has been as complete as possible at this moment, and this should yield reliable range charts of the various species. However, the final check will ultimately lie in the Geulhemmerberg section, which will have to sampled extensively across the IVf-6/-7 and IVf-7/Va-1 boundaries in future, as well as across the Vroenhoven Horizon. With the exception of typically Maastrichtian echinoids (see above), section IVf-7 at the Ankerpoort-Curfs quarry has not yet yielded similarly diverse echinoderm faunas as those from the Blom quarry. Moreover, preliminary observations have shown that the fossil hash levels in that section comprise heavily abraded and highly fragmented material only, and that size sorting has occurred. This then could hardly be expected to yield sufficient samples.

The present range charts (Figs. 3-6) are based only on stratigraphically well-documented samples. Although for the present discussion only the distribution within the Meerssen Member is illustrated, it should be noted that various species extend their range downwards, i.e. into the underlying Nekum Member or lower still. Moreover, it should be borne in mind that the highest occurrence of a species in these range charts need not represent the very last individual of that taxon (the Signor-Lipps effect; see Donovan, 1989; MacLeod & Keller, 1996; Hallam & Wignall, 1997). Affected by this sampling problem are in particular the rarer species; the last appearance datum (or extinction level) of several commoner species would yield the best approximation of the level of mass extinction event.

In addition, the effect on fossil distribution by shifts in facies and fluctuations in sedimentation rate should be considered. It is these fluctuations in local conditions that have been amply demonstrated for the Geulhem-Berg en Terblijt area. The lenticular nature of the various units of the Meerssen Member has been hinted at in various stratigraphic and faunal studies, and this of course influences lithostratigraphic correlations. For the Ankerpoort-Curfs and Geulhemmerberg sections, Brinkhuis & Smit (1996) discussed the importance of palaeohighs and palaeolows (palaeorelief) in preferential preservation of K/T boundary strata in the area. In their proposed scenario of depositional and erosional history across the K/T boundary, the latest Maastrichtian Berg en Terblijt Horizon (a hardground) formed on top of bioburbated biocalcarenites as a submarine relief. After the Yucatán impact, there was a sea level rise, and the first storm deposits (coarse calcarenites) accumulated in the lows. For the time being, it is with these calcarenites that section IVf-7 at the Blom quarry is correlated.

Sampling series from the lowermost Geulhem Member have been available in particular from the former Albertkanaal sections (Vroenhoven-Riemst), with a second, much more limited set from the Ankerpoort-Curfs quarry. The Vroenhoven Horizon at both localities appears to equate well, and the lithological subdivision of the member into two subunits (boundary corresponding to section Va-3), is also recognised in faunal assemblages. As outlined in the introduction, the uppermost Geulhem Member was only exposed along the Albertkanaal near Kesselt, in a peculiar hardground/boulder facies. Unfortunately, the exact stratigraphic level of this occurrence within the Geulhem Member has never been recorded. This means that faunal data for the Geulhem Member are essentially based on two disjunct sample sets, the stratigraphic distance between which cannot be determined. In Figs. 3-6, the Kesselt faunas are placed in section Va-4, although they probably represent a higher level still within the Houthem Formation, not developed at the Ankerpoort-Curfs quarry.

In summary, sample series used for the present study have been as closely spaced and as extensive as possible at this moment. A stratigraphic gap, of unknown duration, may be expected to coincide with the Berg en Terblijt Horizon, but this does not appear to have influenced echinoderm faunules much (see below).

Now that a reasonably detailed picture of echinoderm diversity and palaeobiology in the latest Maastrichtian and Early (earliest) Palaeocene is given, the question what these may contribute to the discussion on K/T boundary extinction and survival patterns may be addressed. In considering all groups (exclusive of holothuroids), rather than e.g. only echinoids, all ecological niches occupied by echinoderms may be assessed. In this way, distribution patterns of widely differing groups such as roveacrinid crinoids and astropectinid asteroids may be compared.

In the sections above, the palaeobiological aspects of the various groups were briefly outlined. Below, the emphasis will be on the question whether these data allow the distribution patterns across the K/T boundary to be characterised as a catastrophic extinction or not.

Crinoids

None of the crinoid taxa known from the uppermost Meerssen Member continue into the Geulhem Member. These species represent rare stalked forms (i.e., sessile benthos), comatulids (i.e., vagile benthos), as well as a benthic saccocomid. The high diversity of comatulids suggests optimum conditions for perching, hiding in (hardground) cavities, and a high-energy setting, with bidirectional currents (Fig. 7A). The isocrinid is considered to be transported in from nearby, deeper(?) and/or calmer settings with predominantly unidirectional current flow. The saccocomid is assumed to have lodged itself in the substrate, preferably in places where net sedimentation was limited. All crinoids are (semi)passive suspension feeders, with the comatulids characteristing (sub)tropical, shallow-water settings. Material collected at the Blom quarry from a level considered to be above the Berg en Terblijt Horizon (see Fig. 1), a submarine hardground, illustrates the latest Maastrichtian acme of comatulid diversity. The sudden demise of these comatulids may be linked to a combination of primary disappearance of larvae from the water column as a direct result of plankton collapse, and a change in environmental setting. Brinkhuis & Smit (1996) noted that the upward

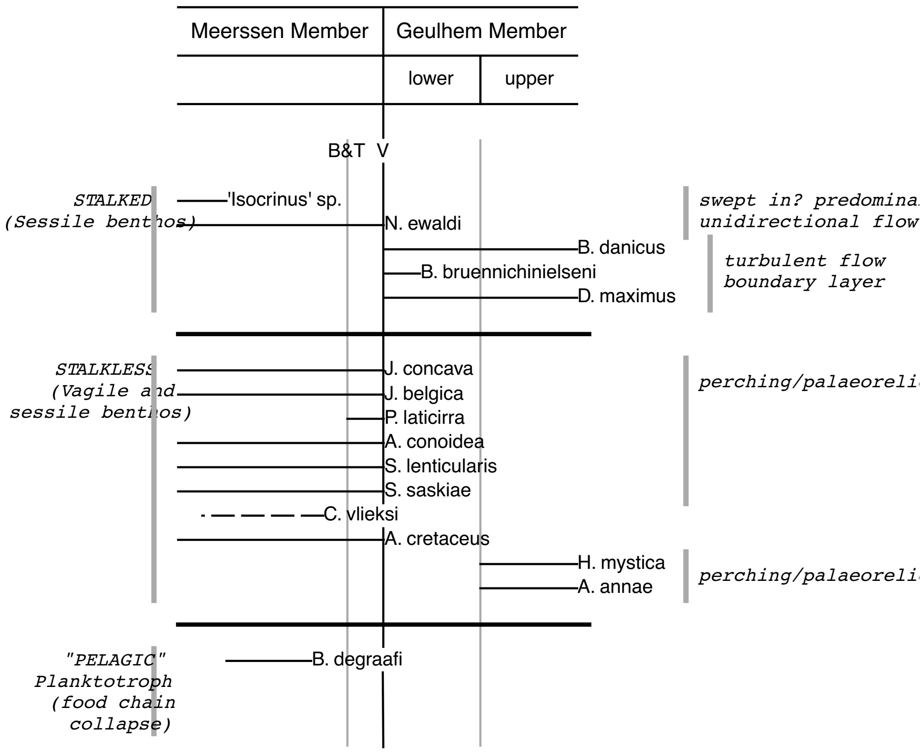


Fig. 7A. Crinoid distribution across the K/T boundary in the type area of the Maastrichtian Stage, and inferred palaeoenvironments. Abbreviations: Vr = Vroenhoven Horizon, B&T = Berg en Terblijt Horizon.

thinning of coarse-grained layers overlying the Berg en Terblijt Horizon, and the fining-up of these up to the E clay could indicate deepening, or alternatively, a change to a more 'shielded' position. The lack of suitable substrates for perching and hiding (during part of the day) in the lower Geulhem Member was not conducive to comatulid settlement. Only in the upper Geulhem Member do conditions appear to have changed and become stable to allow comatulids to return (K strategy; Fig. 7A). Some comatulid species would appear to illustrate local extinction phenomena, while saccocomids and roveacrinids died out at the end of the Maastrichtian worldwide (Fig. 7A). Still others seem to have emigrated elsewhere, continuing lineages in the Early and Middle Danian (e.g., *Placometra*, *Amphorometra*, *Jaekelometra*, and *Cyathidium*) (Fig. 7A).

