Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium — Part 2: Crinoids

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Jagt, J.W.M. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium — Part 2: Crinoids. — Scripta Geol., 116: 59-255, 51 figs., 46 pls, Leiden, May 1999.
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Key words: Echinodermata, Crinoidea, Late Cretaceous, Early Palaeogene, taxonomy, stratigraphy.
All Campanian, Maastrichtian and Danian articulate (cladid) crinoids known to date from the extended type area of the Maastrichtian Stage, are described and illustrated. The geographic and stratigraphic distribution of this unexpectedly diverse echinoderm group are documented. A total of twenty genera (three of them new) and thirty-six species (six of them new) are defined: *Austinocrinus bicoronatus* (von Hagenow, 1840), ‘*Isocrinus*’ sp., ‘*I.*’ *lanceolatus* (Roemer, 1840)?, *Isselicrinus buchii* (Roemer, 1840), *Praeisselicrinus*? *limburgicus* (Rasmussen, 1961), *Nielsenicrinus agassizii* (von Hagenow, 1840) (= ‘*Pentacrinites*’ *kloedeni* von Hagenow, 1840), *N. ewaldi* sp. nov., *Jaekelometra* gr. *belgica* (Jaekel, 1902), *J.* gr. *concava* (Schlüter, 1878) (= *J. columnaris* Gislén, 1924 and including forma *meijeri* Rasmussen, 1961), *J.*? *defectiva* sp. nov., *Placometra* gr. *laticirra* (Carpenter, 1880), *Atuatucametra annae* gen. et sp. nov., *Amphorometra* gr. *conoidea* (Goldfuss, 1839), *Semiometra impressa* (Carpenter, 1881), *S. lenticularis* (Schlüter, 1878), *S. saskiae* sp. nov., *Loriolometra retzii* (Lundgren, 1875), *Hertha* gr. *pygmea* Gislén, 1924, *H.* gr. *plana* (Brünnich Nielsen, 1913), *H.* gr. *mystica* von Hagenow, 1840 (?), *Bourgueticrinus* sp. 1 (aff. *baculatus* Klikushin, 1982c), *Bourgueticrinus* sp. 2, *B. bruennichinielseni* Ødum, in Jessen & Ødum, 1923, *B.* aff. *brydonei* Rasmussen, 1961, *B. constrictus* (von Hagenow, in Quenstedt, 1876), *B. danicus* Brünnich Nielsen, 1913, *B. hureae* (Valette, 1917), *B.*? *suedicus* (Carpenter, 1881), *Democrinus*? *maximus* (Brünnich Nielsen, 1915), *Monachocrinus*? *gallicus* Rasmussen, 1961, *Cyathidium vlieksi* Jagt, 1986, *Applinocrinus cretaceus* (Bather, 1924), *Birgelenocrinus degraafi* gen. et sp. nov., and *Veugelersia diana* gen. et sp. nov. It is demonstrated that comatulids and bourgueticrinids/bathycrinids in particular show a wide range of variation. Awaiting detailed biometric analyses of modern comatulid populations and a reassessment of comatulid taxonomy, for the time being the use of open nomenclature (Bengtson, 1988) is favoured in these instances. Generic reassignments are proposed for *Isocrinus*? *carinatus* Roemer, 1840 [sensu Rasmussen, 1961] and *Bourgueticrinus aequalis* d’Orbigny, 1841: to the cainocrinid genus *Nielsenicrinus* and to the otherwise exclusively North American Late Cretaceous genus *Dunnicrinus*, respectively.

Contents

Introduction

In comparison with other echinoderms, and echinoids in particular, Late Cretaceous (Campanian-Maastrichtian) and Early Palaeogene (Danian) crinoid faunas from the extended type area of the Maastrichtian Stage have virtually been neglected. Based on a limited number of museum collections only, Rasmussen (1961, 1965) documented a total of sixteen crinoid species from these strata. However, it should be pointed out that he still distinguished four species of the atelecrinid comatulid *Jaekelometra* and that his list includes one species not recorded subsequently from the area, the cainocrinid *Nielsenicrinus obsoletus* (Brünnich Nielsen, 1913).

In the present paper, thirty-six species in twenty genera are described. Three genera and six species are new, and a few species are reassigned to other genera. Of note amongst these are in particular new genera and species of pelagic roveacrinids and pterocomid comatulids, as well as cups and large numbers of proximal brachials, which allow *Isocrinus*? *carinatus* (sensu Rasmussen, 1961) to be assigned definitely to the cainocrinid *Nielsenicrinus*. This species may in fact be a member of a phylogenetic lineage leading from the Santonian (-? Early Campanian) '*Isocrinus*' *minutus* (Valette, 1917) to the Early Maastrichtian *N. agassizii* (von Hagenow, 1840) and the Late Maastrichtian *N. rosenkrantzi* Rasmussen, 1961. Although collections available for the present paper are large in comparison to previous studies of crinoids from the area, taxonomic assignments are occasionally fraught with difficulties. In these instances, the use of open nomenclature is favoured, awaiting detailed biometric analyses of 'populations' of species originally described from elsewhere in northwest Europe. This holds especially true for bourgueticrinids/bathycrinids and some comatulids. In general, a wide range of morphological variation is accepted for these species. For bourgueticrinids in particular a conservative attitude is adopted, although it is realised that some taxa (e.g. *Monachocrinus*? *gallicus*) may in fact be no more than ontogenetic stages of other species occurring in the same assemblages.

Most of the material available was collected during the past six to eight years in a number of quarries, both working and disused, and in a few other (natural) exposures in the area between Aachen, Liège and Maastricht (see Jagt, 1999 for details). Included also are museum collections, despite the fact that these, and especially those made prior to 1975, often suffer from lack of stratigraphic details. A number of private collections, notably those of M.J. van Birgelen, M.M.M. Kuypers and M.J.M. Deckers, which comprise stratigraphically well-documented material, have also been screened. Specimens from these collections which are illustrated or referred to in the present paper have been transferred to the collections of the Natuurhistorisch Museum Maastricht and have the prefix NHMM.

The present paper is the second in a series of contributions documenting echinoderm faunas of Late Cretaceous and Early Palaeogene age from the extended Maastrichtian type area. For a discussion of the geographic-stratigraphic setting and general references see Part 1 (Jagt, 1999). This, and subsequent papers, are principally taxonomic in nature. On the basis of these revisions, the crinoids, echinoids, asteroids, and ophiuroids, will then be analysed palaeobiologically and palaeoecologically in the concluding paper of this series. Analyses of functional morphology in turn will provide explanations for changes in echinoderm faunas across the Cretaceous/Tertiary (K/T) boundary in the area (Jagt, in prep. d). Comparisons with extant faunas allow conclusions to be drawn with regard to habitat preference and functional morphology of these fossil echinoderm taxa.

These papers will all comprise a historical account of the research of these echinoderm groups, which is to precede the systematic descriptions, and which will include citations from literature sources which are not easily accessible.

Material and methods

Over the past six to eight years, members of the ‘Vijlen Groep’, and other (amateur) palaeontologists, have taken and processed samples from a number of key sections in the extended type area of the Maastrichtian Stage (see Jagt, 1999). The weight of these bulk samples varied widely and depended mainly on outcrop condition: from a few to more than 500 kg. In their choice of sampling intervals the group members were led primarily by personal observations during fieldwork and by results of bioclast analyses carried out by P.J. Felder. Spacing of the sampled intervals varied to a certain extent, being largely dependent of accessibility, but coverage was such that this sample series compares well with that described by H. Ernst (1984) for the standard section of the Late Cretaceous white chalk in northwest Germany. Special attention was paid to fossil hash levels which document decreases in sedimentation rates, winnowing and hard-part concentration. In this way, the entire section from the Early Campanian Vaals Formation to the Middle Danian Geulhem Member was sampled at regular intervals. Stratigraphic provenance of samples was indicated with reference either to the lower or upper boundary level of a given member, depending on outcrop conditions. Invariably, lithostratigraphic logs as published by W.M. Felder (1975b) and W.M. Felder & Bosch (in press) were used as framework for the various (disused) quarries. This means that stratigraphic control of these samples is excellent.

Generally, the processing of samples was straightforward, resulting in various sieve mesh residues (mostly down to mesh width of 0.3 mm). Glauconitic, partially indurated samples occasionally called for an acid treatment. Handpicked from these residues were all kinds of small to medium-sized fossils, ranging from benthic foraminifera and ostracods to selachian teeth, cirripede valves and jaw elements of nautiloids. Most of the material was incorporated into private collections, but it was decided to constitute a reference collection, representing all groups, for the Natuurhistorisch Museum Maastricht. Crinoid specimens selected for illustration and/or discussion in the present paper are deposited either at that museum (prefix NHMM) or at the Nationaal Natuurhistorisch Museum (Leiden, prefix RGM). By using material from private collections, provided stratigraphic documentation is good, it is felt that many data otherwise doomed to become part of the ‘unpublished fossil record’ (Teichert et al., 1987) remain accessible.

Preservation of the mostly dissociated crinoid ossicles varies considerably. Especially in ‘white chalk’ lithofacies types (e.g. Zeven Wegen, upper Vijlen and Lixhe members) it is good to very good, allowing details of stereom structure to be assessed. In places, at least in part as a result of obrution, crinoids may still be partially articulated, e.g. portions of bourgueticrinid columns and thecae with proximal brachials attached, isocrinid nodals with portions of cirri preserved, and comatulid thecae with portions of cirri and proximal brachials. Extremely rare are occurrences with (near)complete specimens, such as those from the base of the Gronsveld Member (Maastricht Formation) currently under study (Jagt et al., 1998). Particularly in the coarser-grained units (upper Maastricht Formation) stereom overgrowths of the type described by Evamy & Shearman (1965, 1969), Neugebauer (1978, 1979a, b) and Neugebauer & Ruhrmann (1978) occur regularly. In this way details of crinoid microstructures (Roux, 1970) are obliterated, but occasionally such strata also yield pristine specimens, which suggests taphonomic processes to have varied considerably during deposition of these units.

In view of the small size of most crinoid ossicles, it was decided, with few exceptions, to use only scanning electron micrographs. Specimens were mounted on aluminium and brass stubs, gold coated and photographed by Mrs S.M. Kars at the Vrije Universiteit (Amsterdam) using a JEOL JSM-6400 scanning electron microscope.

Specimens illustrated in the present paper are generally the best-preserved and/or most typical ossicles selected from the various samples, on which descriptions are based.

Previous work

In Faujas Saint Fond's (1799) famous work (see also Pasteur, 1802-1804) one searches in vain for a reference to or illustration of crinoids from the type Maastrichtian, which is puzzling, especially so since he did figure (pl. 30) a number of echinoids commonly associated with comatulid crinoids in the Meerssen Member (Maastricht Formation).

Goldfuss (1831, p. 186, pl. 57, fig. 3R) appears to have been the first to describe crinoids from Maastricht. Illustrated under the name of *Apiocrinites ellipticus* Miller is a bourgueticrinid theca from Maastricht ('Petrefactum calcareum, e stratis cretaceis Westphaliae et Belgiae' and 'Dieser, in der Kreide bei Mastricht und zu Lemförde bei Osnabrück vorkommende, Apiocrinit ...').

D'Orbigny (1841, pp. 95-98) erected the genus *Bourgueticrinus*:

> **'5e Genre. BOURGUETICRINUS** (d'Orb.).
>
> *Apiocrinites* auctorum.
>
> CARACTÈRES. Ensemble formé d'une racine articulée, d'une tige ronde ou comprimée, simple, toujours dépourvue de rayons à sa surface articulaire souvent transversale; d'un calice pyriforme, très-petit, composé: 1° d'un ou de deux articles de la tige un peu plus larges que les autres; 2° d'une série de cinq pièces basales; 3° d'une série de cinq pièces supérieures pourvues, en dessus, d'attaches brachiales simples, et d'un seul canal brachial. *Cavité interne* du sommet nulle, réduite au canal médian, la cavité étant supérieure au calice.
>
> *Bras* au nombre de cinq, au point de départ.'

He mentioned (p. 96) a number of species, amongst which '... les B. *ellipticus* et *æqualis*, se trouvent exclusivement dans la craie blanche supérieure de Paris, d'Angleterre, de la Touraine et de Maëstrich [sic]...'. Of the latter species, d'Orbigny (pp. 96, 97) noted that, 'De là il n'en fut plus question jusqu'en 1811, ou Parkinson (3) la donna ainsi qu'une autre (B. *æqualis*), sous les noms de *Botle Encrinite* et de *Strait Encrinite*. L'auteur distinguant avec sagacité ces deux formes et leur attribuant des fragmens de tiges à articulations alternativement oblongues et comprimées latéralement'. He also remarked (p. 97) that, 'Enfin Goldfuss (4) adoptant le genre de Miller dans toute son étendue, y laissa régner la même confusion, et ne distingua même pas les deux espèces si nettement désignées par Parkinson.'

(3) Organic remains, t. II, pl. XIII, f. 75 et 34.

(4) Goldfuss, Petrificata Germaniæ, t. I, p. 186, pl. 57, f. 3.

Careful reading of this text shows that Rasmussen (1961, p. 170) may have been right in designating as lectotype of *Bourgueticrinus aequalis* the specimen illustrated by Goldfuss (1831, pl. 57, fig. 3R) and re-illustrated by d'Orbigny (1841, pl. 17, figs. 10-12). Preservation of dissociated columnals and a single theca in the Goldfuss type collection (no. 396a) at Bonn (Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität) suggests these to have been collected from the base of the Valkenburg Member (Maastricht Formation), directly above the Lichtenberg Horizon, as exposed in the Maastricht area.

Rasmussen (1961, pp. 171, 191) pointed out that Parkinson's (1811) 'straight encrinite', which d'Orbigny assumed to be identical to his *B. aequalis*, should now be assigned to *Bourgueticrinus hureae* (Valette, 1917), a species also known from the extended Maastrichtian type area, but confined to strata of Late Campanian age (see 'Systematic palaeontology').

From a number of localities in southern Limburg and contiguous German territory, Binckhorst van den Binckhorst (1859) recorded (in original spelling) the following crinoid species:

from the 'Coupe du Heunsberg près de Fauquemont' and 'le Proen' (pp. 31-32 = Valkenburg aan de Geul/Sibbe area): *Pentacrinus Agassii* [sic], von Hag., *Bourgueticrinus æqualis*, Mill., *Glenotremites conoideus*, Goldf. and *G. paradoxis* id. [sic],

from the 'Craie de Schaasberg' (p. 54): *Bourgueticrinus ellipticus*, Mill.,

from the 'Marne de Kunraad' (p. 59): *Bourgueticrinus ellepticus*, Mill. [sic] and *Pentacrinus Agassizi*, v. Hag.,

from the 'Marnes de Simpelveld et Vetschau' (pp. 64, 67): *Pentacrinus Agassizi*, Hag. and *Apiocrinus ellepticus* Mill. [sic],

from the 'Craie siliceuse de Kunraad, Benzenraad et Simpelveld' (p. 74): *Apiocrinus ellipticus*, Mill. and *Bourgueticrinus æqualis*, Mill.

His list (pp. 117-129) '... des principales espèces qui, croyons-nous, caractérisent d'une manière spéciale la craie tuffeau et ne descendent pas plus bas dans le dépôt crétacé du Limbourg', includes:

Glenotremites (Comatula) conoideus, Goldf., *G. (C.) paradoxus*, Goldf. and *Pentacrinus Agassizi*, v. Hag.

From the 'Craie blanche à silex noirs et Marnes sans silex', Binckhorst (1859, p. 148) recorded *Pentacrinus Agassizi*, v. Hag., *Bourgueticrinus æqualis*, d'Orb., *Glenotremites*, sp., and from the 'Sables verts à Belemnitella quadrata' (p. 162) *Apiocrinus ellipticus*, Mill., and, finally, from the 'Willkommsberg' near Aachen (p. 163) *Bourgueticrinus ellipticus*, Mill., *B. æqualis*, id. and *Pentacrinus Agassizi*, Hag.

