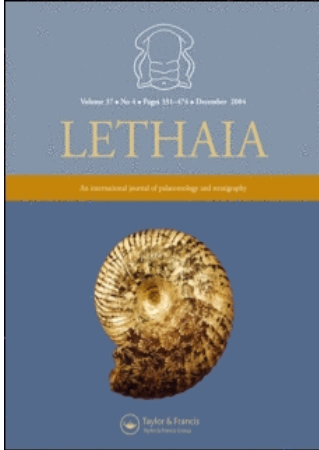


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Field sampling bias, museum collections and completeness of the fossil record

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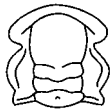
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Museum specimens, particularly old collections, typically lack comprehensive field data and determination of substrate, sampling biases, etc., is problematic. Diversity at the generic level of all identifiable latest Cretaceous (Campanian–Maastrichtian) echinoderm remains in major museum collections from the Mons (southern Belgium) and Danish (Jylland (Jutland) and Sjælland (Zealand)) basins were compared to those of the Liège-Limburg Basin. The last-named has been studied in detail, including microscopical analysis of ossicles picked from bulk samples. Echinoids of the Mons Basin show similarities to those of the Liège-Limburg Basin, but crinoids, asteroids and ophiuroids remain poorly known from the former. Echinoderms of the Danish Basin resemble those of similar chalk lithofacies in the Liège-Limburg Basin, despite significant geographical separation. These disparities can be explained, at least in part, by collector bias in sampling methodology, although differences in substrate presumably also had an influence. □ *Echinoderms, fossil record, museums, sampling, Upper Cretaceous.*

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The fossil record is no more than a sample of past life on this planet and our knowledge of it can be based on no more than a sample of a sample. This (smaller) sample mainly consists of the evidence of field data and museum (and other) collections, and is recorded in the publications that they engender. Many factors influence the quality of the known fossil record, and biases are recognized due to stratigraphic, geographic and taxonomic sampling (see, for example, Raup 1976a, b, 1977; Sheehan 1977; Koch 1978, 1998; Paul 1982, 1985; Benton & Simms 1995, 1996; Donovan 1996; Donovan & Paul 1998; Benton *et al.* 2000). Gaps in the stratigraphic or geographic distributions of a fossil taxon may be real (in life the species did not range into the research area and was not brought in by post-mortem transport), a taphonomic artifact (preservational biases removed [e.g. dissolution] or disguised [e.g. fragmentation] evidence of the taxon), the result of inadequate sampling or a combination of these and/or other factors. While all these possible influences can be considered when collecting in the field, museum specimens generally lack comprehensive field data, particularly those from old collections, so determination of sampling biases, etc., is, at best, problematic (Allmon 2005). Herein, we examine the influence of taphonomic artifacts and collection bias on museum collections of an invertebrate group with

an extensive fossil record, the echinoderms, from a stratigraphic interval and geographic locations that might be considered to have been well collected, that is, the Campanian–Maastrichtian interval of selected parts of northwest Europe. Our ‘sampling bias’ concentrates on museum collections that have been examined in detail by the senior author. Although other parts of the same region are also worthy of similar study (such as northern Germany), the basins chosen nevertheless demonstrate a pattern of bias inherent in the collecting of these regions during the past 200 years.

Macropalaeontologists in search of answers to questions in palaeobiology have learned to deal with the imperfections of their fossil record using many methodologies. These include various statistical techniques and using exceptional preservation in Konservat Lagerstätten as windows into an otherwise ‘empty’ part of the fossil record (Donovan & Paul 1998). An important technique employed by workers on groups that are typically preserved as small disarticulated elements, perhaps more commonly associated with micropalaeontology, is bulk sampling and sieving of time-averaged sediment samples in order to collect, for example, ophiuroid ossicles (Jagt 2000a), crustacean fragments (Collins 1999) or micromammal teeth (van den Hoek Ostende 2003).

Even well-indurated rocks are amenable to such techniques if correctly prepared and thus can produce unexpected results (e.g., Dixon *et al.* 1994). This technique results in a less biased taxonomic record than would be obtained by concentrating upon complete specimens of groups with multi-element skeletons. However, for some groups of macro-invertebrates, such as the Chalk echinoderms of northwest Europe, the very numerous complete specimens available in museum collections mean that such techniques are rarely employed. Although fragments cannot replace complete specimens, where available, faunal studies of groups that are typically easily disarticulated need to include all lines of morphological information to produce a comprehensive picture of biotic diversity. For example, Jagt (1999a–c, 2000a–d) has worked extensively on the type Maastrichtian of Limburg, The Netherlands and Liège, Belgium, and has shown that, by bulk sampling across units and cross referencing with museum collections, a complete record of echinoderm evolution and extinction can be gauged for this interval with a high level of confidence (see also Smith & Jeffery 2000).

It is apparent that the data obtained from bulk sampling add new information to our knowledge of intervals that have been collected since the 19th century or before. This is despite large reference collections in museums being developed at the same time. Existing museum collections have grown on the basis of specimens accumulated to answer different scientific questions from those being asked now (Allmon 2005). Although the fossil record of echinoderms from the Campanian and Maastrichtian stages (Upper Cretaceous) of northwest mainland Europe has been widely studied for over 150 years, the effects of differing substrates, geographical variation and, most importantly, collector bias remain imperfectly understood (J.W.M. Jagt, personal communication 2004). For example, although Desor (1847) gave considerable importance to the echinoderms in defining the Maastrichtian–Danian interval, subsequent research (e.g., Asgaard 1979; Gravesen 1979; Jagt 1999a–c, 2000a–d; Smith & Jeffery 2000) has readdressed and refined our knowledge of their biostratigraphic and biogeographic distribution. The present paper is an attempt to identify the controls that determined the composition of some of these collections.