From the lower part of the overlying Geulhem Member only stalked species are known, and these are common locally. The highly flexible stems of these bourgueticrinids, with synarthrial articulations, suggest these to have grown in a boundary layer with turbulent flow. The heterochronic change to proximale loss through paedomorphosis, noted by Kjaer & Thomsen (1999) for earliest Danian bourgueticrinids, is also seen in the present material. The selection for longer columns could be a result of increased competition in a nutrient-poor, depleted environment. That bourgueticri-

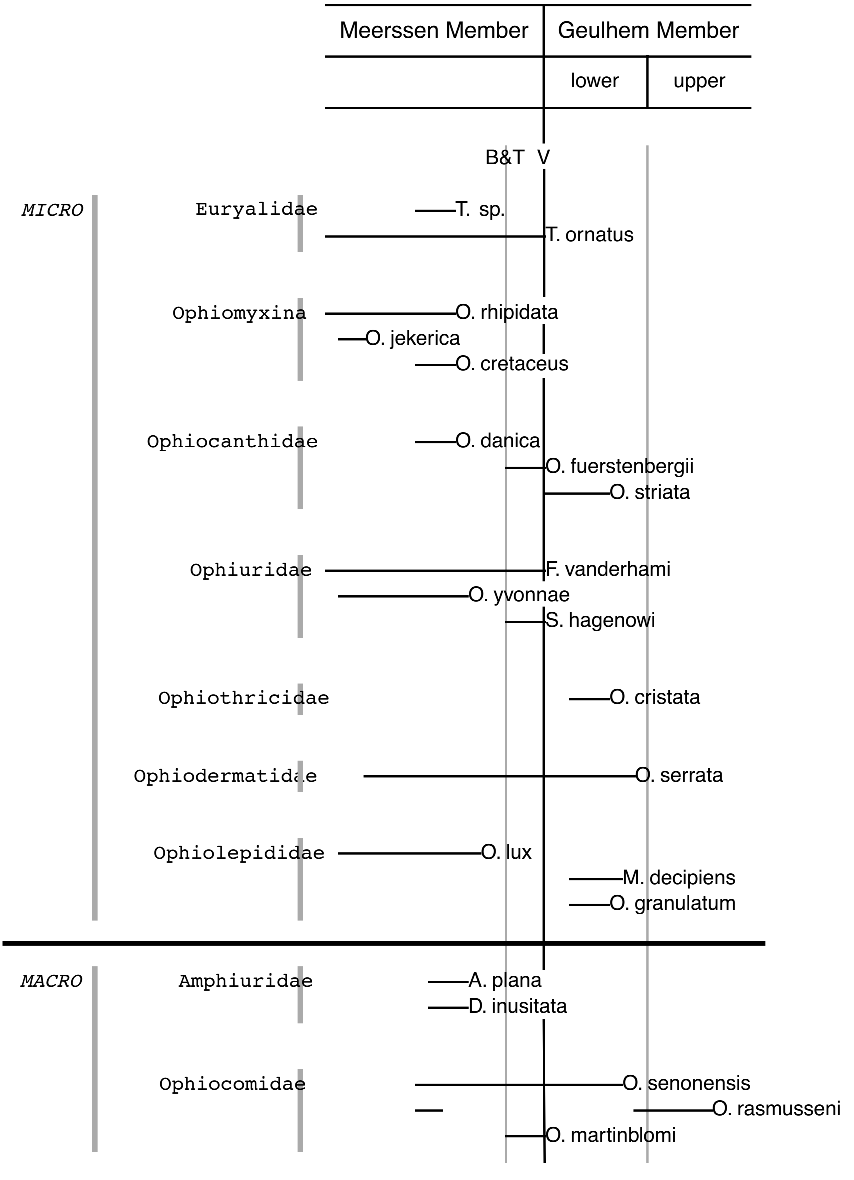


Fig. 7B. Ophiuroid distribution across the K/T boundary in the type area of the Maastrichtian Stage, and inferred modes of life (micro- vs macrophagous feeding strategies). Abbreviations as for Fig. 7A.

nine faunules from the lower (lowermost) Geulhem Member contain all morphologies recognised from the earliest Danian of Denmark, is here seen as proof of a rapid immigration of this group of species into the Maastricht area, directly above the Vroenhoven Horizon (Fig. 8A). This then would also confirm the correlation between that horizon and the top of the Cerithium Kalk of the Stevns Klint sections in Denmark. The turbulent flow might explain the absence of isocrinids in the study area, as compared to their fairly common occurrence in the Lower Danian of Denmark and southern Sweden (Fig. 3).

The upper Geulhem Member yields rare bourgueticrinids, as well as two comatulid morphotypes, broadly similar to forms from the Meerssen Member, but representing a much lower diversity. One of these migrated in from elsewhere, the other appears to have originated in the study area (Fig. 8A). Both these types have been collected from the hardground/boulder facies that has also yielded the wealth of regular echinoids, and suggest a stable, more or less protected environment, in a shallow-water, presumably subtropical setting, more or less comparable to the Middle Danian of Fakse (Denmark).

In short, crinoid distribution across the K/T boundary would fit the catastrophic extinction end-member for the extinction phase, as outlined by Hallam & Wignall (1997).

Ophiuroids

Of ophiuroid taxa known from the Meerssen Member (Fig. 4), seven range into section IVf-7, and two of these actually continue into the lower Geulhem Member. The range across the boundary of one, *Ophiocoma*? *rasmusseni*, is disjunct (Fig. 4); the same holds true for *Ophiomusium granulosum*, which is well known from strata up to the middle of the Maastricht Formation. These could be considered to represent hold-over taxa (Fig. 8B), as could *Ophiothrix*? *cristata* and *Ophiacantha*? *striata*, both first described from the upper Lower Maastrichtian of northeast Germany.

Forms extending into section IVf-7 represent fairly stout, medium-sized ophiocomids and ophiodermatids. Associated is a single species each of ophiacanthid, ophiothricid, and ophiolepidid, not known from the underlying Meerssen Member, but recorded from older Cretaceous strata elsewhere (see Kutscher & Jagt, 2000). These illustrate local extinction (Fig. 8B). Although the ophiuroid assemblage from the lower Geulhem Member comprises various ecological groups (Fig. 7B), microphagous groups (suspension and detritus feeders) tend to dominate. Of note is the absence of burrowing amphiurids (macrophagous feeders) in the (lower) Geulhem Member. Amongst forms that in Recent settings characterise littoral environments there is virtually no change across the boundary, suggesting bottom conditions across it to be more or less comparable.

A similar setting may be assumed for the uppermost Meerssen Member, but here euryalids (genus *Trichaster*?) form a conspicuous element. These do not continue into the Lower Palaeocene in the study area, but closely related forms are known from coeval strata elsewhere (Rasmussen, 1972).

Ophiuroid diversity within the Meerssen Member seems to have decreased prior to the K/T boundary involving mainly bottom-dwelling taxa, but this may in part be a sampling artefact. Various storm-generated levels at the ENCI-Maastricht BV quarry have been extensively sampled during recent years; these naturally represent catastrophic, rapid burial of live populations, which would explain the higher diversity seen.