Although the above records are in need of a modern revision (see 'Systematic palaeontology'), they do document the general trend for comatulid crinoids to characterise the younger strata of the type Maastrichtian, and stalked crinoids (isocrinids and bourgueticrinids) to abound in older strata. Of note is Binckhorst's record of a comatulid (*Glenotremites*, sp.) from the Zeven Wegen, Beutenaken or Vijlen members ('Craie blanche à silex noirs et Marnes sans silex') of the Gulpen Formation, and of a bourgueticrinid from the Vaals Formation ('Sables verts à Belemnitella quadrata').

The pluricolumnal illustrated by J. Müller (1859, p. 5, pl. 7, fig. 1) under the name of '*Pentacrinus Agassizi*, von Hagenow', does appear to be assignable to that species (now *Nielsenicrinus agassizii*), but that probably holds true only for material from two of his localities, 'Bei Vaels in den Mergeln des Schneebergs, ebenso in denselben Schichten über dem Grünsand am "Friedrich" im Aachener Wald, ...'. Specimens from the other localities listed, but not illustrated, by Müller ('... Koenrad und in der weissen Kreide bei Mastricht') are best referred to other isocrinid species (see below under *Nielsenicrinus carinatus*).

Other local workers, and Bosquet, in Staring (1860, p. 408) in particular, listed for 'Nederlandsch en Belgisch Limburg' the following crinoids (in original nomenclature):

853 *Comatula conoidea* Goldf. sp.	m 2-12
854 *Glenotremites paradoxus* Goldf.	
855 *Eugeniacrinus Hagenovi* Goldf.	m?
856 *Bourgetocrinus ellipticus* Müll.	g 23
857 *B. aequalis* d'Orb.	g 23
858 *Pentacrinus Agassizi* v. Hag.	h 28.

Abbreviations are as follows: 'm - Maastrichtsch, g - Gulpensch, h - Herfsch', corresponding (roughly) to the Maastricht, Gulpen and Vaals formations in current terminology, respectively. Of particular note is Bosquet's record of an isocrinid from the Vaals Formation. This may refer to what is now known as the 'pre-Valkenburg facies' (P.J. Felder et al., 1985; Jagt et al., 1987), being in part time equivalent with the Zeven Wegen Member of Late Campanian age, and indicated in the present paper as Benzenrade Member (W.M. Felder & Bosch, in press).

Later, Bosquet (1868) recorded the same species but added a comatulid* (in original nomenclature):

**Hertha mystica*, Hag.	m	
Comatula conoïdea, Goldf.	m	
Glenotremites paradoxus, Goldf.	m?	
Eugeniacrinus Hagenovi, Goldf.	m	
Bourguetticrinus ellipticus, Mill.	s	
» *æqualis*, d'Orb.	s	
Pentacrinus Agassizi, Hag.	h	m.

Of interest is the record of an isocrinid from the 'Maastrichtsch (m)' in this list; this may refer to what is here considered to be a new species of the genus *Nielsenicrinus* (see 'Systematic palaeontology'). The distinction of three bourgueticrinid species may simply be a matter of oversplitting, but it cannot be ruled out that Bosquet's material included specimens from the Campanian (Zeven Wegen Member), in which case there may have been more than one species.

Although the above lists are of limited use in modern palaeontological studies, they do show a general trend and should be looked upon as the first steps towards a crude biozonation of the Cretaceous strata in the Maastrichtian type area.

Things definitely changed for the better with the publication of Schlüter's paper (1878) on fossil comatulid crinoids. He expressed a wish that, '... auch die jüngeren Formationen, das Tertiär- und Kreide-Gebirge noch Neues bieten würden' (p. 30), and noted that fossil remains of comatulids were extremely rare and comprised mostly only the centrodorsal. More important still, he pointed out that that part of the comatulid anatomy had not received much attention in contemporary descriptive zoological literature on modern representatives. Schlüter listed previous literature on fossil comatulids, noting (p. 37) that Goldfuss (1826-1844) had described 'zwei isolirte Knöpfe von Comatulen ohne Radialia aus der Kreide ...', viz. *Glenotremites paradoxus* (erroneously interpreted by Goldfuss as an echinoid) and *G. conoideus*. Von Hagenow (1840) had added a third species, *Hertha mystica*, based on a centrodorsal with radials preserved. From 'Kreidetuff bei Maestricht', Schlüter (1878, p. 46, pl. 3, figs. 1-3) described *Antedon lenticularis* Schlüter and *Antedon concavus* Schlüter (p. 48, pl. 3, figs. 4-7), noting for the latter differences in preservation, a single specimen (out of total of seven) being 'von trefflicher Erhaltung', whereas the others are 'äusserlich abgerieben.'

The publication of C. Ubaghs's (1879) paper was another step forward; naturally, he relied on earlier authors (notably Binckhorst and Bosquet), but added his own observations, made during numerous field work sessions in the Maastrichtian type area. For the 'partie supérieure du tuffeau de Maastricht' (= 'les couches à Bryozoaires'), C. Ubaghs (p. 65) listed the following crinoids (in original nomenclature): *Comatula conoïdea* Goldf. sp. and *Glenotremites paradoxus* Goldf. The fact that he also listed the psychocidarid echinoid *Cidaris Hardouini* Desor (= *Tylocidaris hardouini*) shows that he too included deposits of Early Palaeocene age in the 'type Maastrichtian' (= Maastricht Formation in current terminology) as did his contemporaries, but apparently this has not influenced his crinoid records. For the 'Calcaire de Kunraad', C. Ubaghs listed (p. 112): *Bourgetocrinus ellipticus* Mill. [sic] and for what he (p. 126) termed 'La craie blanche à silex noir' (referring both to the Lanaye and Zeven Wegen members of the Gulpen Formation in current nomenclature), are recorded: *Bourgueticrinus ellipticus* Mill. and *Pentacrinus Agassizi* (très rare) Hag., *Eugeniacrinus Hagenowi* Goldf., and *Bourguetticrinus ellipticus* Mill.

Crinoids listed for the 'Craie marneuse sans silex' by C. Ubaghs (1879, p. 135) are: *Bourguetticrinus ellipticus* d'Orb., *Bourguetticrinus æqualis* d'Orb., and *Pentacrinus Agassizi* Hag. Of interest in the faunal list, which C. Ubaghs (p. 197) stated to have copied from Bosquet (1868) but, '... nous y avons ajouté le résultat de nos propres recherches, soit une augmentation de 80 espèces, ...' is the fact that data on the stratigraphic distribution of the crinoid taxa recognised are more precise:

Hertha mystica, Hag.	M.	
Comatula conoïdea, Goldf.	M.S.	
Glenotremites paradoxus, Goldf.	M.S.	
Eugeniacrinus Hagenovi, Goldf.	M.S.	
Bourguetticrinus ellipticus, Mill.		M.I.

» *æqualis*, d'Orb.	M.I.		
Pentacrinus Agassizi, Hag.	h	s	M.S.

The fact that there is no mention of any crinoids in a catalogue of C. Ubaghs's collection (Ubaghs, 1885), and that there are only few specimens amongst his collections at the Institut royal des Sciences naturelles de Belgique (Brussels), indicates that he ranked crinoids amongst the least important faunal elements for the units he had studied and collected from personally.

C. Ubaghs (1888, p. 4), in a listing of fossils in the collections of Ignaz Beissel, under the heading 'Crinoïden und Asterioidea' recorded the following species from the 'Kreidemergel' of the Aachen area (probably Vijlen Member in original nomenclature): *Eugeniacrinus Hagenovi*?, *Pentacrinus Agassizi* and *Bourgetocrinus ellipticus*, and, on p. 10 in the same paper, *Pentacrinus* sp. from the 'Grünsand von Vaals' (= Vaals Formation).

In his important monograph, Gislén (1924) devoted an entire chapter to crinoids and to the morphology of fossil comatulids, basing his observations on type material wherever possible, rightly stressing the fact (p. 102), 'that those parts of the Comatulids that have been preserved - usually Cd, BB and RR - do not allow a systematization to be carried out as thoroughly as in the recent forms.' A brief historical overview and a survey of which morphological characters of fossil comatulids may be used for classification follows.

Amongst the numerous fossil comatulids described by Gislén are the following species from the Maastrichtian type area (in original nomenclature):
Glenotremites concavus (Schlüter, 1878)
Amphorometra conoidea (Goldfuss, 1839)
Jaekelometra belgica (Jaekel, 1901)
Jaekelometra columnaris Gislén, 1924
Semiometra lenticularis (Schlüter, 1878)
Hertha mystica Hagenow, 1840.

In a comprehensive monograph on Cretaceous (including Early Palaeocene) crinoids, Rasmussen (1961) revised material from Maastricht preserved in the collections of the Humboldt Universität/Berlin (Binkhorst Colln), Institut royal des Sciences naturelles de Belgique/Brussels (C. Ubaghs and Bosquet Collns), Geologisch-Paläontologisch Institut Universität Hamburg (Voigt Colln) and the Natuurhistorisch Museum Maastricht (Meijer and W.M. Felder Collns). This material included the following (new) species:
Austinocrinus bicoronatus (von Hagenow, 1840)
Isselicrinus buchii (Roemer, 1840)
Doreckicrinus limburgicus Rasmussen, 1961
Isocrinus? *carinatus* (Roemer, 1840)
Bourgueticrinus aequalis d'Orbigny, 1841
Cyathidium holopus Steenstrup in Michaelis & Scherk, 1847
Semiometra impressa (Carpenter, 1881)
Semiometra lenticularis (Schlüter, 1878)
Jaekelometra belgica (Jaekel, 1901)
Jaekelometra columnaris Gislén, 1924
Jaekelometra concava (Schlüter, 1878)

Jaekelometra meijeri Rasmussen, 1961
Amphorometra conoidea (Goldfuss, 1839).

It should be borne in mind that for most of these species Rasmussen studied one specimen each, at best a few specimens.

Rasmussen (1965) listed the following crinoid species for southern Limburg:

for the 'Campanian at Heure le Romain and Louvain' and the 'Lower Gulpen Chalk of Vijlenerbos': *Isocrinus carinatus*, *Austinocrinus bicoronatus*, *Isselicrinus buchii* and *Doreckicrinus limburgicus*,

for the 'Gulpen Chalk Cr4 in Limbourg': *Bourgueticrinus aequalis* and *Semiometra impressa*,

for the 'Tuffeau de Maastricht Mb': *Bourgueticrinus aequalis*,

for the 'Tuffeau de Maastricht Mc': *Semiometra impressa* and *Jaekelometra belgica*,

for the 'Tuffeau de Maastricht Md': *Semiometra impressa*, *Semiometra lenticularis*, *Jaekelometra meijeri*, *Jaekelometra concava*, and (?) *Cyathidium holopus*,

and for the 'Tuffeau de Maastricht, horizon unknown': *Amphorometra conoidea* and *Jaekelometra columnaris*.

For the 'Post-Maastrichtian' of Geulhem, Canal Albert and Zolder (Belgium) he recorded: (?) *Cyathidium holopus*, *Bourgueticrinus danicus* Brünnich Nielsen, 1913, *Democrinus maximus* (Brünnich Nielsen, 1915), and *Nielsenicrinus obsoletus* (Brünnich Nielsen, 1913).

In a number of short contributions, Jagt (1986a, b, 1988, 1990, 1992) recorded a holopodid, *Cyathidium vlieksi*, from the Kunrade Limestone facies of the Maastricht Formation, referring Rasmussen's (1961, 1965) records of the typically Middle Danian *C. holopus* to it. He described a number of additional Late Campanian and Late Maastrichtian bourgueticrinids, pointing out that *B. aequalis* had but five arms, compared crinoid faunas from the upper Gulpen Formation (Lanaye Member) as occurring west of the River Maas with those from the Kunrade Limestone facies of the Heerlen-Ubachsberg area, and noted the occurrence of pelagic species in the former. Also discussed was the gregarious occurrence of a number of comatulid species in the upper Maastricht Formation. He pointed out that *Bourgueticrinus aequalis* closely resembled *Dunnicrinus mississippiensis*, and illustrated the unexpectedly highly diverse roveacrinid faunas of Early Campanian to Late Maastrichtian age from Liège and Limburg.

Jagt et al. (1994) noted the occurrence of well-preserved, articulated specimens of '*Bourgueticrinus*' *aequalis* from the base of the Gronsveld Member (Maastricht Formation), and stressed the need for a thorough revision of the Bourgueticrinida. Finally, Jagt (1995c) presented a brief introduction to the present paper, documenting the unexpectedly high diversity in crinoid faunas.

Systematic palaeontology

Abbreviations — The following abbreviations are used to indicate the repository of specimens illustrated and/or referred to in the text:

BMNH	Natural History Museum, London (formerly British Museum of Natural History);
IRScNB	Institut royal des Sciences naturelles de Belgique, Brussels;
MGUH, GM	Geological Museum of Copenhagen University, type and reference collections, respectively;

MNB	Museum für Naturkunde der Humboldt Universität, Berlin;
MNHUK	Museum of Natural History, University of Kansas, Lawrence, KS;
NHMM	Natuurhistorisch Museum Maastricht, with individual collections bearing the following prefixes: BL – L. Blezer Colln JJ - J.W.M. Jagt Colln K - M.M.M. Kuypers Colln MB - M.J. van Birgelen Colln MD - M.J.M. Deckers Colln MM - M. Meijer Colln PK - P.H.M. van Knippenberg Colln RD - R.W. Dortangs Colln;
NITG/TNO	Nederlands Instituut voor Toegepaste Geowetenschappen/TNO (formerly Rijks Geologische Dienst), Vestiging Heerlen;
RFWUIP	Rheinische Friedrich-Wilhelms-Universität, Institut für Paläontologie, Bonn;
RGM	Nationaal Natuurhistorisch Museum, Leiden (formerly Rijksmuseum van Geologie en Mineralogie);
SGPIH	Geologisch-paläontologisches Institut der Universität Hamburg.

Terminology — This follows Breimer (1978), Moore et al. (1978), G. Ubaghs (1978), Donovan (1984), Paul & Donovan (1988), Paul (1992), and Simms (1989b). For some groups, current crinoid classification schemes are still unsatisfactory: Simms's (1988c) classification of post-Palaeozoic crinoids is adopted here (see also Simms, 1989a; Simms & Sevastopulo, 1993 and Simms et al., 1993).

Taxonomic procedure — Firmness of generic assignment of crinoid species described below varies to a certain degree. Although species attribution in isocrinids based on isolated (pluri)columnals generally is relatively easy, generic assignment ultimately must rely on articular facets of proximal brachials. The fossil record of isocrinids is skewed towards (pluri)columnals, which explains why most fossil species in this group are based on only portions of the whole animal. In those cases where ossicles of the dorsal cup and proximal arms are associated with columnals, generic assignment may be more reliable (see e.g. *Nielsenicrinus ewaldi*). Taxonomic treatment of isocrinids vs other articulate crinoids is thus slightly different. Attribution of comatulids, bourgueticrinids/bathycrinids and roveacrinids is based primarily on features of the centrodorsal plate and/or dorsal cup and is therefore more straightforward. However, in comparison with extant comatulids, in which the structure of proximal brachials and pinnules are of prime importance, the taxonomy of fossil representatives of this group appears more or less artificial.

Crinoids are morphologically complex organisms, and as such functional interpretations could very well lead to the construction of robust cladistic analyses (see Smith, 1994). Simms (1988c) noted that there were but few cladistic analyses of post-Palaeozoic crinoids, one notable exception being Taylor's (1983) analysis of the millericrinid *Ailsacrinus*. For a number of reasons, the present paper does not include such analyses:

1) Although the Articulata is now considered to constitute a monophyletic clade (Simms & Sevastopulo, 1993), crinoid taxonomy is not stable, which holds true for extant as well as fossil taxa (Messing & Dearborn, 1990) and detailed revisions at all taxonomic levels are needed. Messing (1996, p. 92) remarked that a preliminary investigation of East-Indian shallow-water comatulids threw 'numerous generic and subfamilial diagnoses into confusion and [reinforced] the need for detailed phylogenetic re-evaluation of comatulid taxonomy'. Simms (1988d) also pointed out that comatulids are inadequately classified, and that atelecrinids (to which the genus *Jaekelometra*, well represented in the Maastrichtian type area, is assigned) were comparatively primitive in that they retained large basals in the cup. Simms et al. (1993, p. 501) noted that, within the Articulata, at lower taxonomic levels, current classification cannot be considered to reflect relationships between these groups, which need to be revised.