This paper reports on a survey of four echinoderm classes (Crinoidea, Echinoidea, Asteroidea, Ophiuroidea) from the Campanian and Maastrichtian of the Mons and Danish basins, based on collections in the Institut royal des Sciences naturelles de Belgique, Brussels (IRScNB), the Natuurhistorisch Museum

Maastricht (NHMM) and the Geological Museum, University of Copenhagen (MGUH). The data obtained have been compared with the more complete knowledge of the Campanian–Maastrichtian interval of the Liège-Limburg Basin of Belgium and The Netherlands, monographed by Jagt (1999a, b; 2000a–d) with the aid of co-workers and including numerous taxa known only from fragments or ossicles gleaned from bulk samples (typically 1–500 kg). The distribution of genera in each of the formations has been noted; samples from each formation represent a time-averaged collection and formations can be correlated between all areas.

This contribution is a survey of echinoderms from selected museum collections made in three regions in northwest Europe. It is not intended to examine in detail the relation of the echinoderms to the structure and stratigraphy of the northern European basins, although relevant comments on these factors are made where appropriate, but to focus on three well-sampled study areas. Data are from museum collections; generally, available sedimentological and lithostratigraphical information is minimal because of the bias in sourcing the material. Differences in biostratigraphic position and sedimentary facies will account for some faunal difference, but this paper examines collections in an attempt to identify any biases in collecting.

Collections

Mons Basin, Belgium (Institut royal des Sciences naturelles de Belgique, Brussels; IRScNB)

Extensive collections are available from a number of disused quarries in the Ciply area of the Hainaut province, southern Belgium. The Mons Basin consists of a succession of rocks ranging from Lower Campanian to Middle Danian. It is an extension of the Paris Basin (Robaszynski 1978) and lies to the south of the Brabant Massif (Christensen 1999). It shows a slightly different depositional history from the Liège-Limburg Basin, from which it is separated by a zone 50 km in width that is sparse in Upper Cretaceous strata. The stratigraphic correlation of this basin, revised by Robaszynski & Christensen (1989) and Robaszynski *et al.* (2002), is summarized in Figs 1 and 2. Fossiliferous exposures in Hainaut are rarer (Robaszynski 1978) than in the other basins considered herein, but a few quarries have yielded numerous echinoderm fossils (*ca.* 800 specimens), particularly the echinoid *Echinocorys*.

| Belemnite Zones | Mons Basin | | | Liege-Limburg Basin | | |
|---|---------------------------------|---|---|-------------------------------|--|--|
| | Formation | General Lithology | Palaeoenvironment | Formation | General Lithology | Palaeoenvironment |
| <i>Belemnitella langei</i> | | | | | | |
| <i>Belemnitella minor</i> | (SPI) Spiennes Chalk Formation | White to whitish grey, coarse-grained chalk; calcarenitic towards top | Deep water carbonate shallowing upwards | Gulpen Formation (lower part) | Light grey to whitish yellow glauconitic, fine-grained clay and calcareous marls and fine-grained chalks | Deep water carbonate (Jagt 1999a) |
| <i>Belemnitella mucronata</i> | (NOU) Nouvelles Chalk Formation | Pure, massive soft, very fine-grained white chalk | Deep water carbonate | | | |
| | (OBG) Obourg Chalk Formation | Fine-grained white to slightly grey chalk with basal conglomerate layer | Deep water carbonate | | | |
| Upper Campanian | (T) Trivières Formation | Fine-grained white to slightly grey chalk with basal conglomerate layer | | | | |
| Lower Campanian <i>Goniatites quadrata</i> | | | Deep water carbonate | (VAA) Vaals Formation | Yellow-greenish grey, glauconitic fine-grained sandstones | Shallow-marine warm water (Jagt 1999a) |

Fig. 1. Lithostratigraphic correlations between the Campanian strata of the two study areas and their relationship to the standard belemnite biozonation (Christensen 1979, 1984; A.V. Dhondt, 1999 and personal communication to A.W.H. September 2004). Sources of published information as in Fig. 2. Key: VAA = Vaals Formation, including the Benzenrade Member of the Gulpen Formation.

Danish Basin (Geological Museum, University of Copenhagen; MGUH)

The reference collections from the interval of interest in the MGUH are comprised of two principal components. Specimens were collected principally from the east coast of Sjælland (Zealand) and northern Jylland (Jutland) by past curators and amateurs, dating from at least the late 19th century. These were supplemented by the bulk and spot samples of H. Wienberg Rasmussen from Sjælland (Zealand) (localities at Stevns Klint and Kongsted) and Møns Klint. All lithofacies considered herein (Figs 1, 2) were correlated by Birkelund (1957) and Christensen (1979, 1984); Håkansson & Hansen (1979) refined the lithostratigraphy of the more distant Jylland (Jutland) localities. About 4,000 specimens were examined, including asteroid and crinoid ossicles.