As far as generic composition of Late Maastrichtian and Early Palaeocene ophiuroid faunas (see Figs. 4, 7B) is concerned, there is no marked change, with the possi-

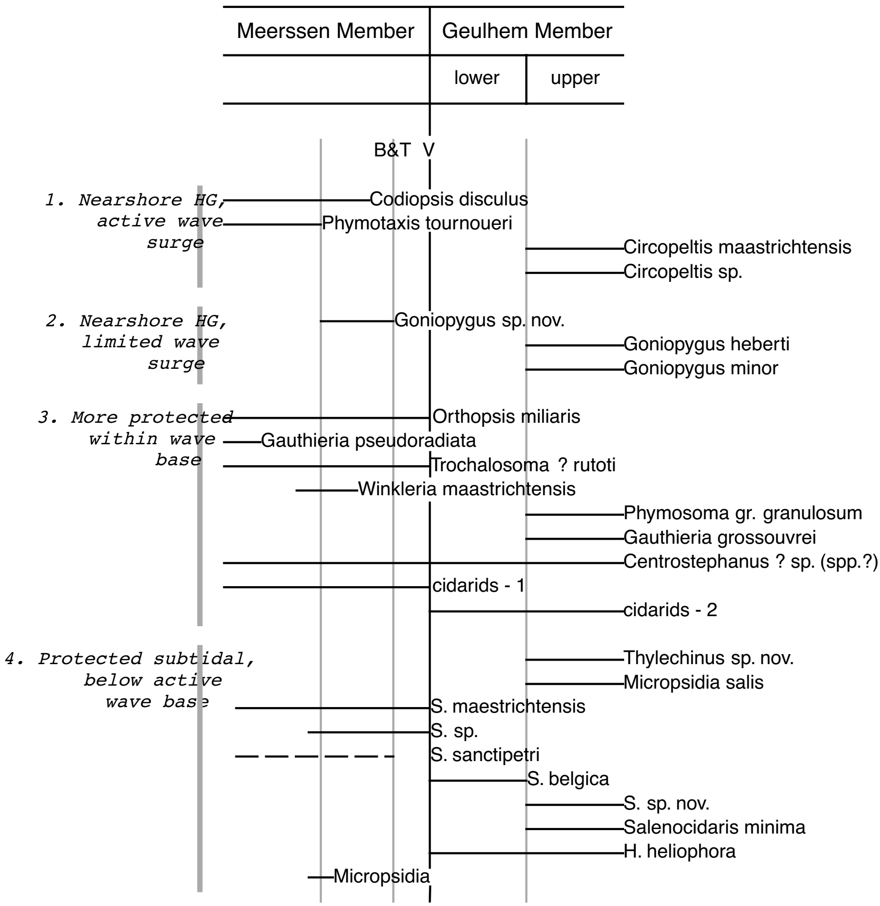


Fig. 7C. Regular echinoid distribution across the K/T boundary in the type area of the Maastrichtian Stage, and inferred palaeoenvironments. Abbreviations as for Fig. 7A.

ble exception of representatives of the euryalids, and ophiomyxids. However, with the exception of *Trichaster*? *ornatus*, these forms are rare even in the Meerssen Member. Genera below and above the boundary comprise closely related species, suggesting that turnover was limited, thus confirming Rasmussen's (1979) observation. However, the limited diversity of Early Palaeocene ophiuroid faunas in comparison to the Late Maastrichtian ones, suggest a biotope subject to changes in physical and/or chemical conditions. Worldwide, the most conspicuous turnover in echinoderm faunas seems to correspond not to the K/T boundary, but to the boundary between the Danian and Selandian (see Rasmussen, 1979). That ophiuroid extinction across the K/T boundary in the study area was selective is demonstrated by the disappearance of some microphagous groups (such as euryalids and ophiomyxines), while others cross over apparently unaffected (Fig. 7B).

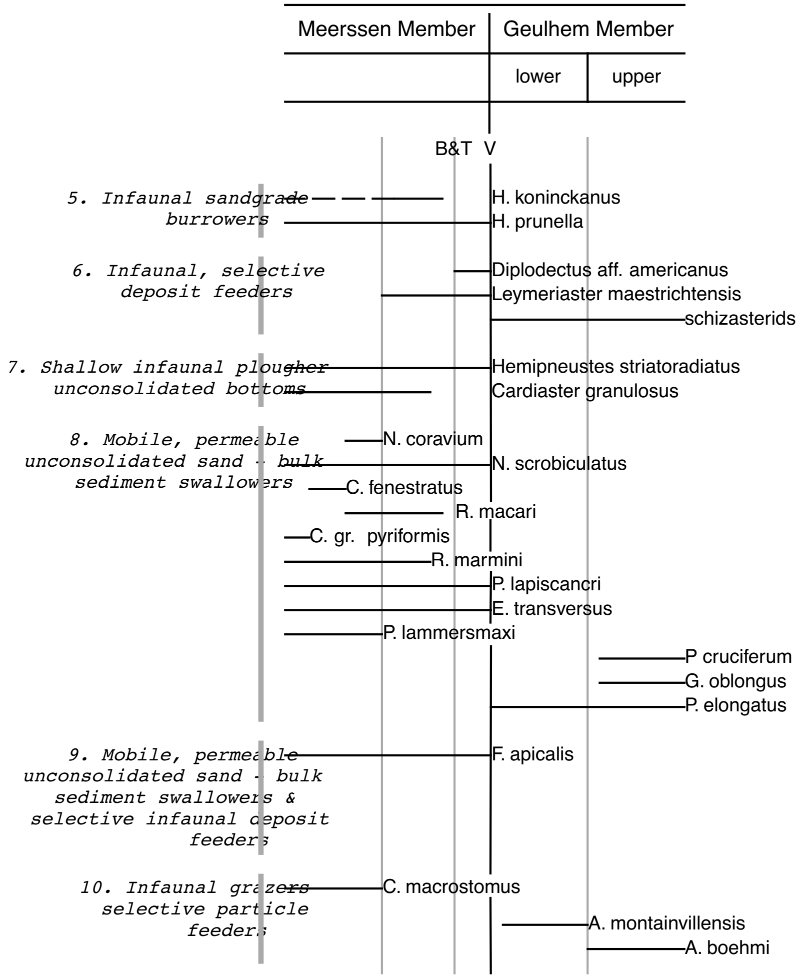


Fig. 7D. Irregular echinoid distribution across the K/T boundary in the type area of the Maastrichtian Stage, and inferred palaeoenvironments. Abbreviations as for Fig. 7A.

Echinoids

Of the thirty-six echinoid taxa known from the Meerssen Member just one, *Centrostephanus*? sp. (? spp.), continues into the Geulhem Member (Figs. 5A, C), but it should be noted that this form has not been identified at the species level, and may in fact, comprise more than one species. Various immigration events may be recognised across the boundary (Fig. 8C).

A comparison of ecological groups across the boundary (see Fig. 7C-D) reveals the following patterns:

The middle/upper Meerssen Member and upper Geulhem Member compare well where species occurring on (nearshore) hardgrounds, within the zone of active wave surge (0-5 m depth) are concerned. These habitats must have been very similar, but generic/species composition varies (*Codiopsis* and *Phymotaxis* in the Meerssen Member; *Circopeltis* in the Geulhem Member).

The upper Meersen Member and upper Geulhem Member both have *Goniopygus* as characteristic element of (nearshore) hardground settings, subtidally within uppermost few metres of water column, but subject to limited wave surge only. This confirms the above interpretation; this time it is only the species that differ.

Amongst shallow-water species (2-10 m), occurring in more protected environments, within wave base, but not subject to strong currents and/or wave surge, *Orthopsis miliaris*, *Gauthieria pseudoradiata*, *Trochalosoma*? *corneti*, and *Winkleria maastrichtensis* disappear near or at the boundary. Only *Orthopsis* does not have a match in the upper Geulhem Member, where a similar environment is represented (with *Phymosoma* gr. *granulosum*, and *G. grossouvrei*). In cidarids, diversity across the boundary remains more or less unaffected, but the turnover at the specific level is drastic, illustrating local extinction.

Amongst species occurring on protected subtidal (> 10 m), soft-bottom substrates, below active wave base, the turnover at the specific level is drastic, with none of the species represented in the Meerssen Member continuing into the Geulhem Member. In the lower Geulhem Member, acmes in the distribution of *Hyposalenia heliophora* should be noted. In view of the fact that finds of tests with associated spines as well as lanterns are known, it may be assumed that these large numbers were a reaction to an increased availability of food, or represent smothered (?spawning) populations. Alternatively, there may have been a lack of competition.