2) There is no agreement at present on the choice and definition of characters in crinoids to be used for the compilation of character-data matrices and the construction of cladograms (see Smith, 1994). This is a particularly difficult problem (Skelton, 1993) and in need of careful consideration. In addition, there is currently no taxonomically standardised computer data base that is globally comprehensive. More objectively defined morphological groupings and morphometric analyses of populations to evaluate age-dependent changes are needed. Simms (1989b) noted that generally, even in neontological studies, morphological similarity determines whether or not two individuals are placed in the same species or not. The selective preservation of fossils complicates the picture and obviously reduces the number of morphological features that can be used for species assignment.

3) As stressed by Baumiller & Gazdzicki (1996) attempts should be made to come up with uniform taxonomic criteria for fossil and extant forms. In doing so they agreed with Simms et al. (1993), who noted that fossil comatulid material is mostly undiagnostic at higher taxonomic levels.

4) Simms (1988b), who outlined the requirements needed for an evaluation of ancestor-descendant relationships, referred to Hallam (1982). That author stressed that, in order for fossil species to be useful in testing evolutionary models, these should be abundant and have a high preservation potential ('populations' allowing assessment of range of intraspecific variation). In addition there should be good, independent biostratigraphic and geographic control to document patterns of migration and to recognise hiatuses. For the Maastrichtian type area many breaks in sedimentation have been documented and quite a number of faunal incursions or migrations of new forms that evolved elsewhere. Facies changes abound throughout the column, and provide explanations for the arrival of new forms the ancestors of which are unknown. For most of the Maastricht Formation biozonations are rather crude (e.g. *Belemnitella junior* Zone encompassing the entire formation with the exception of the uppermost metres).

5) The ontogeny of fossil and Recent articulate crinoids is still poorly known, although this is of prime importance in recognising relationships and in reconstructing the phylogeny of the group. Heterochrony (McNamara, 1986, 1990; Simms, 1988a; Roux, 1987) has been shown to have played an important part in their evolution, in directing morphological change along particular evolutionary pathways. Although

sister group relationships have been recognised in articulates (Simms, 1998c), there are still many problems in the recognition of heterochrony in forms for which ancestors are unknown, e.g. in roveacrinids. Such groupings may in fact turn out to be polyphyletic. The species recognised in the Maastrichtian type area represent but a small portion of their stratigraphic range, and their distribution is most often disjunct.

The above uncertainties and difficulties in the proper taxonomic weighting of crinoids are such that, at present, it appears premature to attempt cladistic analyses. After all, the accuracy of phylogenetic trees depends on the accuracy of taxonomic and biostratigraphic data employed, and only monophyletic groups should be considered in cladistic analyses (see Smith, 1994). None of these requirements can be fulfilled at this moment. To test ancestor-descendant relationships, we need to know more of population structure and faunal migrations, preferably on an over-regional basis.

Class Crinoidea Miller, 1821
Subclass Cladida Moore & Laudon, 1943
Infraclass Articulata Miller, 1821
Order Isocrinida Sieverts-Doreck, in Moore et al., 1952
Suborder Isocrinina Sieverts-Doreck, in Moore et al., 1952
Family Isocrinidae Gislén, 1924

Remarks — Klikushin (1977a, 1982a, 1992) subdivided this family into five subfamilies: Balanocrininae, Diplocrininae, Isocrininae, Isselicrininae, and Metacrininae. His classification has not generally been adopted in subsequent literature. Simms (1988c), in combining in the Isocrinida the Isocrinina, Comatulidina, Bourgueticrinina and Uintacrinina of the Treatise classification (Rasmussen, 1978), pointed out that heterochrony had played an important role in the evolution of most of the articulate crinoids. His suborder Isocrinina comprises the families Isocrinidae, Isselicrinidae and Cainocrinidae. Simms et al. (1993) added a third family, Proisocrinidae, and noted that the Isocrinidae and Cainocrinidae are demonstrably paraphyletic, Proisocrinidae being monotypic and Isselicrinidae monophyletic. Klikushin (1977a, 1982a, 1992) assigned the genus *Austinocrinus* to the Isselicrininae, to which he also referred, in addition to *Isselicrinus*, the genera *Buchicrinus*, *Doreckicrinus*, and *Praeisselicrinus*.

Genus *Austinocrinus* de Loriol, 1889

Type species — *Austinocrinus komaroffi* de Loriol, 1889, by monotypy = *Pentacrinus erckerti* Dames, 1885 (see de Loriol, 1889b).

Austinocrinus bicoronatus (von Hagenow, 1840)
Pl. 1, figs. 1-2.

*1840 *Pentacrinus bicoronatus* von Hagenow, p. 663, pl. 9, fig. 12.
1961 *Austinocrinus bicoronatus* (Hagenow, 1840) — Rasmussen, p. 29, pl. 1, figs. 1-9 (cum syn.).
1987 *Austinocrinus bicoronatus* (Hagenow) — Wright & Smith, p. 202, pl. 44, figs. 1-2.
1995c *Austinocrinus bicoronatus* — Jagt, p. 186, figs. 3, 7.

Type — Neotype is an internodal from glacial deposits (glacially transported rafts?) in Jasmund (Rügen, northeast Germany), as designated by Rasmussen (1961,

p. 29, pl. 1, fig. 1). The specimen was collected and identified by von Hagenow, and is currently in the Voigt Colln (SGPIH).

Material — Six specimens: NHMM GK 573-577, 717 (all W.M. Felder Colln, identified by Rasmussen in 1959).

Description — With the exception of NHMM GK 576, all specimens are internodal pluricolumnals, comprising two to six columnals, the height of which varies slightly.

Measurements (in mm)	H	D
NHMM GK 573	6.9 (3)	10.4
NHMM GK 574	10.7 (5)	7.9
NHMM GK 575	4.4 (2)	10.6
NHMM GK 576	3.5 (1)	10.1
NHMM GK 577	5.0 (2)	10.3
NHMM GK 717	12.6 (6)	10.8

(H - height, D - diameter; numbers in brackets refer to number of columnals)

Columnals are rounded (sub)pentagonal, of varying height, but generally low, separated by noncrenulate sutures and with latera slightly concave and smooth. Articulation facets have smooth and narrow, lanceolate, slightly depressed areolae bordered by short, stout, broadly v-shaped crenulae. Peripheral crenulae are the best developed. In all specimens crenulae are interrupted at the peripheral ends of the petals, where radiating crenulae, of variable length and strength, form ridges or irregular vermiculation.

Discussion — These few specimens compare well with material described and illustrated by Rasmussen (1961); they constitute the only representatives of this genus known to date from the study area. Surprisingly, there are no recent finds of this species in the area, which suggests that it could have been restricted to a very narrow band at the base of the Vijlen Member (Gulpen Formation) (see below).

The ranges of the various northwest and northeast European species are still rather poorly known, but *A. bicoronatus* appears to span the Late Campanian/Early Maastrichtian boundary (Rasmussen, 1961; Wright & Smith, 1987). However, Rasmussen (1961, p. 31) remarked that, '... the stratigraphical range of the species might by a closer study of the localities be reduced to the uppermost Campanian.'

Wood (1988, p. 68) recorded 'early forms of *Austinocrinus bicoronatus*' from the so-called *Austinocrinus* Bed in the '*mucronata* Zone' Beeston Chalk at Caistor St Edmunds (Norfolk), and from the top of the Beeston Chalk and (possibly) the lower part of the Paramoudra Chalk of the St James Pit (p. 90) in the same area. He also noted (p. 72) that, 'The *Austinocrinus* are probably transitional between *A. rothpletzi* Stolley and the later *A. bicoronatus*'. Johansen & Surlyk (1990) showed the 'Beeston Chalk Member' to be roughly equivalent to the northwest German Late Campanian *polyplocum* and *langei* zones (sensu Schulz, 1985) and the 'Paramoudra Chalk Member' to correspond to the *grimmensis/granulosus* Zone and possibly basal Early Maastrichtian *lanceolata* Zone.

Whittlesea (1991) recorded *Austinocrinus* sp. and *A. bicoronatus* from the Early Maastrichtian (*Porosphaera* and pre-*Porosphaera* beds and Paramoudra Chalk) recovered in boreholes at Wroxham (Norfolk), thus spanning the Late Campanian/Early Maastrichtian boundary. Subsequently, Whittlesea (1996a, b) mentioned *Austinocrinus* sp. from the upper beds of the Paramoudra-1 division of the '*mucronata* Zone', thus of Late Campanian age (Christensen, 1995), noting that this crinoid may have had columns of up to 0.3 m in length.

Austinocrinus rothpletzi Stolley, 1892 (p. 252, pl. 10, figs. 7-10, 14) (= *A. turkmenicus* Klikushin, 1975a, p. 98) appears to be characteristic of the Late Campanian, but there are also records from the Late Santonian (Sieverts-Doreck, 1953; Klikushin, 1973, 1975a, 1982a). Typical representatives of this species (see Rasmussen, 1961, pl. 2, figs. 1-5, 7) differ from *A. bicoronatus* especially in petal structure, but transitional forms to *A. bicoronatus* have been recorded from the Campanian/Maastrichtian boundary (Rasmussen, 1953, 1961).

Austinocrinus erckerti (Dames, 1885) seems to be restricted to the Maastrichtian of southern European and Asian Tethyan localities (Dames, 1885; Klikushin, 1975a, 1982a, 1985b, 1992), its northernmost geographic range including southern Germany and Austria (Rasmussen, 1961; Kristan-Tollmann, 1987b). This species differs from *A. bicoronatus* in details of articular faces of columnals and in mostly having ornamented latera.

The recent record of '*Austinocrinus* n. sp.' from the Early Aptian of Jamaica (Donovan et al., 1994) has subsequently been reassigned by Donovan et al. (1996) to the millericrinine *Apiocrinites* sp.

Occurrence — With the exception of NHMM GK 717, which is from exposure 62D-15d, all specimens are from outcrop 62D-15b near the Nieuwe Weg (Zeven Wegen-Vijlenerbosch; see W.M. Felder, 1977), southern Limburg (The Netherlands). This outcrop, now overgrown, exposed the top of the Zeven Wegen Member and the base of the so-called 'Belemnietenkerkhof' (Vijlen Member). Keutgen & van der Tuuk (1991) and Keutgen (1996) noted for the nearby Bovenste Bosch quarry, exposing the Beutenaken and Vijlen members (Gulpen Formation) and the Bovenste Bosch Horizon (sensu W.M. Felder, 1975a, b), that the 'Belemnietenkerkhof' contained belemnite species of various biozones. The Late Campanian *Belemnitella minor* Jeletzky, 1951 (sensu Christensen, 1995) and the Early Maastrichtian *B. (Pachybelemnella) obtusa* Schulz, 1979 and *B. (P.) sumensis* Jeletzky, 1949 have been recorded. The above material of *A. bicoronatus* could thus be either of Late Campanian or Early Maastrichtian age.

Genus *Isocrinus* sensu auct. (? non von Meyer, in Agassiz, 1836)

Type species — *Isocrinus pendulus* von Meyer, 1836, by original designation.

'*Isocrinus*' sp.
Pl. 3, figs. 7-10.

1995c *Isocrinus*? n. sp. — Jagt, p. 188, figs. 3, 7.

Material — Five (pluri)columnals: NHMM MB 322a, 414-4b, 506-17a, 601-3a, and 754b. Large numbers of generally poorly preserved and abraded isolated (pluri) columnals from the Kunrade Limestone facies (Maastricht Formation) as exposed in the Kunrade-Heerlen area may also belong here (NHMM MB 506-17b, 644, 651, 652b, 754d).

Description — Columnals are pentalobate to (sub)pentagonal in cross section, relatively thick and slightly variable in height and diameter, of two orders (Pl. 3, fig. 7), and separated by crenulate sutures. Latera are either evenly convex and smooth (Pl. 3, figs. 8-9) or slightly concave radially with a median ridge which becomes prominent and tubercle-like interradially (Pl. 3, figs. 7, 10). Radial pores occur in sutural depressions of varying strength. Nodals (Pl. 3, figs. 8-10) are up to 1.5 times higher than internodals, and have five medium-sized, near-circular cirral facets, placed adjacent to the upper (proximal) articulum and directed strongly upwards. The distal facet rim protrudes markedly (Pl. 3, figs. 9-10). Profile of nodal latus is convex to strongly convex. Cirral facets are moderately concave and occupy between 60-70% of nodal height. The oval cirral lumen and two triangular synarthrial articular ridges are situated above the middle of the cirral facet. Specimen NHMM MB 601-3a (Pl. 3, fig. 9) preserves a single cirral, which has smooth latera. Columnal articular facets have broad areolae with 8 short crenulae each. Petals are closed and crenulae continue around the tips, the most distal ones lying parallel to radius. Lumen is round in cross section. Distal articular facet of nodal is cryptosymplectial, showing only faint distal crenulae.

Discussion — Only few specimens are available, and the majority of these is from the Kunrade Limestone facies of the Maastricht Formation. This material probably represents a second species of the genus *Nielsenicrinus*, but so long as associated proximal brachials are unknown it is best left in open nomenclature. That these specimens could represent ontogenetic stages of *N. ewaldi* sp. nov. (see below), with which they co-occur in places, appears unlikely. To a certain extent the present material resembles the Early-Late Danian *'Isocrinus' divergens* (Brünnich Nielsen, 1913) (see Rasmussen, 1961, p. 122, pl. 15, figs. 18-21).

Occurrence — Known to date from the Kunrade Limestone facies (Maastricht Formation, *junior* Zone auctt.) at Benzenrade (RW 76 motorway exposures), at Kunrade-Kunderberg and from the base of the Meerssen Member (Maastricht Formation, *junior* Zone auct.) at the Nekami-Ankerpoort quarry (Bemelen) (Fig. 48).

'Isocrinus' lanceolatus (Roemer, 1840)?
Pl. 2, fig. 4.

*1840 *Pentacrinites lanceolatus* Roemer, p. 27, pl. 6, fig. 3.
1961 *Isocrinus*? *lanceolatus* (Roemer, 1840) — Rasmussen, p. 133, pl. 19, figs. 3-5.
1975 *Iscocrinus*? [sic] *lanceolatus* (Roemer, 1840) — Schmid, p. 244, pl. 23, figs. 4-7.

Type — The specimen illustrated by Roemer (1840) came from erratic flints in northern Germany; both Rasmussen (1961, p. 133) and Schmid (1975, p. 245) were unable to locate it in the Roemer Colln at Hildesheim.

Material — Six (pluri)columnals: NHMM GK 1815 (W.M. Felder Colln); NHMM 1239 (van Birgelen Colln).

Description — Only few specimens, all internodals, are currently available, and their assignment is fraught with difficulties. Columnals are subcircular to subpentagonal in cross section, of slightly varying height, separated by crenulate sutures. Latera are very slightly convex in the middle and along the sutures, corresponding to a faint median ridge, especially radially. One specimen shows radial pores. Articular facets have broad areolae of variable width, each surrounded by up to 14 rather short crenulae. Petals are closed and crenulae continue along their tips. Crenulae are separated from the edge of the columnals by a narrow smooth margin. Specimen NHMM GK 1815 (Pl. 2, fig. 4) is an infranodal with a well-developed undulate row of small granules across the latera, in which the diameter of the symplectial facet differs markedly from that of the cryptosymplectial/synostosial facet.

Discussion — Comparison with specimens in the literature and with comparative material of '*I.*' *lanceolatus* (NHMM JJ 9634) from the uppermost Maastrichtian of Denmark shows that these specimens cannot be assigned to *Nielsenicrinus agassizii* nor to *Isselicrinus buchii* with which they co-occur. The presence of a narrow smooth margin which separates the crenulae from the edge of the columnals corresponds to material described from Denmark and northern Germany by Rasmussen (1961) and Schmid (1975), but ornament of latera and columnal height differ slightly. Until more material becomes available, and nodals in particular, the present specimens are referred to '*I.*' *lanceolatus* with a query.