Liège-Limburg Basin (Natuurhistorisch Museum Maastricht; NHMM)

Older collections of echinoderms from the Campanian and the type area of the Maastrichtian (Fig. 1) are in the IRScNB, the NHMM, the Nationaal Natuurhistorisch Museum, Leiden, and elsewhere. These have been considerably augmented by new material collected by a team of geologists known as the Vijlen Group, who have sampled every unit in the Maastrichtian of the region. Jagt (1999a, b, 2000a–d) published a comprehensive monograph on the echinoderm fauna of the region, based on his PhD research; these publications, documenting many hitherto unrecognized or new taxa, based in part on extensive fragmentary remains as well as complete specimens, is the closest approximation to the true diversity of this fauna available, based on the

| Belemnite Zones | Mons Basin | | | Liège-Limburg Basin | | | Danish Basin | | |
|--|---|--|--------------------------------|----------------------------|--|---|---|--|---|
| | Formation | General Lithology | Palaeo-environment | Formation | General Lithology | Palaeo-environment | Formation | General Lithology | Palaeo-environment |
| <i>Belemnella kazimiroviensis</i> | | | | (MAA) Maastricht Formation | Poorly indurated white-yellow to yellowish grey, fine- to coarse-grained chalk | Middle sub-Littoral subtropical warm water Carbonate platform (Dhondt 1999) | (SKK1-2†) 'White Chalk' | White fine-grained chalk | Deep water carbonate |
| <i>Belemnitella junior</i> | | | | (SSY) St-Symphorien | Poorly cemented calcarenite with grey-green phosphatised granules and pebbles | Shallow sublittoral subtropical | (GUL (U)) Gulpen Formation (upper part) | White, fine grained chalk & yellowish-grey, glauconitic fine-grained chalk | Deep water carbonate shallowing up to sublittoral subtropical carbonate (Dhondt 1999) |
| Upper Maastrichtian | | | | | | | | | |
| Lower Maastrichtian | | | | | | | | | |
| <i>Belemnella sumensis</i> - <i>B. fastigata</i> | | | | | | | | | |
| <i>Belemnella obtusa</i> | (CIP) Cipy-Malogne Phosphatic Chalk Formation | Calcarenite (phosphate granules within chalky matrix); intensely bioturbated | Shallow sublittoral warm water | | | | (SKK3) 'White Chalk at Mons Klint' | White fine-grained chalk | Deep water carbonate |
| <i>Belemnella pseudobtusa</i> | | | | | | | | | |
| <i>Belemnella lanceolata</i> | | | | | | | (SKK4) 'White Chalk at Kongsted' | White fine-grained chalk | Deep water carbonate |

Fig. 2. Lithostratigraphic correlations between the Maastrichtian strata of the three study areas and their relationship to the standard belemnite biozonation (Christensen 1979, 1984). Based on data in Albers & Felder (1979), Bromley (1979), Christensen (1975, 1979, 1984, 1999), Håkansson & Hansen (1979), Birkelund (1993), Jagt (1999a), Robaszynski & Christensen (1989), Robaszynski *et al.* (2002), Surlyk (1979) and Surlyk & Håkansson (1999), and provided by A.V. Dhondt (personal communication to A.W.H. September 2004).

examination of 750,000 to 1,000,000 complete and fragmentary echinoderm specimens (J.W.M. Jagt, written communication to S.K.D. 2003). This research led to a much greater diversity of fossils being recognized than in earlier studies, particularly for those groups that are most commonly found as fragments, such as the ophiuroids.

Methodology

In the collections of the IRScNB (Mons Basin) and MGUH (Danish Basin), outlined above, every echinoderm fossil of relevant stratigraphic position and locality was examined and assigned to genus, considered for this study to be the highest taxonomic unit that confidently could be assigned to many of

the fragmentary fossil echinoderms, although it is accepted that species-level classification is possible for approximately 60% of the specimens (e.g., Fig. 3). It was also considered inappropriate to use a species-level classification for comparison across biogeographic provinces, as the echinoderms of neither the Mons nor Danish basins had received recent systematic revision. A generic classification of disarticulated elements proved problematic for certain specimens/taxa, such as with certain echinoid spines and nodals of isocrinids, and a looser systematic assignment was deemed appropriate, such as '*Cidaris*' sp. and '*Isocrinus*' sp., respectively. Such 'lumping' is recognized as such, and may conceal patterns or details that will only become apparent as our knowledge of fragmentary ossicles continues to improve. Following this process, the MGUH and IRScNB



Fig. 3. Examples of fragmentary echinoderms (isocrinid crinoids) from Denmark used in this study. □A. *Austinocrinus bicoronatus* (von Hagenow) from Kongsted, MGUH 26889. □B. *Praeissellicrinus? limburgicus* (Rasmussen) from Møns Klint, MGUH 26890. Scale bars represent 5 mm.

collections were then available for comparison with the more extensive collections of the NHMM (Liège-Limburg Basin) (Jagt 1999a, b, 2000a–d).

Most systematic assignments were completed with some confidence, as a significant proportion of the collections of the IRScNB and MGUH had already been classified to at least generic level by other specialists, such as Rasmussen, and Smith and Jeffery. The Danish material was also reviewed for the symposium on ‘Cretaceous–Tertiary boundary events’ in September 1979 (Asgaard 1979; Gravesen 1979). The quality and quantity of material, and taxonomic groups represented in any collection, were naturally influenced by the interests of that museum’s donors, curators and collectors. For example, the abundance of crinoids, ophiuroids and asteroids in the MGUH is a product of Rasmussen’s research programme (e.g., Rasmussen 1950, 1953, 1961).

Results

Dataset

Tables 1 and 2 present the occurrence of taxa for all data sets. Because the results from the type Maastrichtian (Liège-Limburg Basin) represent the only data set to be produced using fragmentary specimens and ossicles picked from large bulk

samples, it is considered to be the benchmark (that is, 100% taxa present) for all comparisons. Results show that regular echinoids (in which spines and test fragments are considered, particularly for cidaroids) have the greatest similarity to the Liège-Limburg Basin, in both the Mons (66%) and Danish (75%) basins. Although complete specimens of irregular echinoids are commoner in collections, a not unsurprising observation (Kier 1977; Smith 1984), the Mons (44%) and Danish (38%) basins have markedly lower generic diversities than the benchmark. Remaining data show a much greater disagreement. The Danish Basin shows a considerable similarity to the Liège-Limburg Basin (crinoids 75%; asteroids 66%; ophiuroids 70%), results that are in stark contrast to the Mons Basin (crinoids 8%; asteroids 26%; ophiuroids 0%).