Infaunal, medium-fine sandgrade burrowers suffer heavy losses; neither species of *Hemiaster* continues into the Geulhem Member, although hemiasterids of *Bolbaster* morphotype are known to occur, albeit rarely, in the Lower Danian of Denmark.

The turnover amongst infaunal, medium-fine, sandgrade burrowers, selective deposit feeders is at the generic level, although the genus *Diplodetus* is known to continue into the (Early) Palaeocene elsewhere. *Leymeriaster* does indeed become extinct at the K/T boundary, worldwide (Fig. 8C). Burrowing schizasterids appear to be fairly common in the (lower) Geulhem Member, thus providing an indication of the nature of the sediment, i.e. fairly coarse-grained, permeable calcareous sands. From the Maastricht Formation, extremely rare schizasterids are known from the Nekum Member and the Kunrade Limestone facies.

The shallow infaunal/semi-infaunal ploughers in stable, unconsolidated bottoms; selective deposit feeders harvesting sediment at or close to water/sediment interface suffer heavy losses. *Hemipneustes* occurs in the upper part of section IV-7, i.e. well above the Berg en Terblijt Horizon, but disappears at the Vroenhoven Horizon. Close relatives of *Cardiaster* are known from the Palaeocene elsewhere, but in the Maastrichtian type area this ecological niche was no longer exploited by echinoids, after the K/T boundary event. The absence in the Geulhem Member of representatives of the genus *Echinocorys*, which characterise Lower Palaeocene strata across northern and northeastern Europe (see e.g., Jeffery, 1997) cannot be explained at this moment.

Diversity amongst infaunal bulk sediment swallowers diminished considerably across the boundary, but two of the three genera left are also known from the Maastrichtian.

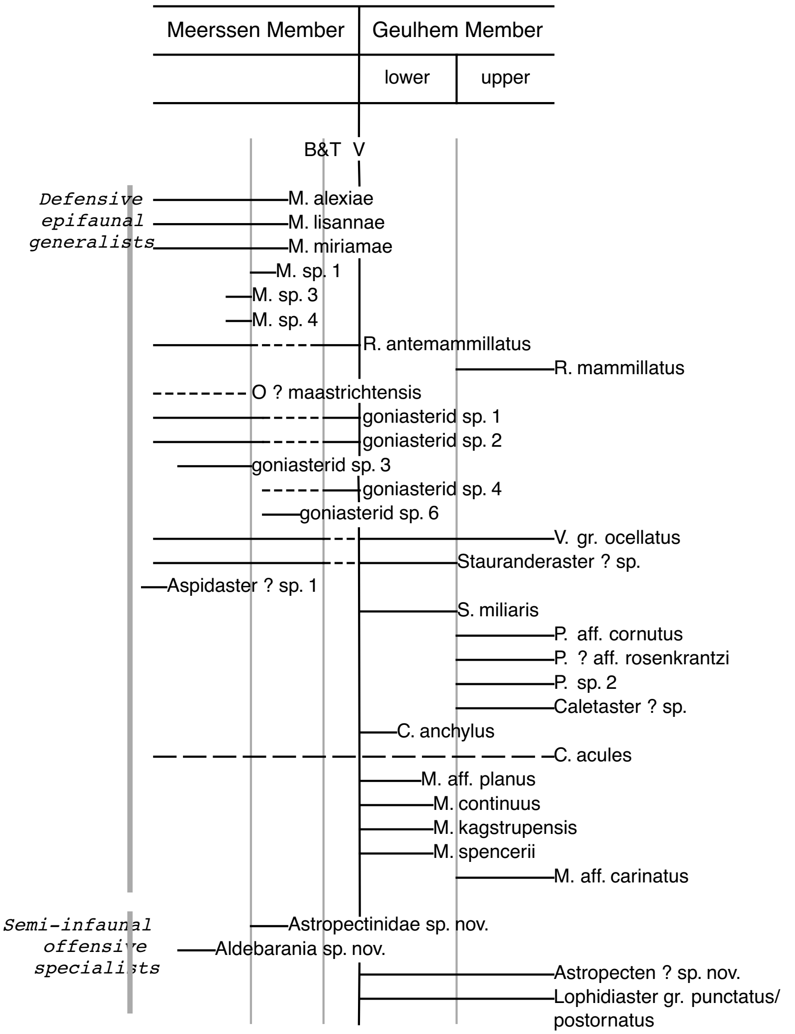


Fig. 7E. Asteroid distribution across the K/T boundary in the type area of the Maastrichtian Stage, and inferred modes of life (epifaunal vs infaunal, defensive vs offensive, generalists vs specialists). Abbreviations as for Fig. 7A.

The selective infaunal deposit feeder *Faujasia apicalis* becomes extinct at the boundary.

Amongst infaunal grazers/detritivores, selective particle feeders, within coarse permeable sands in 0-10 m depths, diversity remains constant.

Of note is the occurrence of marsupiate forms at some levels in the Meerssen and Geulhem members (*Micropsidia*? sp., *Thylechinus* sp. nov., *Goniopygus minor*; Fig. 7C). Following McNamara (1994) these would suggest changes in environmental stability, and more specifically, predictability of nutrient supply, rather than changes in water temperature. Their occurrence in the middle Meerssen Member and upper Geulhem Member suggest that conditions during deposition of these portions of the sequence were comparable, as also deduced from the distribution of crinoids and non-marsupiate echinoids.

Within the Geulhem Member, the upper part is of particular note in that regular echinoids are especially common and diverse, reflecting a hardground/boulder setting, with generally minimal transport, and thus site fidelity (compare Greenstein, 1991, 1993). A high diversity of regular echinoids suggests preferred stabilised bottoms under shallow- water conditions, and with minimum influence of strong wave action.

In short, 'specialists' seem to have suffered most from environmental changes across the K/T boundary, with selective infaunal deposit feeders and bulk sediment swallowers, globular species of sandgrade burrowers, and shallow infaunal/semi-infaunal ploughers (selective deposit feeders) being especially hard hit. This turnover thus appears to have been selective, as well as rapid.

Asteroids

Only two of the eighteen asteroid taxa known from the Meerssen Member continue into the Geulhem Member (Fig. 6A), but it should be noted that for both these taxa a wide range of variation has been assumed. This means that, given additional material, these may prove distinct after all. From the uppermost Meerssen Member (IVf-7), four taxa are known, and none of these continues into the Geulhem Member, suggesting local extinction (Fig. 8D). However, *Recurvaster antemammillatus* and *R. mammillatus* might well be members of the same lineage.

In number of species and generic composition of asteroid faunas across the boundary, changes are few. Faunas on both sides of the boundary contain offensive specialists (astropectinids) as well as defensive generalists (goniasterids) in about equal numbers, the only notable difference being the occurrence in the upper Geulhem Member of at least three pycinasterid species.

This distribution pattern suggests that bottom conditions and trophic structures did not change appreciably across the boundary, and that in the upper Geulhem Member the decrease in number of species of *Metopaster* matched an increase in number of species of *Pycinaster*.

However, of note is the occurrence directly above the Vroenhoven Horizon of highly typical Early Danian goniasterids such as *Metopaster spencerii*, *M. kagstrupensis*, *Crateraster anchylus*, and the stauranderasterid *Stauranderaster*? *miliaris*. In the Stevns Klint sections, these forms are virtually restricted to the Early Danian, but exactly when they first occur is still unknown. In comparison with data for crinoids mentioned above, it is likely that the occurrence of these asteroids also presents a flood immigration into the Maastrichtian type area during the Early (though not earliest) Palaeocene (Fig. 8D). These immigrations also seem to have continued during the (Middle?) Danian, as asteroids from the upper Geulhem Member are closely related to, if not conspecific with, taxa from Denmark (Fig. 8D). Only a minor endemic element is represented, amongst which is a (?short-lived) offshoot of the *Metopaster stainsforthi* lineage, in the lower Geulhem Member.

In short, asteroid diversity across the boundary does not markedly change in generic composition, and ecological structure, but at the species level the turnover is complete.