Rasmussen (1961) recorded this species from the Maastrichtian of northern Germany and Denmark, noting the overall similarity with the Early-Late Danian *Nielsenicrinus fionicus* (Brünnich Nielsen, 1913) (see Rasmussen, 1961, p. 103, pl. 14, figs. 1-11). Schmid (1975) showed it to range through the entire Maastrichtian at Hemmoor (northern Germany).

Klikushin (1982a) recorded '*Pentacrinus*? *lanceolatus* Roemer' from the 'Senonian' of Daghestan, Mangyshlak and Turkmenia.

Occurrence — Known only from the Vijlen Member (Gulpen Formation, *sumensis* Zone) of the Mamelis-Selzerbeek outcrops and from a temporary outcrop at Aachen-Vaalserstraße (Fig. 1).

Family Isselicrinidae Klikushin, 1977

Genus *Isselicrinus* Rovereto, 1914 (emend. Rasmussen, 1954)

[= *Lipocrinus* Rasmussen, 1953]

Type species — *Isselicrinus insculptus* Rovereto, 1914, by monotypy =? *Pentacrinus didactylus* d'Orbigny, in d'Archiac, 1846.

Isselicrinus buchii (Roemer, 1840)

Pl. 1, figs. 5-10; Pl. 3, figs. 1-2.

*1840 *Pentacrinites Buchii* Roemer, p. 27, pl. 6, fig. 2.
1961 *Isselicrinus buchii* (Roemer, 1840) — Rasmussen, p. 50, pl. 4, figs. 1-15 (cum syn.).
1975 *Isselicrinus buchii* (F.A. Roemer, 1840) — Schmid, p. 239, pl. 21, figs. 1-5, 7-12 (cum syn.).
1987 *Isselicrinus buchii* (Roemer) — Wright & Smith, p. 204, pl. 44, figs. 9-10.
1992 *Buchicrinus buchii* (Hagenow in Roemer, 1840 sub *Pentacrinites*) — Klikushin, p. 120, pl. 16, figs. 1, 2, 4-8.
1995c *Isselicrinus buchii* — Jagt, p. 188, figs. 3, 7.

Type — Rasmussen (1961, p. 50) was unable to trace the original of Roemer's illustration (1840, pl. 6, fig. 2) amongst specimens from the Early Maastrichtian of Rügen (northeast Germany) in the collections of the Roemer Museum at Hildesheim. A lectotype has not been designated.

Material — Six (pluri)columnals: NHMM GK 1110 (W.M. Felder Colln); NHMM MB 398, 522, 1239a, c.

Description — The material comprises a single nodal, internodal pluricolumnals and part of a noditaxis consisting of a nodal and ten internodals. Columnals (sub)pentagonal to subcircular and of varying height and diameter (Pl. 1, fig. 8). Latera are smooth and slightly tumid and show radial furrows which are deepest at the sutures and have radial pores (Pl. 1, fig. 8). Columnals are separated by noncrenulate

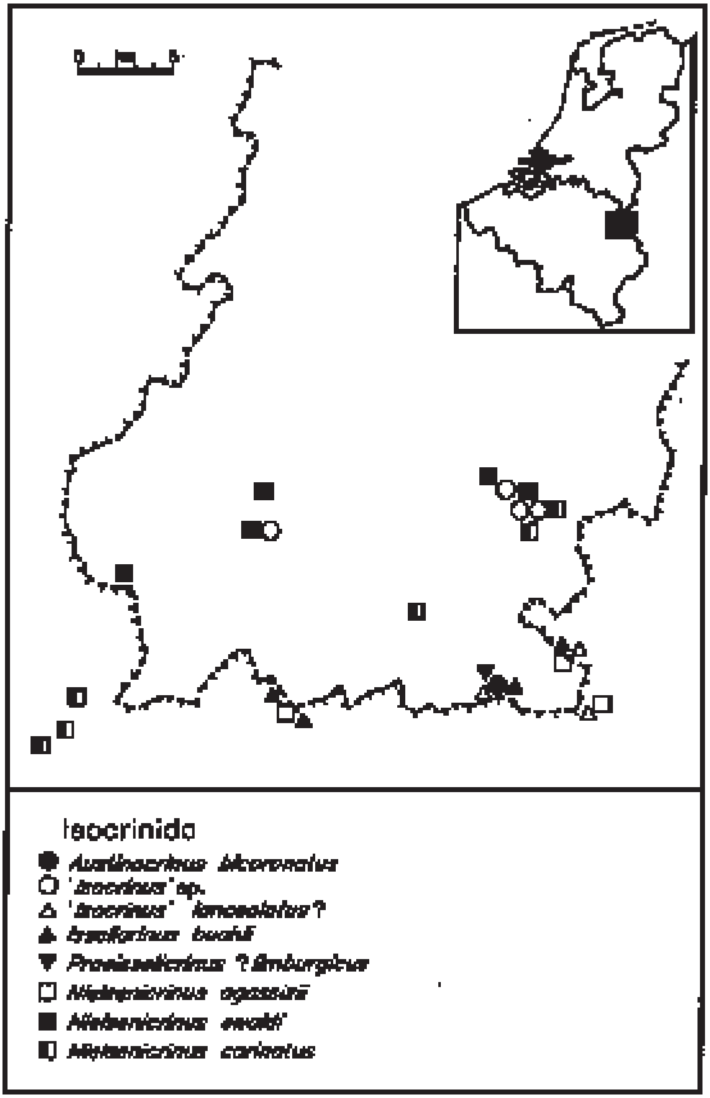

Fig. 1. Geographic distribution of Late Cretaceous isocrinids in the type area of the Maastrichtian Stage.

to faintly crenulate sutures. Articular facets have up to 13 (-14) crenulae, of varying length and width, which line the outer margin of each areola, and either reach the margin or are bordered by a smooth area around the margin (Pl. 1, figs. 5, 7). Areolae are broad and tear-shaped, and are generally more sunken towards the margin and show many pores (Pl. 1, fig. 5). A double radial ridge (Pl. 1, figs. 5, 7, 9), separated by a furrow, does not reach the lumen, which is (near)circular, nor the periphery. Nodals are of comparable size to the largest internodals (Pl. 1, fig. 8) and have two or three cirral facets (Pl. 3, figs. 1-2) situated on the distal margin. The facets protrude (Pl. 3, fig. 2), are elliptical and concave with well-developed synarthrial articular ridges on opposite sides of the circular cirral lumen. The distal articular facet of the nodal is cryptosymplectial (Pl. 3, fig. 1).

Discussion — The present material is closely comparable to specimens illustrated by Rasmussen (1961), Schmid (1975), Wright & Smith (1987), and Klikushin (1992). Rasmussen (1961) recorded the species from the Early and Late Maastrichtian; Schmid's (1975, p. 240, fig. 2) careful records show it to appear first 9 m above the Campanian/Maastrichtian boundary at Lüneburg and c. 14 m above that boundary at Kronsmoor (Saturn quarry) (middle *obtusa* Zone; see Schulz et al., 1984, fig. 2; Schönfeld et al., 1996b), while at Hemmoor the species is common in the Early Maastrichtian and reaches into the lower part of the Late Maastrichtian. Wright & Smith's (1987) material is from the Early Maastrichtian '*lanceolata* Zone' of Norfolk. Klikushin (1982a, 1992) recorded *I. buchii* from the Early Maastrichtian of the Crimea, Caucasus, Mangyshlak, Turkmenia and Central Asia. Klikushin (1977a, p. 92) erected the subgenus *Isselicrinus (Buchicrinus)* for *Pentacrinites buchii*, restricting use of the name *I. (Isselicrinus)* to Eocene-Miocene isselicrinids, noting differences in α stereom (see Roux, 1977b). Subsequent authors (e.g. Simms, 1989b; Oji, 1990) have doubted the validity of this distinction.

Isselicrinus africanus (de Loriol in Peron, 1893) (see Rasmussen, 1961, p. 47, pl. 7, figs. 18-20; Schulz, 1983, pl. 1, fig. 1), from the Maastrichtian of Tunisia, Algeria and southern Germany, might very well be a junior synonym of *I. buchii*, said to differ in details only.

Occurrence — Currently known from the Vijlen Member (Gulpen Formation) at Nieuwe Weg (outcrop 62D-15b, Zeven Wegen, Vijlenerbosch), Mamelis-Selzerbeek outcrops, Altembroeck ('s Gravenvoeren) and 's Maartensvoeren (Fig. 1), all of Early Maastrichtian age (? *obtusa* and *sumensis* zones).

Genus *Praeisselicrinus* Klikushin, 1977

Type species — *Isselicrinus atabekjani* Klikushin, 1973, by original designation.

Praeisselicrinus? *limburgicus* (Rasmussen, 1961)
Pl. 1, figs. 3-4.

*1961 *Doreckicrinus limburgicus* Rasmussen, p. 79, pl. 8, fig. 5.
1982a *P. limburgicus* (Rasmussen, 1961) — Klikushin, p. 305.
1992 *Praeisselicrinus limburgicus* (Rasmussen, 1961 sub *Doreckicrinus*) — Klikushin, p. 126.
1995c *Praeisselicrinus*? *limburgicus* — Jagt, p. 186, figs. 3, 7.

Type — Holotype and only specimen known is NHMM GK 1178 (W.M. Felder Colln).

Material — No recent finds of this species are known.

Description — Rasmussen (1961) provided a detailed description of the present species, which need not be repeated here.

Discussion — Klikushin (1977a) was probably right in removing this species from the genus *Doreckicrinus*, to which it was originally assigned (Rasmussen, 1961). Indeed, differences in columnal structure and details of articular facets are such that the present species does not appear closely related to the Middle-Late Danian *D. convexus* (Brünnich Nielsen, 1913) (see Rasmussen, 1961, p. 76, pl. 8, figs. 3-4), the Early Danian *D. miliaris* (Brünnich Nielsen, 1913) (see Rasmussen, 1961, p. 80, pl. 8, figs. 6-13) and to the 'Senonian' *D. italicus* Rasmussen, 1961 (p. 78, pl. 8, figs. 1-2). Klikushin (1992) subsequently assigned to *Doreckicrinus* the Late Cretaceous *Balanocrinus doliolum* Valette, 1917 (see Rasmussen, 1961, p. 124, pl. 19, figs. 6-7), *D. indentatus* Klikushin, 1985a (Campanian of Tuarkyr) and *Balanocrinus senonensis* Valette, 1917 (see Rasmussen, 1961, p. 85, pl. 9, fig. 4).

Placement of the present species in the genus *Praeisselicrinus* is not without doubt, in view of differences in articular facets and in position of the cirral facets between this species and the type of the genus (see Klikushin, 1992, pl. 18, figs. 15-16).

Occurrence — Currently known only from exposure 62D-15b, where it is associated with *Austinocrinus bicoronatus*, to which reference is made with regard to interpretation of stratigraphic provenance.

Family Cainocrinidae Simms, in Paul & Smith, 1988

Remarks — This family was introduced by Simms (in Paul & Smith, 1988, p. 284) to include all isocrinids with cryptosyzygial articula at IBr1-2 and synarthrial articula at IIIBr1-2 (sic: should read IIBr1-2); type genus *Cainocrinus*. Klikushin (1977b, 1982a, 1992) assigned the genus *Nielsenicrinus* to the Metacrininae, together with *Cainocrinus*.

Genus *Nielsenicrinus* Rasmussen, 1961

Type species — *Pentacrinus obsoletus* Brünnich Nielsen, 1913, by original designation.

Remarks — This genus was diagnosed by Rasmussen (1961, p. 94) as follows, 'Isocrinidae in which the articular face of the columnals has lanceolate to subguttiform petals surrounded by adradial and marginal crenulae. The crenulae attain their greatest length about the gradual transition from marginal to adradial position. The nodal has five outward-directed cirri. The infrabasals are rudimentary or absent. There are two primibrachials. The articulation IBr1-2 is syzygial with plane faces. The articulation IIBr1-2 is synarthrial but not embayed. The first pinnule is found on the abaxial side of IIBr2. The articulation IIBr2-3 is oblique muscular and IIBr3-4 is plane syzygial. Secundiaxillaries are present at least in some species.'

Rasmussen (1961, p. 94) remarked that, 'Isolated brachials found indicate that several other species, in which the arms are insufficiently known, presumably belong to this genus'. This observation is substantiated below for *N. ewaldi* sp. nov. and for '*Isocrinus*' *carinatus*.

Oji et al. (1996, p. 965), who emended the diagnosis of the genus ('Isocrinids with cryptosyzygial articulation in IBr1-2 and flat synarthrial articulation in IIBr1-2, IIBr3-4 cryptosyzygy, not symmorphy'), noted that *Cainocrinus* differs from *Nielsenicrinus* in having symmorphial rather than cryptosyzygial articulations in IBr3-4.

Nielsenicrinus agassizii (von Hagenow, 1840)
Pl. 2, figs. 1-3, 5-10; Pl. 3, figs. 3-6; Pl. 12, fig. 9.

*1840 *Pentacrinites Agassizii* von Hagenow, p. 662, pl. 9, fig. 10.
*1840 *Pentacrinites Kloedeni* von Hagenow, p. 662, pl. 9, fig. 11.
1961 *Nielsenicrinus agassizii* (Hagenow, 1840) — Rasmussen, p. 94, pl. 11, figs. 1-10 (cum syn.).
1975 *Nielsenicrinus agassizii* (Hagenow, 1840) — Schmid, p. 241, pl. 22, figs. 5-13.
1975 *Nielsenicrinus kloedeni* (Hagenow, 1840) — Schmid, p. 243, pl. 23, figs. 8-13 (partim?).
1982a *Nielsenicrinus agassizi* (Hagenow, 1840) — Klikushin, p. 305.
1992 *Nielsenicrinus agassizii* (Hagenow, 1840 sub *Pentacrinites*) — Klikushin, p. 129, pl. 19, fig. 1.
1995c *Nielsenicrinus agassizii* — Jagt, p. 187, figs. 3, 7.
1996 *Isocrinus* sp. — Keutgen, p. 195.

Type — Rasmussen (1961, p. 95) pointed out that the original specimen to von Hagenow's illustration had been lost during the 2nd World War; a neotype has not yet been designated. The same holds true for '*Pentacrinites kloedeni*'.

Material — Several dozens of (pluri)columnals and a few isolated proximal and distal brachials, including NHMM 1997027, NHMM 1997028, NHMM 1997030 (?), NHMM GK 1814 (W.M. Felder Colln); NHMM MB 93-8b, 387-6b, 522-3, 1239a, b, d-f; RGM 396 207-396 208.

Description — Columnals rounded (sub)pentagonal to (sub)pentalobate in cross section, with slight variation in height and diameter and ornament of latera. Latera with a prominent median ridge (Pl. 2, figs. 1, 5-6), which is either (near)smooth or coarsely granulate, and either straight or undulate. Granules may line the crenulate sutures (Pl. 2, fig. 1). Radial depressions occur along the suture, with or without radial pores. Articular facets have elliptical areolae of variable width (Pl. 2, figs. 2, 5, 9), petals being closed and crenulae continuing around their tips (Pl. 2, figs. 9-10). The lumen is (near)circular to pentagonal. Nodals are slightly higher and wider than internodals, the interradial edges being tumid and granulate-tuberculate/nodulose. The nodal/infranodal articulation is cryptosymplectial/synostosial and (near)smooth (Pl. 2, fig. 3). Cirral facets elliptical, covering almost the entire nodal height, and with margins slightly protruding. The articular ridge is situated slightly above the middle, and comprises articular tubercles on opposite sides of the cirral lumen.

Associated proximal brachials, amongst which IBr1 (Pl. 12, fig. 9) and IBr2 (Pl. 3, figs. 3-4) and cryptosyzygial secundibrachials (Pl. 3, figs. 5-6) are closely comparable to material illustrated by Rasmussen (1961, pl. 11, figs. 7, 10).

Discussion — *Nielsenicrinus agassizii* was originally assumed to be confined to the Early Maastrichtian of northwest Europe, but Schmid's (1975) careful records show it spanning the Early/Late Maastrichtian boundary, extending into the *junior* Zone (Schulz et al., 1984). Kjaer (1993) also recorded it from the Late Maastrichtian of Denmark. Whittlesea's (1996a, b) records of the present species from the Late Campanian of Norfolk (Norwich area) probably should be referred to the closely related (?) precursor *N. carinatus* (see below).