Crinoids

The large, cylindrical ossicles of *Bourgueticrinus sensu lato* occur throughout the study area. In the Mons Basin, *Bourgueticrinus* is the only crinoid genus recorded, comatulids and, more surprisingly, isocrinines being unknown. In contrast, all of these groups are present in the Danish and Liège-Limburg basins. Two examples of the known distribution of distinctive crinoid taxa are instructive. Common and

Table 1. Presence/absence chart of crinoids, asteroids and ophiuroids from the study areas (abbreviations for lithostratigraphic horizons as in Figs 1, 2 and GUL(L) = lower Gulpen Formation). Data collected by A.W.H., supplemented by Jagt (1999b, 2000a, c) for MAA, GUL(U), GUL(L) and VAA. Key: + = identified genera; +? = identification uncertain; (+) = probably present, but identification based on poorly preserved material.

| | Maastrichtian | | | | | | | | Campanian | | | | | | |
|-------------------------|---------------|-----|-----|---------|------|------|------|------|-----------|-----|-----|---|---------|----------|--|
| | SSY | CIP | MAA | GUL (U) | SKK1 | SKK2 | SKK3 | SKK4 | SPI | NOU | OBG | T | GUL (L) | VAA (BZ) | |
| <i>Isocrinus</i> | | | + | + | + | + | + | | | | | | + | | |
| <i>Austinocrinus</i> | | | | + | | | | + | | | | | | | |
| <i>Isselocrinus</i> | | | | + | + | + | + | | | | | | | | |
| <i>Nielsenocrinus</i> | | | + | + | + | + | + | | | | | | + | + | |
| <i>Praeisselocrinus</i> | | | | + | | | + | | | | | | + | | |
| <i>Jaekelometra</i> | | | + | | | | | | | | | | | | |
| <i>Placometra</i> | | | + | + | | | | | | | | | + | + | |
| <i>Amphorometra</i> | | | +? | +? | + | | + | | | | | | | | |
| <i>Semiometra</i> | | | + | | | + | | | | | | | + | | |
| <i>Hertha</i> | | | +? | + | + | | + | | | | | | | | |
| <i>Dunnocrinus</i> | | | + | + | | | | | | | | | | | |
| <i>Bougueticrinus</i> | + | + | + | + | + | + | + | | | | | | + | | |
| <i>Cyathidium</i> | | | + | + | | | | | | | | | | | |
| <i>Applinocrinus</i> | | | + | + | | | | | | | | | + | | |
| <i>Birgelenocrinus</i> | | | + | | | | | | | | | | | | |
| <i>Veugelersia</i> | | | + | | | | | | | | | | | + | |
| <i>Loriolometra</i> | | | | | | | | | | | | | | + | |
| <i>Monachocrinus</i> | | | | | + | | | | | | | | + | | |
| <i>Astropecten</i> | | | + | + | + | + | + | | | | | | | | |
| <i>Lophidiaster</i> | | | + | + | | | | | | | | | + | | |
| <i>Aldebarania</i> | | | + | | | | | | | | | | | | |
| Benthopectinidae | | | + | + | | | | | | | | | + | + | |
| <i>Metopaster</i> | | + | + | + | + | + | + | | | | | | + | + | |
| <i>Parametopaster</i> | | | + | | | | | | | | | | | | |
| <i>Recurvaster</i> | | + | + | + | + | + | + | | | | | | + | | |
| <i>Nymphaster</i> | | | | + | + | + | + | | | | | | + | | |
| <i>Chomataster</i> | | | + | + | + | + | + | | | | | | | | |
| <i>Ophryaster</i> | | | + | + | + | + | | | | | | | + | | |
| <i>Crateraster</i> | | +? | | + | + | | + | | | | | | + | | |
| <i>Valettaster</i> | | | + | + | + | | | | | | | | + | | |
| <i>Stauranderaster</i> | | +? | + | | + | + | + | | | | | | | | |
| <i>Coulonia?</i> | | | | | | | | | | | | | + | + | |
| <i>Haccourtaster</i> | | | | | | | | | | | | | + | | |
| <i>Asterias</i> | | | | | | + | + | | | | | | | | |
| <i>Pycinaster</i> | | | | + | + | | | | | | | | + | | |
| <i>Ophiomusium</i> | | | + | + | + | + | + | | | | | | + | + | |
| <i>Amphiura</i> | | | + | + | + | + | + | | | | | | + | | |
| <i>Asteronyx</i> | | | | + | + | + | + | | | | | | | | |
| TOTAL | 1 | 5 | 26 | 26 | 20 | 14 | 16 | 1 | 0 | 0 | 0 | 0 | 21 | 8 | |

distinctive isocrinines include *Austinocrinus*, known from the Lower Maastrichtian of Kongsted and Møn, Danish Basin (Rasmussen 1953, 1961) (Fig. 3A). *Austinocrinus bicoronatus* (von Hagenow, 1840) occurs at the base of the Vijlen Member, Gulpen Formation, Liège-Limburg Basin (Jagt 1999b), and this species is widely recorded from the uppermost Campanian and lowermost Maastrichtian of Norfolk, England, and Rügen, Germany (Rasmussen 1961; Smith & Wright 2002). Similarly, the distinctive columnals of *Praeisselocrinus? limburgicus* (Rasmussen) (Fig. 3B) are now known from the Lower Maastrichtian of Møns Klint, Danish Basin, as well as the basal Vijlen Member of the Liège-Limburg Basin (Rasmussen 1961; Jagt 1999b).

Asteroids and ophiuroids

Rasmussen's (1945, 1950, 1979) interest in Late Cretaceous–Danian asteroids and, to a lesser extent, ophiuroids has meant that the collection of these classes from the Danish Basin (MGUH) is of a high standard. Ophiuroids remain unknown from the Mons Basin.