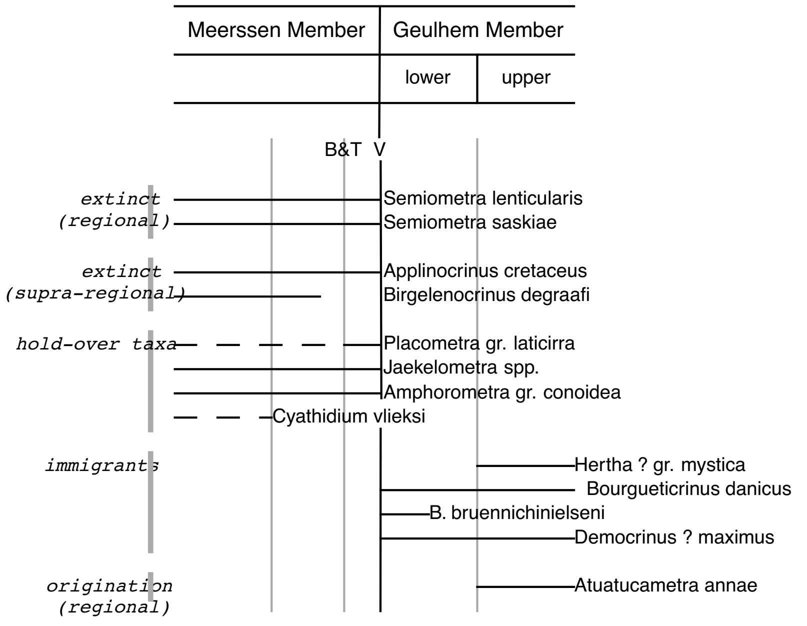
General conclusions

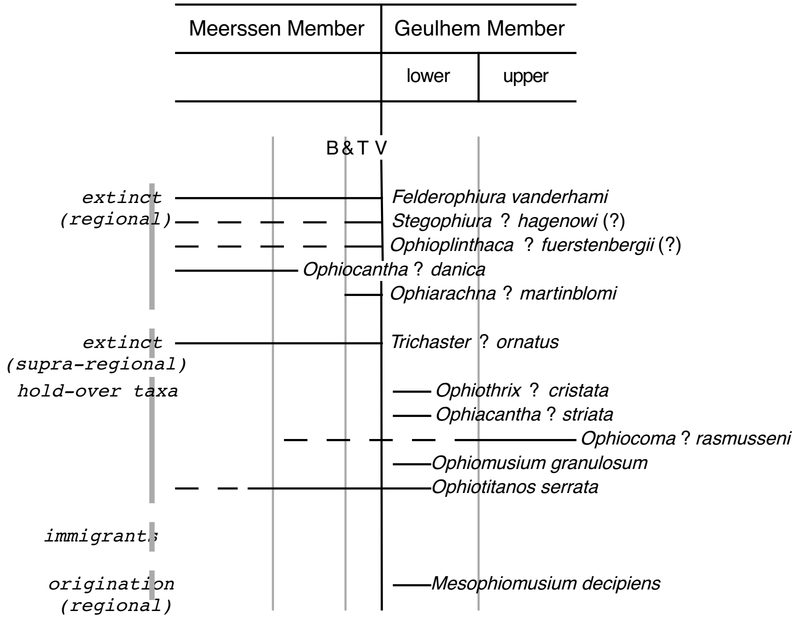
Data on diversity across the K/T boundary for the various echinoderm groups thus conflict to some extent. Crinoids, as (semi)passive suspension-feeders, seem to have been particularly hard hit, with planktotrophics disappearing as well as shallow-water, (sub)tropical comatulids. Bourgueticrinid immigrations suggest muddy bottom waters (selection for longer columns, r strategy), and the existence of a boundary layer with turbulent flow. The change in ophiuroid faunas across the boundary seems to have been selective, showing the demise of some microphagous groups amongst bottom-dwelling and clinging forms, as well as more or less unchanged composition in other groups. The former implies a change in suspension feeding, comparable to that seen in the crinoids. Asteroids experienced a complete turnover in specific composition, but as far as genera are concerned changes are few. Trophic groups (e.g., defensive generalists and semi-infaunal offensive specialists) appear to have remained stable across the boundary, suggesting that bottom conditions did not change appreciably. Amongst echinoids, 'specialist' taxa suffered most from environmental changes across the K/T boundary, suggesting a strong correlation between palaeorelief and echinoid diversity in the study area. In particular, changes were drastic in nearshore hardground bottoms (within or outside active wave surge), and amongst selective infaunal deposit feeders, shallow infaunal ploughers as well as bulk sediment swallowers in unconsolidated bottoms. This would suggest dramatic changes in bottom conditions across the boundary.

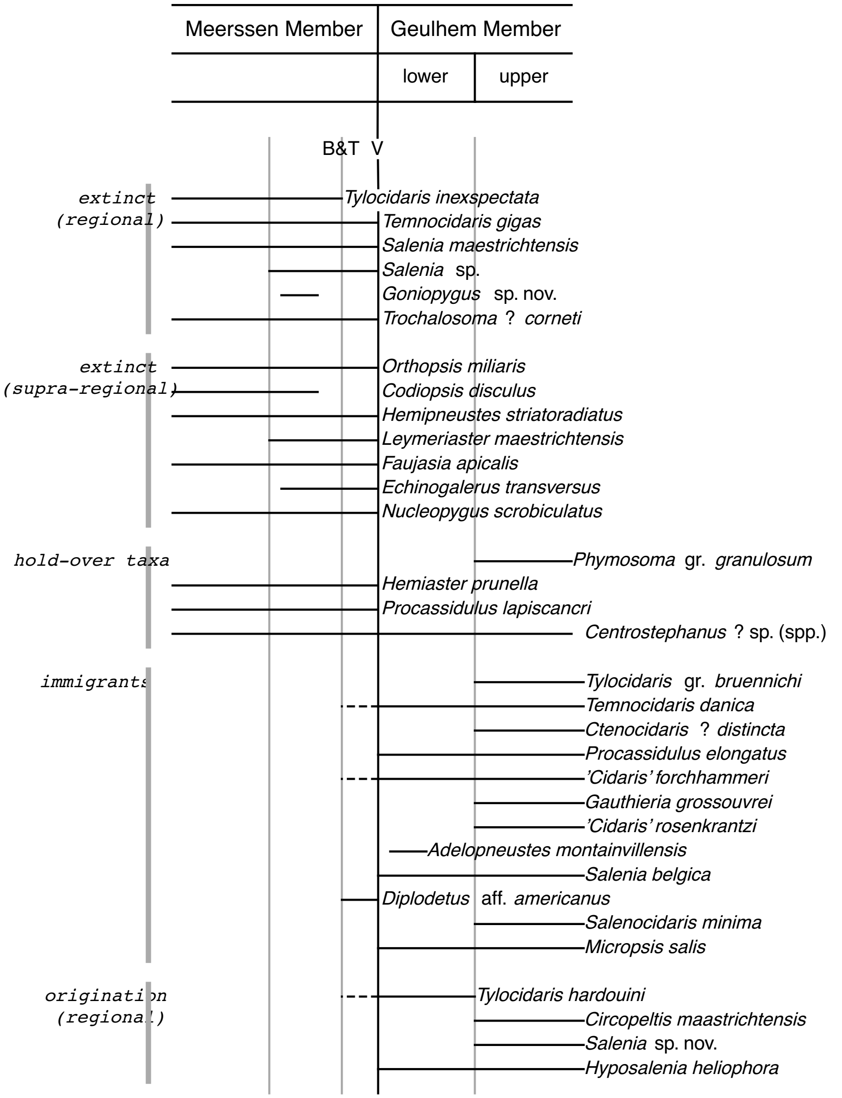
How do these results relate to previous studies of K/T boundary sections elsewhere ? First, it should be stressed that the Maastrichtian type area is a bit of 'an odd man out' as far as the Late Cretaceous in northwest Europe is concerned. The typical 'tuffaceous chalk facies' of the Maastricht Formation represents a facies type not generally preserved elsewhere in Europe, with the exception of some isolated occurrences in north(east) Germany, and it thus allows us a detailed look into a generally turbulent, shallow-water, (sub)tropical setting in which most benthic faunas differed markedly in generic and specific composition from coeval faunas in the Maastrichtian white chalk facies, which extended from northern Ireland to well into the Ukraine.