The present material comprises also a number of juvenile columnals (Pl. 2, fig. 7), especially from the Mamelis-Selzerbeek outcrops, which corroborate Rasmussen's (1961) view that *Pentacrinites kloedeni* is conspecific with *N. agassizii*. Puzzling in this respect is the fact that Schmid (1975) showed what he called *N. kloedeni* to be commoner in the Late Maastrichtian than in the Early Maastrichtian. He suggested that because of the small size of *kloedeni*-type columnals these might frequently have been overlooked. It is quite possible that juvenile columnals of the Late Maastrichtian *N. rosenkrantzi* Rasmussen, 1961, the range of which overlaps in part with *N. agassizii*, cannot be differentiated from those of the latter species and have a comparable *kloedeni* morphology.

Occurrence — Known to date from the Vijlen Member (Gulpen Formation) of Mamelis-Selzerbeek, Altembroeck ('s Gravenvoeren), Aachen-Vaalserquartier and Aachen-Vaalserstraße (Fig. 1).

Nielsenicrinus ewaldi sp. nov.
Pl. 4, figs. 1-10, ? 11; Pl. 5, figs. 1-3, 8.

1995c *Nielsenicrinus*? n. sp. — Jagt, p. 188, figs. 3, 7.

Type — Holotype is NHMM 1997029 (Pl. 4, figs. 3-6; ex Reijnaers Colln, no. 100), paratypes are NHMM MB 601-3b, 3c.

Type locality and horizon — ENCI-Maastricht BV quarry, Maastricht (southern Limburg, The Netherlands); Maastricht Formation, Nekum Member, between Kanne and Caster horizons, Late Maastrichtian (*junior* Zone auctt.).

Derivation of name — Named after Ewald Reijnaers (Roosendaal), who collected and donated the type.

Diagnosis — Columnals of varying height and diameter (columnal alternation), with prominent, sharp median ridge, which may be tuberculate and/or nodulose, eight internodals per internode, cirrals with tuberculate latera, dorsal surface of proximal brachials smooth.

Material — Several dozens of (pluri)columnals, a few axillary primibrachials and some secundibrachials, including NHMM K1013, 1124, 2031, 1345, 2292, 3442; NHMM MK 3933 (W.M. Felder Colln); NHMM BL 0138; NHMM JJ6735-1; NHMM MB 322a-b, 377-19, 414-4a, 506-17a, 601-3b, c/601-4a, 652a, 655-4b/655-5, 754-754a, 784-5, 866-6.

Description — The description is based primarily on the holotype (Pl. 4, figs. 3-6), which preserves a complete noditaxis and internode, as well as a proximal cirral (Pl. 4, fig. 4). Columnals are (sub)pentagonal to (sub)pentalobate in cross section, with internodals of varying height and diameter (columnal alternation), rather low, and with a sharp, irregularly granulate median ridge, and separated by crenulate sutures. In Webster's (1974) notation, the internodal order (Pl. 4, figs. 3-4) appears to be (N)32341323. The strength of the median ridge varies considerably; in some specimens it is blunt and corresponds more or less to a row of granules (Pl. 4, fig. 8). Internodal articular facets have narrow elliptical areolae (Pl. 4, figs. 1, 5, 7, 9-10) surrounded by 10-18 prominent crenulae. Petals are closed with crenulae continuing around their tips. Lumen is (sub)pentagonal (Pl. 4, figs. 7, 9-10). Radial areas of articular facets either smooth or with crenulae touching (Pl. 4, figs. 1, 5, 7, 9-10). The holotype presents two complete internodes, both of eight internodals, and appears to represent the regular and fixed arrangement of columnals such as occurs away from the main area of growth along the stem (see Donovan, 1984). Moreover, it has well-developed synostoses/crytosymplexies (see below) which show it to have come from within several centimetres below the base of the dorsal cup (see Baumiller & Gazdzicki, 1996). Nodals are larger and up to twice the height of the largest internodals (Pl. 4, figs. 3-4, 8) and have tumid, nodulose or granulate latera interradially. The nodal/infranodal articulation is cryptosymplectial/synostosial (Pl. 4, figs. 6, 8). Cirral facets are elliptical, deeply concave (Pl. 1, figs. 2, 7-8), occupy almost full nodal height and have moderately prominent, almost symmetrical synarthrial ridges on either side of the cirral lumen (Pl. 4, figs. 2, 8). Cirral facets are slightly directed upwards (Pl. 4, fig. 4); the single cirral preserved on the holotype has a granulated latus.

Associated proximal brachials include a few IBrr2 (Pl. 5, figs. 1-3) and cryptosyzygial secundibrachials (Pl. 5, fig. 8), which clearly show the present species to be assignable to the genus *Nielsenicrinus*.

Discussion — The present species appears to be distinct from all other Cretaceous-Cainozoic congeners known to date (Rasmussen, 1961; Jäger, 1981a, b; Klikushin, 1980, 1982a, b, 1985a, 1992; Eagle, 1993; Eagle & Hayward, 1993; Oji et al., 1996). It can be differentiated by details of internodal articular facets, distinct columnal alternation (expressed in internodal height and diameter) and apparently smooth dorsal surfaces of (proximal) brachials. Although it appears likely that all isocrinid material from the Nekum and Meerssen members (Maastricht Formation) should be referred to the present species, it cannot be ruled out that more species are represented (see under '*Isocrinus*' sp. above). The generally poorly preserved, small (pluri)columnals from the Kunrade Limestone facies (Pl. 4, fig. 11) include a few specimens which might belong to the present species.

For Japan, Oji (1985) demonstrated that isocrinids persisted in shallow-water settings until the mid-Cretaceous, and that on account of primibrachial articulation two types could be distinguished. One type has a synarthrial, the other a cryptosyzygial (including 'synostosis' and 'symmorphy' of authors) articulation between IBr1 and IBr2. Cryptosyzygial articulations have been demonstrated to be a type of articulation specialised for autotomy, comparable to comatulid crinoids, and to represent an anti-predator adaptation (Oji & Okamoto, 1994a, b). Oji (1985) referred to the group with synarthrial articulation as the 'Old Group' and to the other as the 'New Group'. The genus *Nielsenicrinus* is thus a member of the 'New Group'. The fact that a species (or more species) of this genus occur(s) in shallow-water deposits, in association with commoner comatulids, of the Nekum and Meerssen members is of particular interest. Jagt (in prep. d) is referred to for a more detailed discussion.

Occurrence — Material from the Nekum and Meerssen members as exposed at the ENCI-Maastricht BV, Nekami-Ankerpoort and Blom quarries clearly belongs here (Figs. 1, 47-49). Specimens from the Kunrade area (Kunrade Limestone facies) comprise a number of apparently conspecific isolated columnals and primibrachials, but the remainder is indeterminate, and is better placed in '*Isocrinus*' sp. for the time being (see above). The various outcrops in the Kunrade Limestone facies have recently been correlated by P.J. Felder & Bless (1989). These authors suggested that the RW 76 motorway outcrops (Benzenrade area) were coeval with the Lanaye Member of the Gulpen Formation elsewhere in southern Limburg, and that outcrops in the Kunrade area did not extend above the base of the Emael Member, and would thus correspond to the Valkenburg to Schiepersberg members elsewhere.

Nielsenicrinus carinatus (Roemer, 1840) sensu Rasmussen, 1961
Pl. 5, figs. 4-7, 9-10; Pls 6, 7; Pl. 8, figs. 1-9, ? 10, 11; Pls 9-11; Pl. 12, figs. 1-6, 8.

*1840 *Pentacrinites carinatus* Roemer, p. 26, pl. 6, fig. 1.
1961 *Isocrinus*? *carinatus* (Roemer, 1840) — Rasmussen, p. 115, pl. 20, figs. 3-8 (cum syn.).
?1982a *Pentacrinus*? *carinatus* Roemer, 1840 — Klikushin, p. 307.
?1992 *"Pentacrinus" carinatus* Roemer, 1840 (*Pentacrinites*) — Klikushin, p. 131, pl. 20, figs. 15-17.
1995c *Nielsenicrinus carinatus* — Jagt, p. 187, figs. 3, 7.
1995c *Nielsenicrinus minutus* — Jagt, p. 187, figs. 3, 7.

Type — The pluricolumnal illustrated by Roemer (1840, pl. 6, fig. 1) has not been traced in any collection, and is here presumed lost. The fact that Roemer used this name for isocrinids from Rügen, flint erratics in northern Germany and even from the Santonian of the Hannover area (Germany) has greatly complicated subsequent interpretations of this taxon. Rasmussen (1961, p. 116) was of the opinion that the name *Nielsenicrinus agassizii* could well be used for material from the first two localities. Santonian specimens, however, differed consistently from *N. agassizii*, and occurred commonly in France and Germany. Rasmussen suggested using the name '*Isocrinus*' *carinatus* for these specimens, and noted that this 'taxon' appeared to occur in Coniacian and Campanian strata as well. The present material, of Late Campanian age, includes cups and proximal brachials, on which evidence it can be assigned to the genus *Nielsenicrinus* without doubt. However, all these ossicles differ from material first described and illustrated by Giebel (1855) from the Coniacian/Santonian of the Quedlinburg area (Germany), and assigned by Rasmussen (1961, pl. 20, fig. 4) to *Isocrinus*? *carinatus*. The material from the extended type area of the Maastrichtian Stage shows it to be closely related to the Early Maastrichtian *N. agassizii*, from which it appears to differ in details only, and to possibly constitute its precursor. Rasmussen's (1961) assignment of columnals from the Late Campanian of Belgium to *Isocrinus*? *carinatus* is here followed for the time being. However, it is realised that this course of action still does not stabilise the nomenclature, and that in future it may be necessary to introduce a new name for the Late Campanian material.

Material — Two cups and several tens of thousands of (pluri)columnals, primi-, secundi- and tertibrachials, cirrals and pinnulars including RGM 396 209-396 221 (all ex Jagt Colln); NHMM JJ 4835, 7280R, 9486a-c, 6041; NHMM K1827; NHMM MB 619-17b, 732, 761-24, 770-9, 808-7, 808-11a, 808-12a/j, 838-4 (?), 865-26(?), 868-6, 1044-1044a/z, aa/ee; GM 1997.6 (ex Jagt Colln).

Description — Columnals small to medium-sized (up to c. 6 mm in diameter), (sub)pentastellate to (near)circular in cross section (Pls 6-8), and, in specimens of average size, of alternate height and diameter, and separated by crenulate sutures.

There are eight internodals in an internode in two noditaxes (NHMM JJ 7280R), and in Webster's (1974) notation these would both correspond to (N)32313232. Columnal alternation, however, is generally slight and seems to match differences in strength of the median ridge; in juvenile specimens it is even less clear (Pl. 5, figs. 4, 6). Ornament of latera varies considerably and seems to be dependent on preservation, at least in part. The median ridge is generally prominent, straight or undulate and spinose to varying degrees (Pl. 5, fig. 4; Pl. 6, figs. 3, 6), or web-like to varying degrees (Pl. 6, fig. 7; Pl. 7, fig. 9). Especially in small-sized specimens there are additional rows of tubercles or spines along both sutures (Pl. 5, figs. 4-7), except at the nodal/infranodal suture (Pl. 5, figs. 5-6, 9). In this respect, these specimens are closely comparable with *Isocrinus*? *minutus* (Valette, 1917) as understood by Rasmussen (1961, p. 141, pl. 15, figs. 7-17). In fact, Rasmussen's pl. 15, fig. 10 may well be conspecific with the present material (see Pl. 6, fig. 3). *Isocrinus*? *minutus* (Valette, 1917) (p. 149, fig. 23; see also Valette, 1920, p. 27[11], fig. 5; Rasmussen, 1961, p. 141, pl. 15, figs. 7-17; Klikushin, 1982a, p. 307, pl. 7, figs. 3-4; Wright & Smith, 1987, p. 204, pl. 44, figs. 5-6), from the Santonian-Early Campanian, could well be the precursor of the present species. A dorsal cup with IBrr1 preserved from the Early Campanian of the Hannover area described by Jäger (1982) is closely comparable to material illustrated here. Jagt (1995c) used the name *Nielsenicrinus*? *minutus* for diminutive columnals from the Late Campanian of Liège province. Now that large 'populations' are available it appears that these in fact represent juveniles of *N. carinatus* (see above). The nodal/infranodal articulation is cryptosymplectial/synostosial (Pl. 5, fig. 6; Pl. 7, figs. 1-2, 5, 10; Pl. 8, figs. 4, 6). In some nodals the lumen is covered by a stereom bulge (Pl. 7, figs. 1-2, 5) (see also *N. agassizii*, Pl. 2, figs. 3, 8), showing these to have been the distalmost columnal and suggesting that relocation may have taken place (compare Rasmussen, 1977; Messing et al., 1988). Nodals are up to 1.5 times higher than internodals (Pl. 5, figs. 6-7). Ornament of latera, which are more tumid than those of the internodals, consists of series of tubercles (of varying strength) or collar-like extensions (Pl. 5, figs. 9-10; Pl. 6, fig. 8). Cirral facets are concave and elliptical and occupy almost the entire nodal height, being slightly directed upwards (Pl. 5, figs. 6-7, 9-10; Pl. 8, figs. 1, 3). Triangular synarthrial ridges occur on either side of the cirral lumen.

Illustrations of articular facets of nodals and internodals here considered to belong to a single species (Pls 6-7) serve to document the wide range of variation encountered in this taxon. Proximalmost columnals (Pl. 6, fig. 9; Pl. 7, figs. 7-8) show intercalation patterns of newly formed columnals. Tubuli (Pl. 6, figs. 2, 5-6) are clearly seen. Lumen (near)circular to rounded pentagonal (Pl. 6).

There are many nodals preserving one or more (proximal) cirri (Pl. 5, figs. 5-6; Pl. 8, figs. 4-6), in one specimen they are preserved to length of c. 25 mm. Like that of columnals, the ornament of cirrals seems to be in part dependent of preservation: compare e.g. Pl. 10, figs. 6, 11 and Pl. 11, figs. 1, 4-5. Isolated cirrus fragments of varying lengths (Pl. 11, figs. 2-3) are common, as are claw-like distalmost cirrals (Pl. 11, figs. 6-7). Proximal cirrals short and disc shaped, with W > H, while distal cirrals are longer, more slender, with H > W.

The present material comprises also pathological anomalies: deformed or injured columnals (Pl. 8, figs. 1-3, 7-8) and some with four-fold symmetry (Pl. 7, fig. 6).

Associated dorsal cups (Pl. 9, figs. 1-3), basals (Pl. 9, figs. 4-6), radials (Pl. 9, figs. 8-

10), cryptosyzygial primibrachials (IBr1 and IBr2; Pl. 9, figs. 7, 11; Pl. 10, figs. 1-2; Pl. 12, figs. 6, 8), synarthrial secundibrachials IIBr1-2 (Pl. 10, figs. 3-6), distal axillary secundibrachials (Pl. 10, figs. 7-9), cryptosyzygial secundibrachials (Pl. 11, figs. 8-10; Pl. 12, figs. 1-3, 5) and (?)tertibrachials (Pl. 12, fig. 4; compare Pl. 26, figs. 2, 12) all allow this taxon to be characterised more fully, and to show beyond any doubt that it is assignable to *Nielsenicrinus*. In fact, all ossicles show a characteristic ornament of coarse spine-like tubercles, closely comparable to that of *N. agassizii* (see Rasmussen, 1961): compare e.g. the cryptosyzygial IBr1 of both species (Pl. 12, figs. 8-9).