Echinoids

Regular echinoids are common in the Mons Basin and compare favourably with the other study areas. The most obvious bias are reports of distinctive spines of *Tylocidaris* species in the Maastrichtian formations,

Table 2. Presence/absence chart of echinoids from the study area (abbreviations for lithostratigraphic horizons as in Figs 1, 2 and GUL(L) = lower Gulpen Formation). Data collected by A.W.H., supplemented by Jagt (2000b) for MAA, GUL(U), GUL(L) and VAA, and by Asgaard (1979) and Gravesen (1979). Key: + = identified genera; +? = identification uncertain.

| | Maastrichtian | | | | | | | | | Campanian | | | | |
|-----------------------|---------------|-----|-----|--------|------|------|------|------|-----|-----------|-----|---|---------|---------------|
| | SSY | CIP | MAA | GUL(U) | SKK1 | SKK2 | SKK3 | SKK4 | SPI | NOU | OBG | T | GUL (L) | VAA & GUL(BZ) |
| <i>Tylocidaris</i> | + | + | + | | + | + | + | | | | | | | |
| <i>Temnocidaris</i> | | + | + | + | + | + | + | | | | | | + | |
| <i>Cidarid s.l.</i> | + | + | + | + | + | + | + | | + | + | + | + | | |
| <i>Orthopsis</i> | | | + | | | | | | | | | | | |
| <i>Salenia</i> | | + | + | + | + | | | | | | | | + | |
| <i>Salenidia</i> | | + | + | | + | | + | | | | | | | |
| <i>Codiopsis</i> | | | + | | | | | | | | | | | |
| <i>Phymosoma</i> | | | | + | + | | + | | | + | + | | + | |
| <i>Gauthieria</i> | + | | + | | + | | | | + | + | + | | + | + |
| <i>Gauthiosoma</i> | | + | | + | | | | | | | | | + | |
| <i>Trochalosoma</i> | + | + | + | | | | | | | | | | + | |
| <i>Phymotaxis</i> | | | + | | | | | | | | | | + | |
| <i>Winkleria</i> | | | + | | | | | | | | | | | |
| <i>Coenholectypus</i> | | | + | | | | | | | | | | | |
| <i>Galerites</i> | | + | | + | + | | | | | | | | | |
| <i>Plagiochasma</i> | | | + | | | | | | | | | | | |
| <i>Echinogalerus</i> | | + | + | + | | | | | | | | | | |
| <i>Catopygus</i> | + | + | + | | | | | | | | | | | |
| <i>Oolopygus</i> | | | + | + | + | | | | | | | | | |
| <i>Rhynchopygus</i> | | | + | | | | | | | | | | | |
| <i>Procassidulus</i> | | | + | | | | | | | | | | | |
| <i>Rhyncholampas</i> | | | + | | | | | | | | | | | |
| <i>Nucleopygus</i> | | + | + | + | | | | | | | | | | |
| <i>Echinocorys</i> | | + | | + | + | | | | + | + | + | + | + | + |
| <i>Cardiaster</i> | | + | + | + | + | | | | + | | + | | | + |
| <i>Hemipneustes</i> | + | + | + | + | | | | | | | | | | |
| <i>Cyclaster</i> | | | | + | | | | | | | | | | |
| <i>Diplodetus</i> | | | + | + | | | | | | | | | + | + |
| <i>Hemiaster</i> | + | | + | + | | | | | | | | | + | + |
| <i>Galeola</i> | | | | | | | | | | + | | | + | |
| <i>Cardiotaxis</i> | | | | | | | | | | | | | + | |
| <i>Hagenowia</i> | | | | | | | + | + | | | | | + | |
| <i>Micraster</i> | | | | | | | | | + | + | + | | + | |
| TOTALS | 7 | 14 | 24 | 15 | 14 | 3 | 6 | 1 | 5 | 6 | 7 | 2 | 13 | 5 |

taxa otherwise considered to be limited to the Danian. The most probable explanation is that fissures of post-Cretaceous age, that are infilled with Danian sedimentary rocks bearing echinoids, crosscut the Maastrichtian strata (J.W.M. Jagt, personal communication to A.W.H. 2003).

Maastrichtian echinoids from the Mons Basin are quite distinctive, with common small taxa (<30 mm) such as *Salenidia* and *Gauthieria*. Cidaroid spines suggest a greater diversity in the Mons Basin than elsewhere in the study area. The different echinoid associations of the Mons Basin are apparently specific to different calcarenite lithofacies, which is one of the principal controls on community structure (Hunter research in progress). In the Danish Basin regular echinoids also compare favourably with those of the Liège-Limburg Basin. Most notably, in the Low Countries *Tylocidaris* did not appear until the Danian, with the exception of *T. (T.) inexpectata* Jagt &

van der Ham, whereas *T. (Oedematocidaris) baltica* (Schlüter) is known from the upper Maastrichtian of Denmark. The collection from the Mons Basin is dominated by irregular echinoids, particularly *Echinocorys*, a genus that is also the commonest echinoid in the Danish Basin (S.L. Jakobsen, personal communication to A.W.H. 2003).

Discussion

Not considering fossils because they are poorly preserved, fragmentary or difficult to identify can lead to an impaired understanding of the fossil record (Donovan 1996; Donovan & Paul 1998). The perceived imperfection of the fossil record (Darwin 1859) is true for unmineralized tissues and organisms, although our knowledge of such groups continues to improve (Briggs & Gall 1990). Invertebrate groups

with multi-element skeletons characterized by robust hard parts, such as echinoderms or decapod crustaceans, need to be studied from both complete and fragmentary specimens in order to have an approximation of their true diversity (Donovan 2001, 2003).