Up to the base of the Lanaye Member (Gulpen Formation) interregional correlations with e.g. Norfolk and northern Germany are relatively straightforward, but

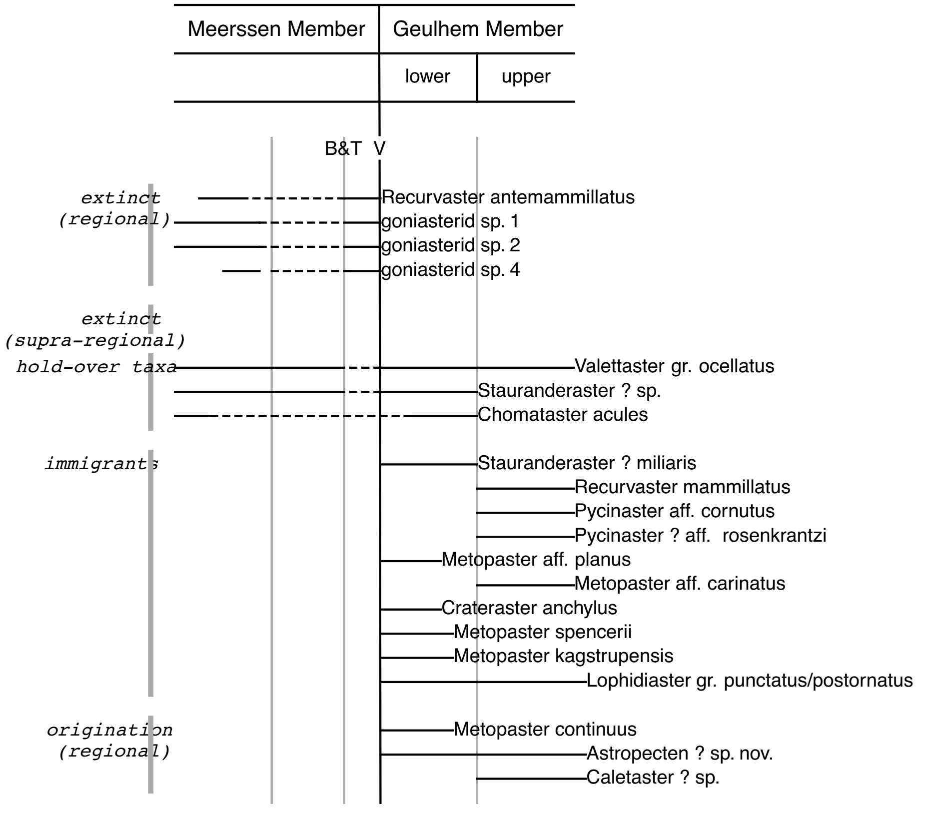
Fig. 8A-D. Echinoderm distribution across the K/T boundary in the type area of the Maastrichtian Stage, showing taxa which are inferred to have become extinct on a regional or supra-regional level, to have immigrated into the area, or to have originated there. Hold-over taxa (compare terminology of refugia species in Kauffman & Harries, 1996) refer to representatives of groups (i.e., genera) that disappear from the area, but are known to continue lineages elsewhere. In addition, under this heading are assembled forms known from older strata (in the study area, or elsewhere), absent from the uppermost Maastrichtian but occurring in the Lower Palaeocene, as well as forms which apparently cross the K/T boundary unchanged. Abbreviations: V = Vroenhoven Horizon, B&T = Berg en Terblijt Horizon. A: crinoids; B: ophiuroids; C: echinoids; D: asteroids


Meerssen Member
Geulhem Member
lower
upper
B&T V
extinct
(regional)
Semiometra lenticularis
Semiometra saskiae
extinct
(supra-regional)
Applinocrinus cretaceus
Birgelenocrinus degraafi
hold-over taxa
Placometra gr. laticirra
Jaekelometra spp.
Amphorometra gr. conoidea
Cyathidium vlieksi
immigrants
Hertha ? gr. mystica
Bourgueticrinus danicus
B. bruennichinielseni
Democrinus ? maximus
origination
(regional)
Atuatucametra annae


Meerssen Member
Geulhem Member
lower
upper
B & T V
extinct
(regional)
Felderophiura vanderhami
Stegophiura ? hagenowi (?)
Ophioplinthaca ? fuerstenbergii (?)
Ophiocantha ? danica
Ophiarachna ? martinblomi
extinct
(supra-regional)
Trichaster ? ornatus
hold-over taxa
Ophiothrix ? cristata
Ophiacantha ? striata
Ophiocoma ? rasmusseni
Ophiomusium granulosum
Ophiotitanos serrata
immigrants
origination
(regional)
Mesophiomusium decipiens



with the change to a marginal marine setting during deposition of that unit, things began to change. Warmwater-loving animals invaded the area, and where there to stay, until the upper third of the Meerssen Member (Maastricht Formation). Throughout this sequence, benthic faunal assemblages change, occasionally quite dramatically, and peak diversity in almost all invertebrate as well as vertebrate groups is reached in the upper Nekum and lower/middle Meerssen members. In a progressively shallower setting, with reef-like patches consisting of scleractinian corals and rudistid bivalves occurring in some places, a brief period of rapid subsidence (?related in time to the onset of Deccan Trap volcanism) had a severe impact on several biota. However, the vagile benthos appears to have been minimally affected, and echinoderm diversity remains almost constant to right below the K/T boundary.



Although the Maastrichtian type area thus represents an environment that is rarely preserved in the fossil record, this also means that comparison with other regions is not at all straightforward, especially when diversity patterns are being considered. Smith (1994, p. 177) noted that, 'One of the major problems associated with establishing extinction patterns is that of distinguishing local from global effects. In a shallow marine environment, for example, small-scale stratigraphic heterogeneity of lithofacies, each with its own distinctive fauna, is typical. Each change represents the local extinction of the earlier assemblage within the section, although taxa may simply have migrated to nearby areas along with the lithofacies. The large-scale sea-level fluctuations that cause major lithofacies reorganization over the continental shelf undoubtedly generate some total extinction [....] but they also create significant problems of sampling.'

Jeffery (1997), in a study of a shallow-water Maastrichtian setting in Kazakhstan, pointed out that still little was known about how exactly marine benthic macrofaunas were affected at the K/T boundary, both geographically and through biological selectivity patterns, but that most affected were taxa with narrow geographical ranges. Comparable to the Mangyshlak sections documented by Jeffery (1997), the Maastricht type area sees a proportion of taxa becoming extinct locally, with others emigrating from these sections, and still others migrating in from elsewhere.

There is a general consensus amongst authors that the facies change between the

Meerssen and Geulhem members was slight (e.g., Bless, 1989), and that biomass composition (bioclast assemblages) was closely comparable. Van Harten (1972) noted a smaller grain size for the Geulhem Member, and the occurrence of clayey intercalations, suggesting periods of relatively low energy, in a generally high-energy setting. However, according to Bless (1989) the occurrence of glauconite and the relative abundance of globular and keeled planktonic forams would suggest a (?)temporary influx of cold, upwelling oceanic water. That author postulated, on ostracod evidence, a change across the K/T boundary in regional environment rather than an overall extinction event, and a concomitant return to boreal conditions. Other authors have also noted a cooling trend for the latest Maastrichtian (Herngreen et al., 1998), as well as for the earliest Palaeocene (Brinkhuis et al., 1998) with a gradual return to stable, relatively warm conditions.