Discussion — Rasmussen (1961) assigned the associated dorsal cup/proximal column from the Coniacian/Santonian of the Quedlinburg area as illustrated by Giebel (1855) to *Isocrinus*? *carinatus*. Giebel referred this specimen to the Neocomian *I. annulatus* (Roemer, 1836), a species described in detail by Jäger (1981b). From the illustration in Rasmussen (1961, pl. 20, fig. 4) it is obvious that this is not conspecific with the present Late Campanian material, which has a quite different dorsal cup and IBr1 structure. Jäger (1982) described an isocrinid theca from the Late Santonian of Gehrden (NW Germany), which showed all typical proximal brachial articulations of the genus *Nielsenicrinus* and could well belong to *Isocrinus*? *nodulosus* (Roemer, 1840). According to Rasmussen (1961) typical columnals of the latter species are easily differentiated from those of *Isocrinus*? *carinatus*, but occasionally the distinction presented problems. For the latter species, Rasmussen (1961, p. 117) assumed an internode length of twenty-three internodals. He also considered *Isocrinus icaunensis* Valette, 1917 (p. 139, fig. 19) and *I. courvillensis* Valette, 1917 (p. 142, fig. 20) to be synonymous, both of Santonian age, with the former ranging into the Early Campanian.

Schmid (1975, p. 242) noted the possible conspecificity of *Isocrinus*? *carinatus* and *N. agassizii*, which could be considered as yet another indication of their close relationship.

In the literature there are many records of '*Pentacrinus carinatus* A. Roem.' (Arnold, 1964) and '*Pentacrinus*? *carinatus* Roemer' (Klikushin, 1982a), but it is often far from clear to which of the above species reference is made. The latter author recorded it from the Coniacian-Campanian of the western Ukraine, Crimea, Caucasus, Volga-Emba region, and Mangyshlak.

Occurrence — As here understood, *N. carinatus* is known from the Late Campanian as exposed at the Heure-le-Romain, CPL SA and CBR-Lixhe quarries (Figs. 1, 43-44). The limited material from the Benzenrade Member (Vaals Formation) of Benzenrade and de Wingerd quarry (Pl. 8, fig. 9) is here considered to be conspecific, as is a single internodal from the Beutenaken Member of Pesaken (NHMM MB 838-4).

Order Comatulidina A.H. Clark, 1908

Remarks — Simms et al. (1993, p. 501) pointed out that the Treatise classification (Rasmussen, 1978) of comatulid crinoids is unsatisfactory and probably does not reflect phylogenetic relationships within the group. Based on extant East-Indian shallow-water comatulids, Messing (1996) noted that a detailed phylogenetic reevaluation of comatulids is urgently needed. For fossil species, important characters used in the classification of extant comatulids (see e.g. Hoggett & Rowe, 1986; Messing, 1995b), such as the type of articulation between proximal brachials [(crypto)synarthry or syzygy] are often poorly known or not known at all. This accounts for the doubts expressed in generic assignment of many forms (see also Baumiller & Gazdzicki, 1996), a problem already addressed by Gislén (1934).

In the study area, comatulids are much commoner than isocrinids, in places occurring in large numbers. Such occurrences are comparatively rare in the fossil record (compare Radwanska, 1987). The comatulid design arose after the mid Carnian (Triassic) extinction (Hagdorn & Campbell, 1993) and their 'free-living' mode of life subsequently turned out to be the most successful strategy amongst post-Palaeozoic articulate (cladid) crinoids.

Infraorder Comatulidia A.H. Clark, 1908
Family Atelecrinidae Bather, 1899
Genus *Jaekelometra* Gislén, 1924

Type species — *Atelecrinus belgicus* Jaekel, 1902, by original designation.

Remarks — Rasmussen (1978, p. T896) removed the present genus from the Conometridae, in which it had been originally placed (Gislén, 1924) and reassigned it to the Atelecrinidae. In the structure of the basals and radials, *Jaekelometra* indeed closely resembles species of the genera *Atelecrinus* (see Rasmussen, 1978, figs. 583-584; Messing & Dearborn, 1990) and *Sibogacrinus*. Proximal and distal brachials attributed to the genus *Jaekelometra*, as described below, do not contradict such an assignment.

Jaekelometra gr. *belgica* (Jaekel, 1902)
Pl. 15, figs. 3-12.

*1902 *Atelecrinus belgicus* Jaekel, p. 1084, fig. 15b.
1961 *Jaekelometra belgica* (Jaekel, 1901) — Rasmussen, p. 321, pl. 47, fig. 6 (cum syn.).
1995c *Jaekelometra belgica* — Jagt, p. 190, figs. 4, 7.

Material — Several hundreds of centrodorsals, as well as a few cups and isolated basals, including RGM 396 225-396 236 (ex Jagt Colln); NHMM JJ 10635-10637, 10639 and 10842c; NHMM RD 15; NHMM BL 0130; NHMM K1022, 1156b, 1348a, 1421b, 2623, 2673, 2688-8b, 2986b; NHMM MB 234-3/8/9/10a/15, 386-3b, 414-4c, 506-Ha, 601-4b, 754f, 866-6/11b.

Description — As here interpreted, specimens assigned to this group have either low and wide, bluntly conical centrodorsals ('Type 1': Pl. 15, figs. 8, 10, 12), usually slightly taller than wide or as tall as wide (Fig. 3), or pointed conical centrodorsals, with straight sides in lower half ('Type 2': Pl. 15, fig. 6), and taller than wide (Fig. 2). Centrodorsals generally (sub)pentagonal in outline (Pl. 15, figs. 4, 10). The number of cirral facets or scars (Fig. 3) varies considerably, even amongst specimens of comparable centrodorsal diameter. Gislén (1924) and Rasmussen (1961) both recorded c. 15 cirral facets for this species; these are occasionally arranged in ten indistinct rows, alternate or are mostly irregularly arranged, with sizes of individual (sub)circular facets varying considerably (Pl. 15, fig. 9). Specimens of 'Type 2' generally have but five rows of cirral facets, the facets becoming larger proximally where they tend to alternate. Distal facets may become obsolete, and more or less flush with centrodorsal dor-

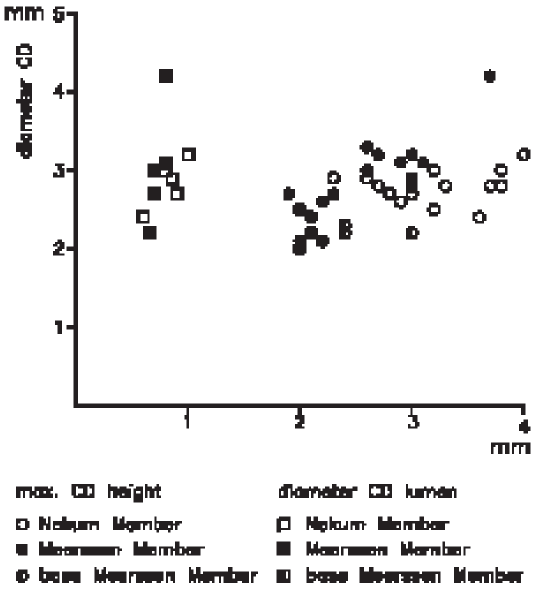

Fig. 2. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Jaekelometra* gr. *belgica* (Jaekel, 1902) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

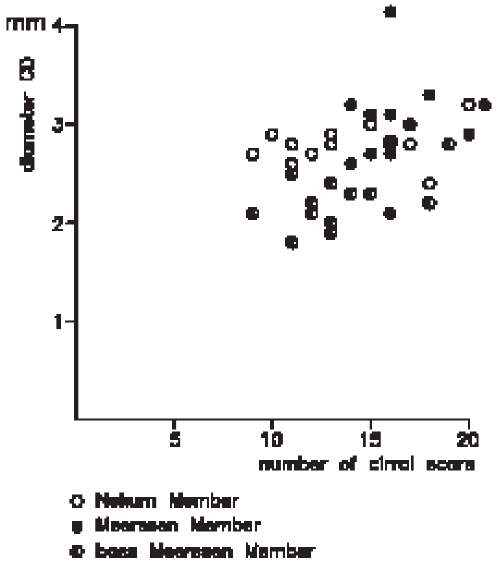

Fig. 3. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Jaekelometra* gr. *belgica* (Jaekel, 1902) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

sal surface. Cirral scars are either moderately deep (Pl. 15, figs. 9-10) or almost even and show weak horizontal synarthrial ridges and a narrow cirral lumen. There is no ornament around the facet margin, but the strength of this margin varies. Ventral surface of centrodorsal is also quite variable, being generally slightly concave with indistinct, shallow grooves for basals, a rather large, (sub)circular central pit, especially in smaller specimens (Fig. 2). The height of the continuous basals also shows a wide range of variation (Pl. 15, figs. 3, 8, 12), being slightly wider than tall or much taller than wide. Their dorsal surface is smooth, and curves outwards to varying degrees. The radials also form a continuous ring of moderately thin plates, wider than tall (Pl. 15, fig. 12) or, generally, taller than wide (Pl. 15, fig. 8). There is much variation in the strength of the dorsal crest (Pl. 15, figs. 8, 12), which may extend to the lower end of the radial. The outward curvature of the radial ring also varies (Pl. 15, figs. 8, 12). Articular facets of radials are wide and (sub)triangular (Pl. 15, figs. 7, 11), with dorsal ligament pit being large, wide and fairly deep, interarticular ligament pits indistinct and ventral muscle pits low and comparatively wide and deep on both sides of a median ridge. Nerve canal large and oval.

Discussion — Rasmussen (1961) noted that the holotype, the specimen illustrated by Jaekel (1902, fig. 15b) and refigured by Gislén (1924, fig. 219-221) (van den Binkhorst Colln, MNB), had a centrodorsal height of 2.7 mm, and a total height and width (inclusive of basals) of 7 and 2.6 mm, respectively. He differentiated *J. belgica* from congeners by its low centrodorsal with few cirral facets. This distinction is here adopted for the time being, but future studies may show that *J. belgica* and *J. concava* (= *J. columnaris*, see below) in fact represent but a single biological species. The structure of the basals and radials here assigned to *J.* gr. *concava* (see below) are inseparable from those of *J.* gr. *belgica*, and measurements (Figs. 2-3) of centrodorsal height, diameter, diameter of centrodorsal lumen as well as number of cirral facets all show a wide scatter and partial overlap (compare Figs. 5-6). The form here referred to as 'Type 2' (Pl. 15, figs. 3-6) might represent a distinct species, but too few cups or specimens preserving basals are available to be sure of this.

Occurrence — Known to date from the Nekum and Meerssen members and the Kunrade Limestone facies (Maastricht Formation) of various quarries and outcrops in Liège-Limburg and southern Limburg; representatives of this (group of) species and the next (see below) are extremely common locally (Jagt, 1990) (Figs. 4, 46-49).

Jaekelometra gr. *concava* (Schlüter, 1878)
Pl. 16, figs. 1-7, 9, 12, ? 8, ? 10-11;? Pl. 17;? Pl. 18, figs. 1-8.

*1878 *Antedon concavus* Schlüter, p. 48, pl. 3, figs. 4-7.
*1924 *Jaekelometra columnaris* Gislén, p. 163, figs. 228-229.
1961 *Jaekelometra columnaris* Gislén, 1924 — Rasmussen, p. 322, pl. 47, figs. 1-5.
1961 *Jaekelometra concava* (Schlüter, 1878) — Rasmussen, p. 324, pl. 47, fig. 9.
1995c *Jaekelometra concava* — Jagt, p. 189, figs. 4, 7.
1995c *Jaekelometra columnaris* — Jagt, p. 189, figs. 4, 7.

Material — Several hundreds of centrodorsals, a few specimens preserving basals, as well as isolated radials, primi- and secundibrachials, including RGM 396 237-396 244 (all ex Jagt Colln); NHMM 1997033, NHMM MK 1545 (W.M. Felder Colln);

NHMM K1015, 1017a, 1024, 1072a, 1123a, 1156a, 1158, 1421a, 1348b, 2287c, 2688-8a, 2986a; NHMM JJ 10638, 10842b; NHMM MB 95-2a, 99-1, 108-14/15c, 234-10b, 377-1a, 377-5a, 386-3a, 649-12 (?), 655-4e, 861-1(?); GM 1997.9 (ex Jagt Colln).

Description — Centrodorsal (sub)pentagonal to subcircular in outline, bluntly conical or pointed conical with height generally about equal to diameter (Fig. 5). Cirral facets or scars mostly arranged regularly in ten distinct rows, of three to five facets each (Pl. 16, figs. 2, 4, 6-7). In a few specimens (Pl. 16, figs. 9, 12) cirral facets tend to alternate, and these are thus reminiscent of *J.* gr. *belgica*. Total number of scars gener-

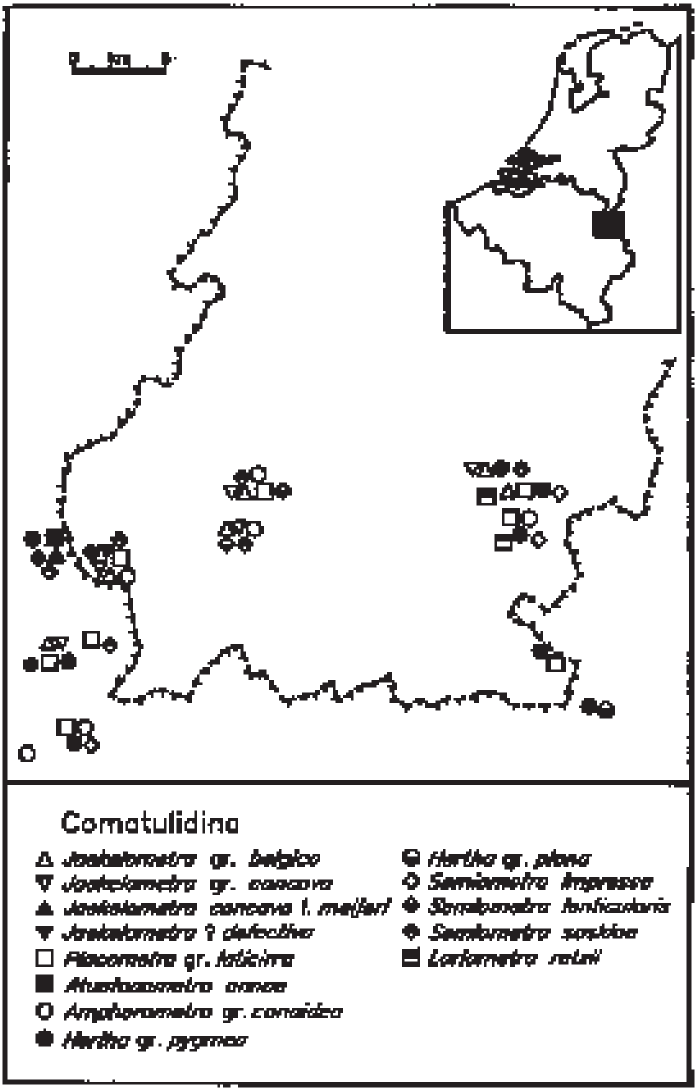

Fig. 4. Geographic distribution of Late Cretaceous-Early Palaeogene comatulids in the type area of the Maastrichtian Stage.