How great a similarity might be expected between the echinoderm faunas of the three northwest European basins under consideration and do estimates of diversity have any true validity? The echinoderm faunas were probably quite similar at the generic and species level in the Late Cretaceous. As noted by Koch (1998, p. 202), about 50% of the Late Cretaceous bivalves of the US Atlantic and Gulf coastal plains also occur in northern and western Europe. Even at that time, the geographic separation of these two regions was greater than that between the shelf basins considered herein. Further support for such assumptions comes from the diversity of wide-ranging nektic, planktonic and benthic invertebrates of recognized biostratigraphic value that occur within this interval. Jagt's (1999a, b, 2000a–d) detailed monographic study, using abundant disarticulated ossicles as well as complete tests and relying on a dataset several orders of magnitude greater than that available from elsewhere, is a sublime study of Late Cretaceous echinoderms. Although rarities were conceivably missed, surely all common taxa were recognized, whatever the state of preservation.

The principal groups of crinoids considered were *Bourgueticrinus*, isocrinines and comatulids. Sessile *Bourgueticrinus* and isocrinines would have anchored to the chalk substrata, whereas comatulids were vagile, walking and/or swimming with their arms (Messing 1997); isocrinines are also capable of relocation (Messing *et al.* 1988). In the Mons Basin comatulids are absent and the only isocrinine is *Nielsenicrinus*, known from a thin unit of calcarenites on the Silurian basement produced by a short-lived marine incursion onto the Brabant Massif (although inadequate labelling of this specimen in the IRScNB collections makes a more precise locality difficult to define). This contrasts with the Liège-Limburg and Danish basins, where all three groups are found at all levels of the succession. In contrast to the Liège-Limburg Basin, the Mons Basin had more siliciclastic input, probably explaining in part the faunal differences between these basins. Recent sampling in southern Sweden, close to the unconformity at the base of the Campanian (Surlyk & Christensen 1974), has demonstrated similar differences to the more calcarenitic strata of the type Maastrichtian (Hunter research in progress). There is no satisfactory explanation for the general absence of crinoids from the Mons Basin; it may be that they were simply not collected. If they are very rare, then high-resolution collecting of the Danish and

Liège-Limburg basins has demonstrated how even rare crinoids may be recognized.

Significant environmental variations are indicated by the varied sedimentology of the Danish Basin (Rasmussen 1971; Surlyk 1979; Surlyk & Håkansson 1999), data that are of relevance in determining the habitat preferences of the echinoderms from this succession. However, such information is not recorded with specimens collected from float. Further, at Stevns Klint, fallen blocks from the Maastrichtian and Danian are mixed together on the foreshore. Collections from Møns Klint are similarly mainly derived from float and restricted to only about a third of the 6 km of section. This, and other, aspects of the present study indicate that the ecological signal determined by substrate is commonly 'overprinted' by collector bias, producing a skew away from those echinoderms (crinoids, asteroids, ophiuroids) that are commonly preserved as disarticulated ossicles and are perceived as difficult to determine systematically. While taphonomic bias of the fossil record cannot be improved, collector bias can be reduced.

Of the echinoderms of the Mons Basin, only the echinoid diversity shows similarities with the data from the Liège-Limburg Basin. Of these, it is the regular echinoids that show the closest similarity, having the most consistently reproducible fossil record across the part of the Chalk Sea considered herein. This is in contrast to the generally accepted poor fossil record of the regular echinoids (Kier 1977; Smith 1984; but see Greenstein 1994). The irregular echinoids of the Mons Basin also compare favourably with those of the Liège-Limburg Basin. This is explained by the high preservation potential of such infaunal and semi-infaunal echinoids, and also by the geographic isolation of the Danish Basin, producing a geographic province where taxa such as *Micraster* are absent. However, the overall diversity of irregular echinoids in the Danish Basin is low. In contrast to the generally disarticulated crinoids, asteroids and ophiuroids, echinoid tests are usually preserved more or less intact (Jagt 2000d). This is particularly true for burrowing taxa; in contrast, regular echinoids are rarely complete, but are nevertheless identifiable from spines and test fragments. Such taphonomic influences may be deduced from museum collections, but palaeoenvironmental factors are less easily determined. The bias of museum collections towards complete specimens suggests that fragmentary crinoids, asteroids and ophiuroids remain to be collected systematically from the Mons Basin.

As would be predicted, those fossil groups that are typically fragmentary, but have been well studied, such as the asteroids of the Danish Basin (Rasmussen 1950), are more closely correlated with information available

from nearby basins (Liège-Limburg Basin) than where such studies have not been attempted (Mons Basin). However, Rasmussen's studies were conducted without reference to the echinoids, relatively poorly represented at MGUH and in need of major revision (Asgaard 1979; Gravesen 1979). The monograph by Ravn (1928) on these echinoids illustrates well the intensive work that is necessary to classify the available spines and fragments of tests and even the most recent survey of echinoids from this region by Smith & Jeffery (2000) used well-preserved tests as a basis of diversity.

Greenstein (1992, 1994, 1995) demonstrated the role of lithofacies in the distribution of shallow-water echinoids. Differences in water depth, energy conditions and terrestrial input, even in what is often perceived to have been rather a homogeneous Chalk Sea environment, may have had profound influences on the population and community structure of echinoderm groups, influences that cannot be readily determined from most museum collections. In the present study, the available field data for the Mons Basin have been seen to be particularly poor. It may be that groups such as ophiuroids are truly absent from this basin, yet the evidence of the Liège-Limburg and Danish basins (Rasmussen 1950; Jagt 2000a), as well as other Mesozoic successions with calcarenitic lithofacies similar to those encountered in the Mons Basin (e.g. Hunter 2004), have repeatedly demonstrated that such echinoderms are cosmopolitan.