For Lower Palaeocene strata in the Molenbeersel borehole, correlatives of the Houthem Formation, Bless et al. (1993) noted repeated changes from shallow subtidal to intertidal settings, and temporary emergence(?). Moreover, they suggested that only well above the K/T boundary did conditions become stable with relatively shallow waters, well within the photic zone. In the study area, however, conditions seem to have varied considerably even over short distances. Based on benthic foram evidence, Herngreen et al. (1998) postulated water depths less than 30 m for unit IVf-7 at the Ankerpoort-Curfs quarry, and a middle (30-100 m) to outer (100-200 m) setting for the Geulhemmerberg section.

With few exceptions, echinoderm turnover across the boundary is almost complete at the specific level, but it is less pervasive at the generic or familial level, as has also been demonstrated for brachiopods (Johansen, 1989). Data presented here suggest this (these) event(s) to have been selective in a shallow-water, high-energy subtropical setting, with marked palaeorelief, followed by a change to a ?deeper, colder-water environment with a boundary layer of turbulent flow, and a subsequent return (locally only?) to shallow-water, high-energy conditions by the Middle Danian. In this respect, the picture that emerges is in part comparable to that postulated for the Braggs (Alabama) section (Bryan & Jones, 1989). Those authors demonstrated local and temporary ecological selectivity to have occurred across the boundary, with the earliest Palaeocene yielding comparatively low-diversity faunas. The fact that amongst crinoids and asteroids in particular, and to a lesser extent amongst echinoids, the lower Geulhem Member has yielded typically earliest Palaeocene species known from the type area of the Danian Stage, suggests (a) ?rapid immigration event(s) from the north/northeast.

In this respect, two recent studies by Heinberg (1999) and Håkansson & Thomsen (1999) are of interest. Using bryozoan, brachiopod and echinoderm assemblages (crinoids in particular) from the Nye Kløv section (Jylland, Denmark), Håkansson & Thomsen (1999) concluded that benthic extinction across the K/T boundary was abrupt, and that the earliest Danian fauna was already well established and essentially represented an impoverished Maastrichtian fauna, either through direct survival or limited evolution within well-established clades, already present in the Maastrichtian of the area. The lower 2-3 metres of the Danian (corresponding to the Cerithium Kalk or Cerithium Limestone) yield an impoverished 'dead zone' fauna, dominated by bourgueticrinid crinoids and other presumed soft-ground specialists. Higher up, these faunas are replaced by ‘more ordinary’ faunas, and some 6 m above the K/T boundary the typical, Early Danian bryozoan community is fully established. Håkansson & Thomsen (1999) also noted that the pervasive benthic depletion which at Nye Kløv characterises the lowermost metres of the Danian, was known from all Danish K/T boundary sections. The new incoming, Early Palaeocene taxa are ecological specialists with documented Late Maastrichtian predecessors in the same area, which shows that, in places, less adverse conditions must have prevailed during the ‘dead zone’ interval, suggesting a kind of ‘refuge’ to have been in existence. According to these authors, the benthic faunal recovery pattern found in the Danish region may thus be characterised as predominantly migrational rather than evolutionary, with a pronounced local signature.

On bivalve evidence, Heinberg (1999) concluded that at Stevns Klint the faunal change across the K/T boundary showed an overall reduction in number of species (by drastic reduction of the number of epifaunal taxa, by near-complete lack of calcitic forms in the Cerithium Kalk, as well as by a high extinction rate amongst multispecies genera). The bivalve recovery pattern is characterised by a lack of deposit feeders in the lower portion of this interval and by a subsequent, gradual increase in the number of new (i.e. non-Maastrichtian) species. A large number of the infaunal Danian species are Maastrichtian survivors, with some of them being found in the chalk below, and others representing immigrants from either the Polish basin or from the Paris Basin. Heinberg (1999) noted that the lack of calcitic forms in the Cerithium Kalk had no obvious ecological connection; this type of sediment may represent a ?chemically precipitated ‘chalk’ (micrite) (see Håkansson & Thomsen, 1999). Heinberg concluded that at Stevns Klint all patterns recorded in the bivalve faunas across the K/T boundary were within the range of ordinary population dynamics, linked to ordinary changes in the depositional environment. Seen in that light, it might be better, according to Heinberg, to refer to these changes as faunal adjustments to new environmental conditions rather than as recovery.

Combining these results with the picture drawn here for the Maastricht area results in the following best constrained scenario. The demise of the highly diverse latest Maastrichtian echinoderm faunas, typical of shallow-water settings with local palaeorelief and associated unconsolidated bottoms, was rapid, suggestive of a catastrophic event (e.g. increased storm activity as a result of an asteroid impact; see above). What follows is the possible equivalent of the ‘dead zone’ of the Danish sections, capped by the Vroenhoven hardground at the base of the Geulhem Member. As outlined above, from the Geulhemmerberg underground workings not enough bulk samples are currently available to test the range of echinoderms between the Berg en Terblijt and Vroenhoven horizons (= section IVf-7 of the Meerssen Member). The earliest Danian echinoderms (e.g. bourgueticrinid crinoids and goniasterid asteroids) occur in fossil hash levels resting on top of the Vroenhoven Horizon, which suggests some time-averaging to have taken place. The immigration of these elements into the study area suggested above thus seems rapid; it may be plotted on the palaeogeographical map of the K/T boundary interval in Håkansson & Thomsen (1999, fig. 1), and extend their ‘K/T boundary sea’ to well south of the Ringkøbing-Fyn High, a structural high. The absence of such typical elements as representatives of the echinoid genus *Echinocorys* and isocrinid crinoids from the lower Geulhem Member

Table 2. Distribution of the crinoids.

	Meerssen	Geulhem
Isocrinidae		
'*Isocrinus*' sp.	+	
Cainocrinidae		
Nielsenicrinus ewaldi	+	
Atelecrinidae		
Jaekelometra gr. *belgica*	+	
Jaekelometra gr. *concava*	+	
Pterocomidae		
Placometra gr. *laticirra*	+	
Atuatucametra annae		+
Conometridae		
Amphorometra gr. *conoidea*	+	
Notocrinidae		
Semiometra lenticularis	+	
Semiometra saskiae	+	
Antedonidae		
Hertha gr. *mystica* ?		+
Bourgueticrinidae		
Bourgueticrinus bruennichinielseni		+
Bourgueticrinus danicus		+
Democrinus? *maximus*		+
Holopodidae		
Cyathidium vlieksi	+	
Saccocomidae		
Applinocrinus cretaceus	+	
Roveacrinidae		
Birgelenocrinus degraafi	+	

Table 3. Distribution of the ophiuroids.

	Meerssen	Geulhem
Euryalidae		
Trichaster? *ornatus*	+	
Trichaster? sp.	+	
Ophiomyxidae		
Ophiomyxa? *rhipidata*	+	
Ophiomyxa? *jekerica*	+	
Ophioscolex? *cretaceus*	+	
Ophiacanthidae		
Ophiacantha? *danica*	+	
Ophiacantha? *striata*		+
Ophioplinthaca? *fuerstenbergii* ?	+	
Ophiuridae		
Felderophiura vanderhami	+	
Ophiocten? *yvonnae*	+	
Stegophiura? *hagenowi* ?	+	
Amphiuridae		

Amphiura? *plana*	+	
Deckersamphiura inusitata	+	
Ophiothricidae		
Ophiothrix? *cristata*	+	
Ophiocomidae		
Ophiarachna? *martinblomi*	+	
Ophiocoma? *rasmusseni*	+	+
Ophiocoma? *senonensis*	+	+
Ophiodermatidae		
Ophiotitanos serrata	+	+
Ophiolepididae		
Ophiomusium granulosum		+
Ophiomusium lux	+	
Mesophiomusium decipiens		+

Table 4A. Distribution of regular echinoids.