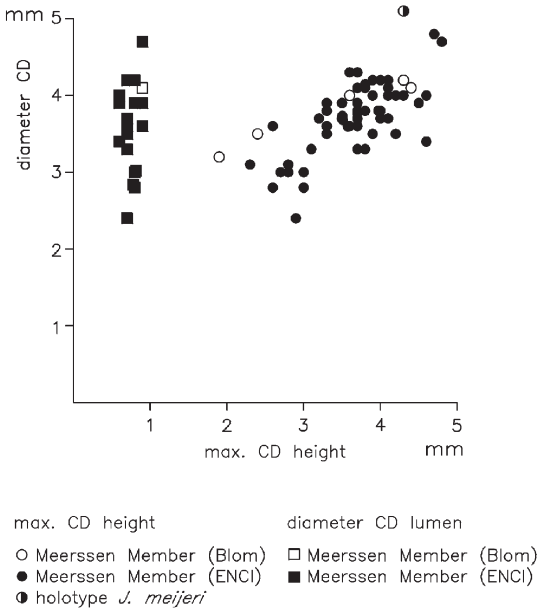

Fig. 5. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Jaekelometra* gr. *concava* (Schlüter, 1878) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

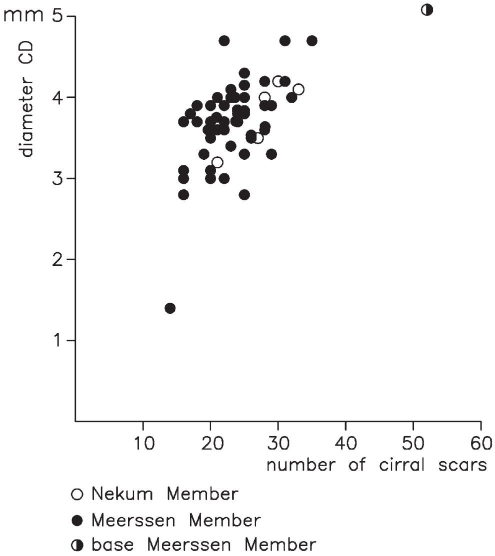

Fig. 6. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Jaekelometra* gr. *concava* (Schlüter, 1878) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

ally varying between 20 and 30 (compare forma *meijeri* below; Fig. 6). In size, facets are uniform with the exception of the lowermost ones which apparently become obsolete during ontogeny, and occasionally a small, new facet at the top of some of the rows (Pl. 16, figs. 2, 6, 9). Cirral facet rows are separated by a smooth radial area, of highly variable width and extent (Pl. 16, figs. 2, 4, 6-7). Cirral facets are deeply concave (Pl. 16, fig. 6) or moderately so, generally have a well-developed synarthrial ridge (Pl. 16, figs. 2, 4-7) and a subcircular to oval cirral lumen (Pl. 16, figs. 2, 5-6).

The ventral surface of centrodorsal is concave to varying degrees (Pl. 16, figs. 1-3, 5), the (sub)circular central pit or lumen being comparatively narrow (Fig. 5). In some specimens shallow radial pits (Pl. 16, fig. 3) are seen, their depth and outline varying considerably, and they are well separated from the central pit. Grooves for the basals (Pl. 16, figs. 1, 3) are thin and shallow, at times hardly discernible.

The basals, preserved in the type of *J. columnaris* (van den Binkhorst Colln (MNB), illustrated by Gislén, 1924, figs. 228-229), are low in comparison to those of *J.* gr. *belgica*, their height equalling half their width or corresponding to width (Pl. 17, fig. 9).

Discussion — In 'populations' of *J.* gr. *concava* from the upper Meerssen Member (Maastricht Formation), often yielding more than 100 specimens, also centrodorsals showing features typical of *J. belgica* are encountered, but these are invariably low in number. Based on this observation, all isolated radials (several dozens) and basals (surprisingly few) found in these samples are here considered to belong to this group. As noted above, these radials (Pl. 16, figs. 8, 10-11) are inseparable from those of *J. belgica*. Associated in these samples are also other brachial ossicles, which are here tentatively assigned to the genus *Jaekelometra*, and to *J.* gr. *concava* in particular. These are IBr1 (Pl. 17, figs. 5, 7, 10), which show a proximal muscular articular facet and a distal synarthry, corresponding to that of the proximal articular facet of IBr2 (Pl. 17, fig. 3). The IBr2 shows a prominent median crest (Pl. 17, figs. 1, 3), which matches that seen on the IIBr1 (?) (Pl. 17, figs. 4, 6, 8), which shows a muscular proximal articular facet and a distal synarthry. In displaying these brachial articulations, assignment of the genus *Jaekelometra* to the Atelecrinidae appears justified (compare Rasmussen, 1978, p. T872). More distal brachials, broadly cuneate in outline, encountered in the same samples show either muscular or synostosial/cryptosyzygial articulations (Pl. 18, figs. 1-8), with oval-elliptical lumen and oblique articular ridges. These are here also assigned to *Jaekelometra*.

As can be seen from the synonyms above, *J. columnaris* is here considered conspecific with *J. concava* (type is RFWUIP Schlüter Colln, no. 304), which name has priority. Rasmussen (1961) noted that *J. concava* appeared to represent an intermediate between *J. belgica* and *J. columnaris*.

Occurrence — Representatives of this group occur commonly in the Nekum and Meerssen members, and more rarely, in the Kunrade Limestone facies (Maastricht Formation) (Figs. 4, 46-49). A single centrodorsal from the basal Emael Member as exposed at the CBR-Romontbos quarry (Fig. 46) may also belong here.

Jaekelometra concava forma *meijeri* Rasmussen, 1961

*1961 *Jaekelometra meijeri* Rasmussen, p. 326, pl. 47, fig. 7.
1995c *Jaekelometra meijeri* — Jagt, p. 190, figs. 4, 7.

Type — Holotype and only specimen known is NHMM MM 844.

Material — No recent finds are known.

Discussion — With only a single specimen in hand, it is here preferred to consider this to be an extreme form of *J.* gr. *concava*. Indeed, in 'populations' of this group occasionally specimens reminiscent (Pl. 16, fig. 6) of *J. meijeri* are encountered. It is characterised by more numerous (Fig. 6), regularly arranged cirral facets, and facet rows separated by concave radial areas which extend further down, as well as by the structure of the basals, according to Rasmussen (1961). However, a close examination of the type suggests that the 'basals' in fact represent broken-off portions of these ossicles, and that their structure in *J. meijeri* does not differ appreciably from that of other members of the genus (Pl. 15, fig. 5; Pl. 17, fig. 9).

Occurrence — The sole specimen known is from Meijer's Md 4, which corresponds to the upper Meerssen Member (IVf-5 and -6, Maastricht Formation) in current terminology, as formerly exposed in the Albertkanaal sections near Vroenhoven-Riemst (Fig. 4).

Jaekelometra? *defectiva* sp. nov.

Pl. 15, figs. 1-2.

1995c *Jaekelometra*? n. sp. — Jagt, p. 189, figs. 4, 7.

Type — Holotype and only specimen known is NHMM 1997031 (ex Jagt Colln, don. J. Reynders).

Type locality and horizon — ENCI-Maastricht BV quarry (Maastricht), Maastricht Formation, base Emael Member (Late Maastrichtian, *Belemnitella junior* Zone of authors).

Derivation of name — Lat. *defectivus*, meaning broken, damaged.

Diagnosis — Atelecrinid (?) with high conical centrodorsal, subpentagonal in outline and with widely separated cirral facets (c. 35 in number), regularly arranged in ten vertical rows.

Material — No other specimens are known to date.

Description and discussion — Centrodorsal conical, considerably taller than wide, and with blunt distal end. Cirral facets are widely spaced, and arranged regularly in ten alternate rows, of 2 to 4 facets each. Facets are of comparable size, with exception of the lowermost ones, increasing only slightly proximally (Pl. 15, fig. 1). Facets are crater-like and protrude (Pl. 15, fig. 2), are elliptical with a distinct synarthrial ridge and small, oval cirral lumen. The ventral surface of the centrodorsal, although fragmentary and poorly preserved, appears to have been strongly concave with thin and shallow furrows for basals.

The centrodorsal outline and the structure and arrangement of the cirral facets serve to distinguish this form from all other species of *Jaekelometra* occurring in the area. Although no basals or radials are known of this species, assignment to the genus *Jaekelometra* rather than to *Amphorometra* or any other conometrid, is preferred, at least for the time being.

Occurrence — Currently only known from the base of the Emael Member (Maastricht Formation) as exposed at the ENCI-Maastricht BV quarry, Maastricht (Figs. 4, 47). With a single exception (see above), species of the genus *Jaekelometra* are normally confined to the Nekum and Meerssen members and to the Kunrade Limestone facies of the Maastricht Formation.

Superfamily Tropiometracea A.H. Clark, 1908
Family Pterocomidae Rasmussen, 1978

Remarks — To this family, Rasmussen (1978) originally assigned two genera, *Placometra* and *Pterocoma*. Manni et al. (1985) subsequently added the new genus *Rhodanometra* (type *R. lorioli*, Early Callovian, Jurassic), albeit with a query. *Atuatucametra* nov. gen., described below, is here also placed in this family.

Genus *Placometra* Gislén, 1924

Type species — *Placometra mortenseni* Gislén, 1924, by original designation.

Placometra gr. *laticirra* (Carpenter, 1880)
Pl. 14; Pl. 24, fig. 5.

*1880 *Antedon laticirra* Carpenter, p. 551, pl. 23, fig. 6.
*1924 *Placometra mortenseni* Gislén, 1924, p. 162, figs. 230-232.
*1925 *Glenotremites scutatus* Gislén, p. 7, figs. 11-13.
1961 *Placometra laticirra* (Carpenter, 1880) — Rasmussen, p. 352, pl. 52, figs. 3-5 (cum syn.).
1961 *Placometra mortenseni* Gislén, 1924 — Rasmussen, p. 354, pl. 52, fig. 7.
1961 *Placometra scutata* (Gislén, 1925) — Rasmussen, p. 355, pl. 52, fig. 6.
1987 *Placometra laticirrha* Carpenter [sic] — Wright & Smith, p. 210, pl. 46, figs. 3-4.
1993 *Placometra laticirra* (Carpenter, 1880) — Kjaer, p. 148, pl. 6, figs. 9-11.
1995c *Placometra* n. sp. — Jagt, p. 189, figs. 4, 7.

Material — Several dozens of cups, centrodorsals, radial rings, as well as dissociated brachials (Pl. 26, fig. 3; Pl. 27, fig. 8) which might belong here, including NHMM K1411, 2464; NHMM JJ 9525, 9526, 9532; NHMM PK680; NHMM RD164; NHMM MB 108-13/15b, 619-18, 649-1, 678-1, 865-21b/22, 1044-19, 1239.

Description — Centrodorsals are pentagonal in outline, with grooves for basals protruding (Pl. 14, figs. 1-6, 12) and with ventral surface having radiating folds which correspond to the cirral facets; there are no radial pits. Centrodorsal lumen vs centrodorsal diameter (Fig. 8) varies slightly, as does maximum centrodorsal height vs centrodorsal diameter (Fig. 7). Dorsal surface of centrodorsal is either gently arched or almost flat and irregular, occasionally slightly concave. In this respect, specimens from the Maastrichtian type area differ from material from Jasmund/Rügen (Pl. 14, figs. 11-13), in which the dorsal surface is generally strongly arched and irregular. In a few specimens, especially those from the Benzenrade Member there are curved ridges in a star-like arrangement on the dorsal centrodorsal surface. Lateral sides of centrodorsal are steep (Pl. 14, figs. 4, 8), and occasionally show obliquely elongate, large cirral facets, their number apparently independent of centrodorsal diameter (Fig. 9). In some specimens these facets bear rather coarse, radiating crenellae along the margins; in most, however, they are apparently lacking. In part, this may be dependent of preservation, which is clearly demonstrated by specimens from the basal Emael Member (Maastricht Formation, Pl. 14, figs. 4, 8). The articular ridge, consisting of synarthrial tubercles on opposite sides of the comparatively large, oval cirral lumen connected by a prominent ridge, is generally well developed (Pl. 14, figs. 4, 8).

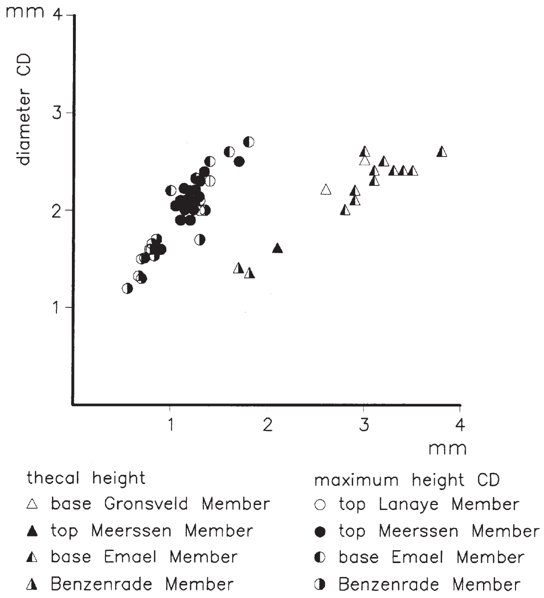

Fig. 7. Relationship between centrodorsal diameter (CD), thecal height and maximum centrodorsal height in *Placometra* gr. *laticirra* (Carpenter, 1880) from the Benzenrade Member (Vaals Formation, Late Campanian), the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Gronsveld, Emael and Meerssen members (Maastricht Formation, Late Maastrichtian).

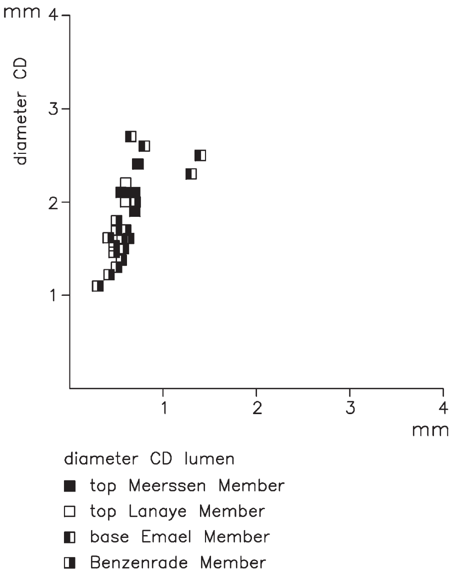

Fig. 8. Relationship between centrodorsal diameter (CD) and diameter of centrodorsal lumen in *Placometra* gr. *laticirra* (Carpenter, 1880) from the Benzenrade Member (Vaals Formation, Late Campanian), the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Emael and Meerssen members (Maastricht Formation, Late Maastrichtian).

Material available comprises fairly many complete cups, their height (thecal height in Fig. 7) vs centrodorsal diameter varying considerably. Radial rings are pentagonal with (weakly) concave sides (Pl. 14, figs. 7, 9), and show small basals on their proximal sides. These apparently rarely extend to the free surface of the radials, and thus differ markedly from the illustrated specimen (Pl. 14, figs. 11-13) from Jasmund/Rügen. The radials are relatively large plates (Pl. 24, fig. 5), which greatly overhang the centrodorsal (Pl. 14, figs. 4, 8); their articular facets are almost vertical, wide and tall. Dorsal ligament pit is large and wide, and deep centrally. Above the subcircular to oval nerve canal follow the ventral muscle pits which are large and deep and separated from the interarticular ligament pits by an oblique ridge. Body cavity is large and wide.

Discussion — As can be seen from the synonyms above, this species is here interpreted widely and referred to as a group. This group includes 'extreme' morphologies held to be typical of the various 'species', which are based mainly on single specimens only. For the present study, a number of 'populations' have been available of Late Campanian and Late Maastrichtian age and from a variety of depositional settings. There are (slight) differences in centrodorsal dimensions and in the structure of cirral facets and basals, but not until 'populations' of *P. laticirra* from elsewhere are analysed can these be properly evaluated. For the moment, it seems best to treat this material as a long-ranging group. *Placometra conica* Rasmussen (1971, p. 286, pl. 1, figs. 2-3; pl. 2, figs. 7-8) from the Turonian of England appears to be a distinct species.

Occurrence — In the study area, representatives of this group are now known from the Late Campanian Benzenrade Member (Vaals Formation) and Zeven Wegen Member (Gulpen Formation), as well as from the Late Maastrichtian Lanaye Member

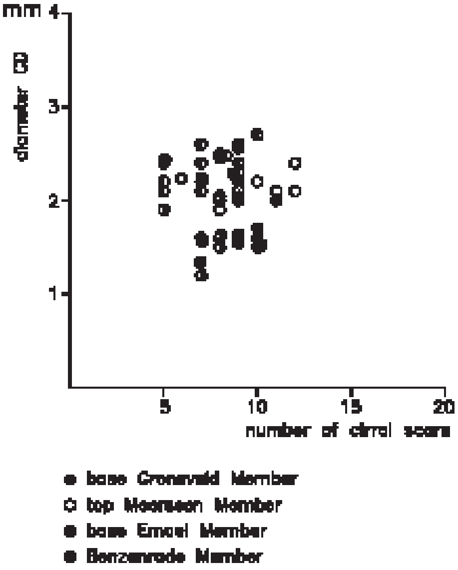

Fig. 9. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Placometra* gr. *laticirra* (Carpenter, 1880) from the Benzenrade Member (Vaals Formation, Late Campanian) and the Gronsveld, Emael and Meerssen members (Maastricht Formation, Late Maastrichtian).