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References

- Albers, H.J. & Felder, W.M. 1979: Litho-, Biostratigraphie und Palökologie der Oberkreide und des Alttertiärs (Präobersanton-Dan/Paläozän) von Aachen-Südl limburg (Niederlande, Deutschland, Belgien). In Wiedmann, J. (ed.): *Aspekte der Kreide Europas. International Union of Geological Sciences, Series A* 6, 47–84.
- Allmon, W.D. 2005: The importance of museum collections in paleobiology. *Paleobiology* 31, 1–5.
- Asgaard, U. 1979: The irregular echinoids and the boundary in Denmark. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 74–77. University of Copenhagen, Copenhagen.
- Benton, M.J. & Simms, M.J. 1995: Testing the marine and continental fossil records. *Geology* 23, 601–604.
- Benton, M.J. & Simms, M.J. 1996: Testing the marine and continental fossil records: reply. *Geology* 24, 381–382.
- Benton, M.J., Wills, M.A. & Hitchin, R. 2000: Quality of the fossil record through time. *Nature* 403, 534–537.
- Birkelund, T. 1957: Upper Cretaceous belemnites from Denmark. *Biologiske Skrifter udgivet af Det Kongelige Danske Videnskabernes Selskab* 9, 1–69.
- Birkelund, T. 1993: Ammonites from the Maastrichtian White Chalk of Denmark. *Bulletin of the Geological Society of Denmark* 40, 33–81.
- Briggs, D.E.G. & Gall, J.-C. 1990: The continuum in soft-bodied biotas from transitional environments: a quantitative comparison of Triassic and Carboniferous Konservat-Lagerstätten. *Paleobiology* 16, 204–218.
- Bromley, R.G. 1979: Chalk and bryozoan limestone: facies, sediments and depositional environments. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 16–32. University of Copenhagen, Copenhagen.
- Christensen, W.K. 1975: Upper Cretaceous belemnites from the Kristianstad area in Scania. *Fossils and Strata* 7, 69 pp.
- Christensen, W.K. 1979: Maastrichtian belemnites from Denmark. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 42–45. University of Copenhagen, Copenhagen.
- Christensen, W.K. 1984: The Albian to Maastrichtian of southern Sweden and Bornholm, Denmark. *Cretaceous Research* 5, 313–327.
- Christensen, W.K. 1999: Upper Campanian and Lower Maastrichtian belemnites from the Mons Basin, Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 69, 97–131.
- Collins, J.S.H. 1999: Fossils explained 25: Crab claws. *Geology Today* 15, 114–117.
- Darwin, C. 1859: *On the Origin of Species*. 502 pp. John Murray, London.
- Desor, E. 1847: Sur le terrain danien, nouvel étage de la craie. *Bulletin de la Société Géologique de France* (2) 4, 179–182.
- Dhondt, A.V. 1999: Upper Maastrichtian bivalve faunas from the Crimea, Maastricht and Mangyshlak. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: Sciences de la Terre* 69, 55–65.
- Dixon, H.L., Donovan, S.K. & Veltkamp, C.J. 1994: Crinoid and ophiuroid ossicles from the Oligocene of Jamaica. *Caribbean Journal of Science* 30, 143–145.
- Donovan, S.K. 1996: Testing the marine and continental fossil records: comment. *Geology* 24, 381.
- Donovan, S.K. 2001: Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166, 177–192.
- Donovan, S.K. 2003: Completeness of a fossil record: the Pleistocene echinoids of the Antilles. *Lethaia* 36, 1–7.
- Donovan, S.K. & Paul, C.R.C. (eds). 1998: *The Adequacy of the Fossil Record*. x+312 pp. John Wiley & Sons, Chichester.
- Gravesen, P. 1979: Remarks on the regular echinoids in the Upper Maastrichtian and Lower Danian of Denmark. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 72–73. University of Copenhagen, Copenhagen.
- Greenstein, B.J. 1992: Taphonomic bias and the evolutionary history of the family Cidaridae (Echinodermata: Echinoidea). *Paleobiology* 18, 50–79.
- Greenstein, B.J. 1994: Is the fossil record of regular echinoids really so poor? A comparison of living and subfossil assemblages. *Palaios* 8, 587–601.
- Greenstein, B.J. 1995: The effects of life habit and test microstructure on the preservation potential of echinoids in Graham's Harbour, San Salvador Island, Bahamas. In Curran, H.A. &