	Meerssen	Geulhem
Psychocidaridae		
Tylocidaris gr. *bruennichi*		+
Tylocidaris hardouini		+
Tylocidaris inexspectata	+	
Cidaridae		
Temnocidaris (T.) danica		+
Temnocidaris (T.) sp. 1	+	
Temnocidaris (T.) sp. 2	+	
Temnocidaris (Stereocidaris) gigas	+	
Temnocidaris (S.) sp. 2	+	
Cidaris? *forchhammeri*		+
Cidaris? *rosenkrantzi*		+
Cidaris? sp.		+
Ctenocidaris? *distincta*		+
Goniocidaris? sp.	+	
Diadematidae		
Centrostephanus? sp. (spp. ?)	+	+
Orthopsidae		
Orthopsis miliaris	+	
Saleniidae		
Salenia (S.) belgica		+
Salenia (Pleurosalenia) maestrichtensis	+	
Salenia (P.) sp.	+	
Salenia (P.) sp. nov.		+
Salenidia (Platysalenia?) sanctipetri	+	
Hyposalenia heliophora		+
Salenocidaris minima		+
Arbaciidae		
Codiopsis disculus	+	
Acropeltidae		
Goniopygus heberti		+
Goniopygus minor		+
Goniopygus sp. nov.	+	

Phymosomatidae		
Phymosoma gr. *granulosum*		+
Gauthieria grossouvrei	+	
Gauthieria pseudoradiata	+	
Circopeltis maastrichtensis		+
Circopeltis sp.		+
Trochalosoma? *corneti*	+	
Phymotaxis tournoueri	+	
Stomopneustidae		
Winkleria maastrichtensis	+	
Temnopleuroida		
Micropsidia salis		+
Micropsidia? sp.	+	
Thylechinus sp. nov.		+

Table 4B. Distribution of irregular echinoids.

	Meerssen	Geulhem
Holectypidae		
Coenholectypus macrostomus	+	
Conulidae		
Adelopneustes boehmi		+
Adelopneustes montainvillensis		+
Plagiochasmidae		
Plagiochasma cruciferum		+
Plagiochasma lammersmaxi	+	
Echinogalerus transversus	+	
Echinogalerus sp. 1	+	
'Nucleopygidae'		
Catopygus gr. *fenestratus*	+	
Faujasiidae		
Faujasia apicalis	+	
Oolopygus gr. *pyriformis*	+	
Rhynchopygus marmini	+	
Procassidulus elongatus		+
Procassidulus lapiscancri	+	
Cassidulidae		
Rhyncholampas macari	+	
Echinolampadidae		
Gitolampas oblongus		+
incertae sedis		
Nucleopygus coravium	+	
Nucleopygus scrobiculatus	+	
Cardiasteridae		
Cardiaster granulosus	+	
Labrotaxidae		
Hemipneustes striatoradiatus	+	
Micrasteridae		
Diplodetus aff. *americanus*	+	
Hemiasteridae		
Hemiaster koninckanus	+	

Hemiaster prunella	+	
Leymeriaster maestrichtensis	+	
Schizasteridae		
'*Linthia breviuscula*'		+
Paraster sindensis		+

Table 5. Distribution of the asteroids.

	Meerssen	Geulhem
Astropectinidae		
Aldebarania sp. nov. ?	+	
Astropecten? sp. nov.		+
astropectinid sp. nov.	+	
Lophidiaster? gr. *punctatus/postornatus*		+
Goniasteridae		
Metopaster alexiae	+	
Metopaster aff. *carinatus*		+
Metopaster continuus		+
Metopaster kagstrupensis		+
Metopaster lisannae	+	
Metopaster miriamae	+	
Metopaster aff. *planus*		+
Metopaster spencerii		+
Metopaster sp. 1	+	
Metopaster sp. 2	+	
Metopaster sp. 3	+	
Metopaster sp. 4 (aff. *elegans*)	+	
Recurvaster antemammillatus	+	
Recurvaster mammillatus		+
Ophryaster? *maastrichtensis*	+	
Chomataster acules		+
Crateraster anchylus		+
Caletaster? sp.		+
goniasterid sp. 1	+	
goniasterid sp. 2	+	
goniasterid sp. 3	+	
goniasterid? sp. 4	+	
goniasterid sp. 6	+	
Sphaerasteridae		
Valettaster gr. *ocellatus*	+	+
Stauranderasteridae		
Stauranderaster? sp.	+	+
Stauranderaster? *miliaris*		+
Aspidaster? sp. 1	+	
Pycinasteridae		
Pycinaster aff. *cornutus*		+
Pycinaster? aff. *rosenkrantzii*		+
Pycinaster sp. 2		+

Table 6. Disttribution of crinoids within the Geulhem Member.

	lower	upper
Pterocomidae		
Atuatucametra annae		+
Antedonidae		
Hertha gr. *mystica* ?		+
Bourgueticrinidae		
Bourgueticrinus bruennichinielseni	+	
Bourgueticrinus danicus	+	+
Democrinus? *maximus*	+	

Table 7. Distribution of ophiuroids within the Geulhem Member.

	lower	upper
Ophiacanthidae		
Ophiacantha? *striata*	+	
Ophiothricidae		
Ophiothrix? *cristata*	+	
Ophiocomidae		
Ophiocoma? *rasmusseni*	+	
Ophiocoma? *senonensis*	+	
Ophiodermatidae		
Ophiotitanos serrata	+	+
Ophiolepididae		
Ophiomusium granulosum	+	
Mesophiomusium decipiens	+	

Table 8. Distribution of echinoids within the Geulhem Member.

	lower	upper
Psychocidaridae		
Tylocidaris gr. *bruennichi*		+
Tylocidaris hardouini	+	
Cidaridae		
Temnocidaris (T.) danica	+	
Cidaris? *forchhammeri*	+	
Cidaris? *rosenkrantzi*	+	
Cidaris? sp.	+	
Ctenocidaris? *distincta*		+
Diadematidae		
Centrostephanus? sp. (spp. ?)	+	+
Saleniidae		
Salenia (S.) belgica	+	
Salenia (P.) sp. nov.		+
Hyposalenia heliophora	+	+
Salenocidaris minima	+	
Acropeltidae		

Goniopygus heberti		+
Goniopygus minor		+
Phymosomatidae		
Phymosoma gr. *granulosum*		+
Gauthieria grossouvrei		+
Circopeltis maastrichtensis		+
Circopeltis sp.		+
Temnopleuroida		
Micropsidia salis		+
Thylechinus sp. nov.		+
Conulidae		
Adelopneustes boehmi		+
Adelopneustes montainvillensis	+	
Plagiochasmidae		
Plagiochasma cruciferum		+
Faujasiidae		
Procassidulus elongatus	+	+
Echinolampadidae		
Gitolampas oblongus		+
Schizasteridae		
'Linthia breviuscula'	+	
Linthia? sp. (spp.)	+	+
Paraster sindensis	+	

Table 9. Distribution of asteroids within the Geulhem Member.

	lower	upper
Astropectinidae		
Astropecten? sp. nov.	+	+
Lophidiaster? gr. *punctatus/postornatus*	+	+
Goniasteridae		
Metopaster aff. *carinatus*		+
Metopaster continuus	+	
Metopaster kagstrupensis	+	
Metopaster aff. *planus*	+	
Metopaster spencerii	+	
Metopaster sp. 2		+
Recurvaster mammillatus		+
Chomataster acules	+	
Crateraster anchylus	+	
Caletaster? sp.		+
Sphaerasteridae		
Valettaster gr. *ocellatus*	+	+
Stauranderasteridae		
Stauranderaster? sp.		+
Stauranderaster? *miliaris*	+	
Aspidaster? sp. 1	+	+
Pycinasteridae		
Pycinaster aff. *cornutus*		+
Pycinaster? aff. *rosenkrantzii*		+
Pycinaster sp. 2		+

demonstrates that echinoderm settlement was strongly influenced by local conditions, depth and/or energy related.

In short, echinoderm distribution across the K/T boundary in the Maastrichtian type area would indicate rapid extinction of (sub)tropical shallow-water communities, and a subsequent recovery phase characterised by (?rapid) immigration from the north/northwest, linked with an earliest Danian (post-Cerithium Kalk) transgressive pulse. Faunal links with the Danian/North Atlantic region seem to have persisted until the Middle Danian, but by that time local conditions appear to have returned to the pre-K/T boundary development of palaeorelief in the area.

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[For additional references see also Parts 1-5 of the current series (Jagt, 1999a, b, 2000a-b; Kutscher & Jagt, 2000).]

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