- White, B. (eds): Terrestrial and Shallow Marine Geology of the Bahamas and Bermuda. *Geological Society of America Special Paper 300*, 177–188.
- Hagenow, F. von. 1840: Monographie der Rügen'schen Kreideversteinerungen. Abtheilung 2. Radiarien und Annulaten nebst Nachträge zur 1. Abtheilung. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1840*, 631–672.
- Håkansson, E. & Hansen, J.M. 1979: Guide to Maastrichtian and Danian boundary strata in Jylland. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 171–188. University of Copenhagen, Copenhagen.
- Hoek Ostende, L.W. van den. 2003: Fossils explained 42: Micro-mammals. *Geology Today* 19, 70–76.
- Hunter, A.W. 2004: Echinoderm palaeoecology from fragments: reconstructing salinity and substrate controlled faunas in the British Middle Jurassic. *The Palaeontological Association Newsletter* 57, 123.
- Jagt, J.W.M. 1999a: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 1: Introduction and stratigraphy. *Scripta Geologica* 116, 1–57.
- Jagt, J.W.M. 1999b: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 2: Crinoids. *Scripta Geologica* 116, 59–255.
- Jagt, J.W.M. 1999c: An overview of Late Cretaceous and early Palaeogene echinoderm faunas from Liège-Limburg (Belgium, The Netherlands). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 69, Supplement A, 103–118.
- Jagt, J.W.M. 2000a: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 3: Ophiuroids; with a chapter on: Early Maastrichtian ophiuroids from Rügen (Germany) and Møn (Denmark) by Manfred Kutscher & John W.M. Jagt. *Scripta Geologica* 121, 1–179.
- Jagt, J.W.M. 2000b: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 4: Echinoids. *Scripta Geologica* 121, 181–375.
- Jagt, J.W.M. 2000c: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 5: Asteroids. *Scripta Geologica* 121, 377–503.
- Jagt, J.W.M. 2000d: Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 6: Conclusions. *Scripta Geologica* 121, 505–577.
- Kier, P.M. 1977: The poor fossil record of the regular echinoid. *Paleobiology* 3, 168–174.
- Koch, C.F. 1978: Bias in the published fossil record. *Paleobiology* 4, 367–372.
- Koch, C.F. 1998: 'Taxonomic barriers' and other distortions within the fossil record. In Donovan, S.K. & Paul, C.R.C. (eds): *The Adequacy of the Fossil Record*, 189–206. John Wiley & Sons, Chichester.
- Messing, C.G. 1997: Living comatulids. In Waters, J.A. & Maples, C.G. (eds): *Geobiology of Echinoderms. The Paleontological Society Papers* 3, 3–30.
- Messing, C.G., Rose Smyth, M.C., Mailer, S.R. & Miller, J.E. 1988: Relocation movement in a stalked crinoid (Echinodermata). *Bulletin of Marine Science* 42, 480–487.
- Paul, C.R.C. 1982: The adequacy of the fossil record. In Joysey, K.A. & Friday, A.E. (eds): *Problems of Phylogenetic Reconstruction*, 75–117. Systematics Association Special Publication 21. Academic Press, London.
- Paul, C.R.C. 1985: The adequacy of the fossil record reconsidered. In Cope, J.C.W. & Skelton, P.W. (eds): *Evolutionary Case Histories from the Fossil Record*. Special Papers in Palaeontology 33, 7–15.
- Rasmussen, H.W. 1945: Observations on the asteroid fauna of the Danian. *Meddelelser fra Dansk Geologisk Forening* 10 (1944), 417–426.
- Rasmussen, H.W. 1950: Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. *Danmarks Geologiske Undersøgelse II. Række* 77, 1–134.
- Rasmussen, H.W. 1953: Cretaceous Crinoidea. Preliminary report on the species found in Denmark. *Meddelelser fra Dansk Geologisk Forening* 12, 415–419.
- Rasmussen, H.W. 1961: A monograph of the Cretaceous Crinoidea. *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter* 12 (1), 428 pp.
- Rasmussen, H.W. 1971: Echinoid and crustacean burrows and their diagenetic significance in the Maastrichtian–Danian of Stevns Klint, Denmark. *Lethaia* 4, 191–216.
- Rasmussen, H.W. 1979: Crinoids, asteroids and ophiuroids in relation to the boundary. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 65–73. University of Copenhagen, Copenhagen.
- Raup, D.M. 1976a: Species diversity in the Phanerozoic: a tabulation. *Paleobiology* 2, 279–288.
- Raup, D.M. 1976b: Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2, 289–297.
- Raup, D.M. 1977: Systematists follow the fossils. *Paleobiology* 3, 328–329.
- Ravn, J.P.J. 1928: De regulære echinider i Danmarks Kridtaflejringer. *Kongelige Danske Videnskabernes Selskab Skrifter; Naturvidenskabelig og Matematisk Afdeling* 9 (1), 1–63.
- Robaszynski, F. 1978: Comparison between the middle Cretaceous of Belgium and some French regions. In Wiedmann, J. (ed.): *Aspekte der Kreide Europas. International Union of Geological Sciences, Series A* 6, 543–561.
- Robaszynski, F. & Christensen, W.K. 1989: The Upper Campanian–Lower Maastrichtian chalks of the Mons Basin, Belgium: a preliminary study of belemnites and foraminifera in the Harmignies and Ciplu areas. *Geologie en Mijnbouw* 68, 391–408.
- Robaszynski, F., Dhondt, A.V. & Jagt, J.W.M. 2002: Cretaceous lithostratigraphic units (Belgium). *Geologica Belgica* 4 (2001), 121–134.
- Sheehan, P.M. 1977: A reflection of labor by systematists? *Paleobiology* 3, 325–328.
- Smith, A.B. 1984: *Echinoid Palaeobiology*. xii+191 pp. George Allen and Unwin, London.
- Smith, A.B. & Jeffery, C.H. 2000: Maastrichtian and Palaeocene echinoids: a key to world faunas. *Special Papers in Palaeontology* 63, 406 pp.
- Smith, A.B. & Wright, C.W. 2002: Echinoderms. In Smith, A.B. & Batten, D.J. (eds): *Fossils of the Chalk* (2nd edition, revised and enlarged). *Palaeontological Association Field Guides to Fossils* 2, 251–295.
- Surlyk, F. 1979: Guide to Stevns Klint, 164–170. In Birkelund, T. & Bromley, R.G. (eds): *Cretaceous–Tertiary Boundary Events, Symposium 18–24 September 1979, I: The Maastrichtian and Danian in Denmark*, 164–170. University of Copenhagen, Copenhagen.
- Surlyk, F. & Christensen, W.K. 1974: Epifaunal zonation on an Upper Cretaceous rocky coast. *Geology* 2, 529–534.
- Surlyk, F. & Håkansson, E. 1999: Maastrichtian and Danian strata in the southeastern part of the Danish Basin, 29–58. In Pedersen, G.K. & Clemmensen, L.D. (eds): *Field Trip Guidebook: 19th Regional Meeting of Sedimentology*, 24–26 August, IAS, Copenhagen.