(Gulpen Formation), and Gronsveld, Emael and Meerssen members (Maastricht Formation) (Figs. 4, 43, 45-47, 49).

Genus *Atuatucametra* gen. nov.

1995c comatulid n. gen. — Jagt, figs. 4, 7.

Type species — *Atuatucametra annae* sp. nov., by monotypy.

Derivation of name — Combination of *Atuatuca (Tungrorum)*, a town now known as Tongeren (Limburg, Belgium), inhabited by the tribe of the Tungri during Roman times (van Es, 1972) and *-metra*, suffix used for many comatulid crinoids.

Diagnosis — Pterocomid with low to slightly conical, irregularly pentagonal centrodorsal with protruding, small, irregularly arranged cirral facets, extensive free surface to greatly overhanging, vertical radials and basals exposed in interradial points.

Atuatucametra annae gen. et sp. nov.
Fig. 10; Pl. 19, figs. 3-7.

Type — Holotype is NHMM 1997088 (Fig. 10a-d; ex van der Ham Colln); paratypes are NHMM 1997089 (Fig. 10e-h; ex van der Ham Colln) and NHMM MB 432.PPa-c (Pl. 19, figs. 3-7).

Type locality and horizon — Temporary Albertkanaal sections near Veldwezelt (Limburg, Belgium), Houthem Formation, Geulhem Member, upper part (Middle Danian, *bruennichi* Zone equivalents).

Derivation of name — Named after my mother, to express the gratitude we feel about her still being amongst us.

Material — Twenty centrodorsals and isolated brachials possibly belonging to the present species, including NHMM MB 432.HHH, 432.PP.

Description — Centrodorsals are relatively small and low (Fig. 11), with cirrus-free (or with a few obsolete cirral facets?, Pl. 19, fig. 7) dorsal area slightly arched to bluntly conical, lacking dorsal pit or star (Pl. 19, figs. 3-4; Fig. 10b, f) but mostly with irregular tubercle-like protuberances (Pl. 19, fig. 3) of varying strength. Centrodorsal outline is irregularly pentagonal (Pl. 19, figs. 3-4, 6; Fig. 10e-f), with interradial areas (grooves for basals) strongly protruding. Cirral facets situated on these protruding interradial sections, apparently arranged in two columns per section, and with 1-2 (or up to 4) facets per column (Fig. 10h). One of the facets generally extends further than the others (Pl. 19, figs. 3, 5), which accounts for the irregular centrodorsal outline. In the holotype cup (Fig. 10b) the most protruding cirral facets are seen to correspond to the sutures between the radials, and this is where the basals are exposed. The (near)circular to oval, regularly concave, cirral facets have a small, oblique-transverse cirral lumen, but lacks margin ornament, articular ridge or articular tubercles (Pl. 19, figs. 3, 5; Fig. 10g-h).

The ventral surface of the centrodorsal shows no radial pits (Pl. 19, fig. 6; Fig. 10e); grooves for the rod-like basals are more or less distinct (Pl. 19, fig. 6), which extend to the end of the centrodorsal. Centrodorsal lumen (Fig. 11) c. 30% of centrodorsal diameter, and of (sub)pentagonal to (near)circular outline (Pl. 19, fig. 6; Fig. 10e). Each section has 2-4 axial canals opening to the pit (Fig. 10e).

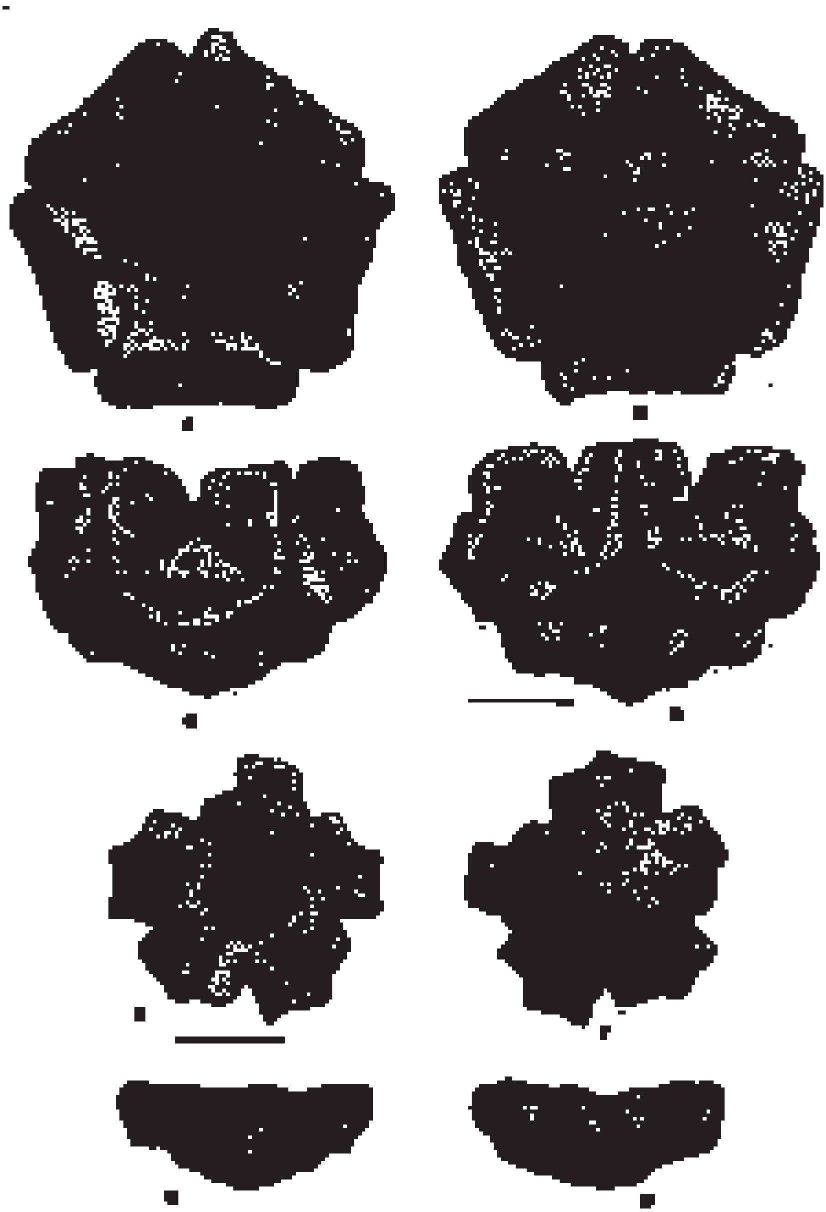

Fig. 10. Camera-lucida drawings of the holotype NHMM 1997088 (a-d) and paratype NHMM 1997089 (e-h) of *Atuatucametra annae* gen. et sp. nov. from the Geulhem Member (Houthem Formation, Middle Danian) of the Albertkanaal sections (Vroenhoven-Riemst, Belgium). Scale bar represents 1 mm (del. R. van der Ham).

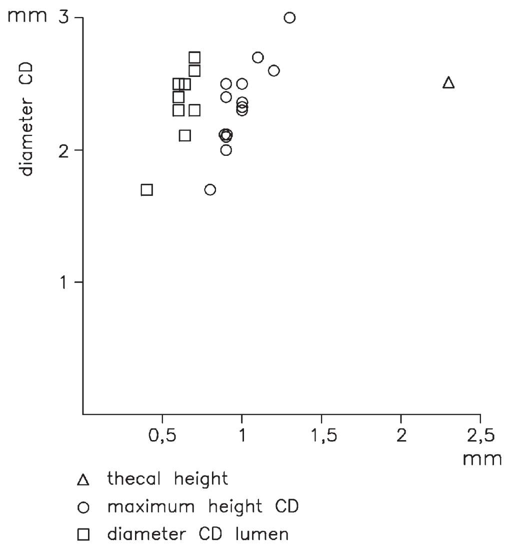

Fig. 11. Relationship between centrodorsal diameter (CD), thecal height, maximum centrodorsal height and diameter of centrodorsal lumen in *Atuatucametra annae* gen. et sp. nov. from the Geulhem Member (Houthem Formation, Middle Danian).

The holotype cup (Fig. 10a-d) preserves radials; these are slightly oblique to almost vertical with free lateral surface extending distally on both sides of radial midline and separating abutting radials (Fig. 10a, c-d). Dorsal ligament pit is transverse, wide and deep, the nerve canal above being circular. Ventral muscle pits are wide but rather low, separated by a deep groove; interarticular ligament pits are comparatively large and separated from ventral muscle pits by an almost straight ridge (Fig. 10c-d). Body cavity is large and funnel shaped, corresponding to almost 50% of total cup diameter (Fig. 10a).

The variation seen in centrodorsal height (Pl. 19, figs. 5, 7) has also been documented for various extant comatulids (see e.g. Messing & Dearborn, 1990) and is not considered important.

Discussion — Placement in the Pterocomidae is based on the general outline of centrodorsal, cup and structure of cirral facets, which are all reminiscent of what can be seen in representatives of the genus *Placometra*. Distinguishing features of the new genus in particular are the cirral facet arrangement and the structure of the radials.

Occurrence — This new taxon is apparently confined to the Middle Danian portion of the Geulhem Member (Houthem Formation), as formerly exposed in the Albertkanaal sections near Veldwezelt (Limburg, Belgium) (Fig. 4).

Family Conometridae Gislén, 1924

Remarks — Baumiller & Gazdzicki (1996, p. 112) noted that this family, placed in the Tropiometracea by Rasmussen (1978), might possibly be better referred to the Notocrinacea.

Genus *Amphorometra* Gislén, 1924

Type species — *Glenotremites conoideus* Goldfuss, 1839, by original designation.

Amphorometra gr. *conoidea* (Goldfuss, 1839)
Pl. 13, figs. 1-5; Pl. 18, figs. 9-12; Pl. 19, figs. 1-2.

*1839 *Glenotremites conoideus* Goldfuss, p. 286, pl. 160, fig. 18.
*1924 *Amphorometra brydonei* Gislén, p. 160, figs. 212- 213.
*1924 *Conometra rugiana* Gislén, p. 166, figs. 233-234.
1961 *Amphorometra brydonei* Gislén, 1924 — Rasmussen, p. 329, pl. 49, fig. 2.
1961 *Amphorometra conoidea* (Goldfuss, 1839) — Rasmussen, p. 331, pl. 48, figs. 2-4 (cum syn.).
1961 *Amphorometra rugiana* (Gislén, 1924) — Rasmussen, p. 336, pl. 48, fig. 5.
1995c *Amphorometra brydonei* — Jagt, p. 189, figs. 4, 7.
1995c *Amphorometra conoidea* — Jagt, p. 190, figs. 4, 7.

Material — A dozen of cups (mostly moderately to poorly preserved), as well as several dozens of centrodorsals, including RGM 396 222, 396 223, 396 245 (all ex Jagt Colln); NHMM 1997034; NHMM JJ 10842d; NHMM K1015, 1017b, 1072b, 1156c, 1348c, 1422, 2616, 2688-8a (?), 2986c; NHMM MB 95-2c, 108-15c, 377/377-1c/17, 386-3c, 761-33, 770-5, 808-21, 865-21c, 866-6a/11c, 1044-13a/b/20, 1239g; GM 1997.10 (ex Jagt Colln).

Description — As can be seen from the list of synonyms above, this ‘species' is here treated as a group, for reasons outlined below. Specimens of Late Campanian (Benzenrade and Zeven Wegen members), Early Maastrichtian (Vijlen Member) and Late Maastrichtian age (Nekum and Meerssen members) (Figs. 12-14) are lumped.

Centrodorsals are conical or bluntly conical (Pl. 18, figs. 10-12; Pl. 19, fig. 1), dorsal pole often worn and abraded (Pl. 13, figs. 1, 5), especially in specimens from the Zeven Wegen, Beutenaken and Vijlen members. Centrodorsal diameter generally exceeding height, with few exceptions (Figs. 12, 14). There is no dorsal pit or impression (Pl. 18, fig. 11). Centrodorsals generally have ten rows (Pl. 18, figs. 11-12; Pl. 19, fig. 1) of 3-5 (6) cirral facets each, with facets becoming increasingly larger proximally. These (near)circular to oval, weakly 8-shaped facets are deeply concave and closely spaced (Pl. 18, fig. 11; Pl. 19, fig. 1), with large, circular to oval cirral lumen and distinct articular tubercles (Pl. 13, figs. 1, 5; Pl. 19, fig. 1). That in some specimens these tubercles appear to be less distinct, is mainly due to preservation (compare e.g. Pl. 18, fig. 12). Cirral facets show a zigzag arrangement radially (Pl. 18, fig. 12; Pl. 19, fig. 1).

The ventral surface of the centrodorsal is irregularly subpentagonal, with furrows for basals extending furthest (Pl. 13, figs. 2-4; Pl. 18, fig. 9) and uneven, being either strongly concave (Pl. 18, fig. 10) or almost flat (Pl. 13, figs. 1, 5). Centrodorsal lumen is relatively large (Pl. 13, figs. 2-4; Pl. 18, fig. 9; Figs. 12, 14), especially in juvenile individuals; there are no radial pits. Narrow, and generally shallow, furrows for basals remain either separate (Pl. 13, figs. 3-4) or form a star-shaped structure on the ventral surface (Pl. 13, fig. 2; Pl. 18, fig. 9). Basals are exposed in the interradial angles (Pl. 19, fig. 1). A cup from the Zeven Wegen Member, which corresponds to Gislén's (1924, p. 161, figs. 217-218) var. *granulata*, shows the structure of the radials; their free lateral surface is wide (Pl. 19, fig. 1), laterally contiguous and granulate, and inturned leav-

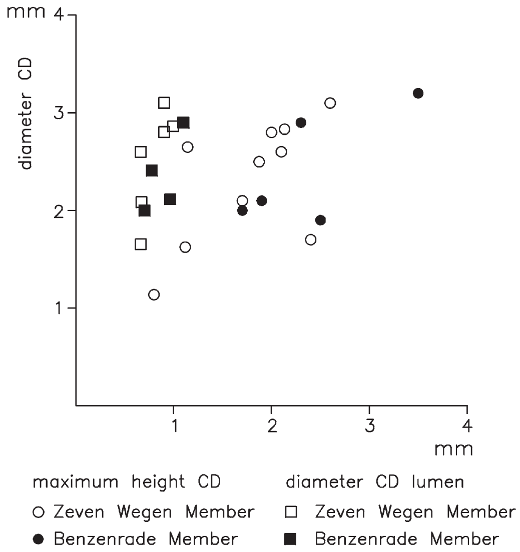

Fig. 12. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Amphorometra* gr. *conoidea* (Goldfuss, 1839) from the Benzenrade Member (Vaals Formation, Late Campanian) and the Zeven Wegen Member (Gulpen Formation, Late Campanian).

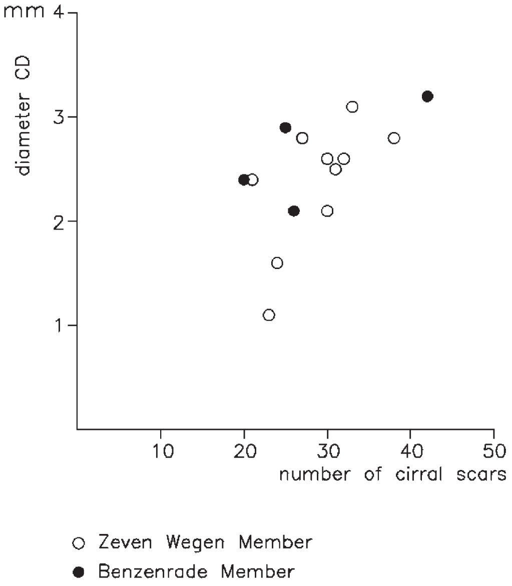

Fig. 13. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Amphorometra* gr. *conoidea* (Goldfuss, 1839) from the Benzenrade Member (Vaals Formation, Late Campanian) and the Zeven Wegen Member (Gulpen Formation, Late Campanian).

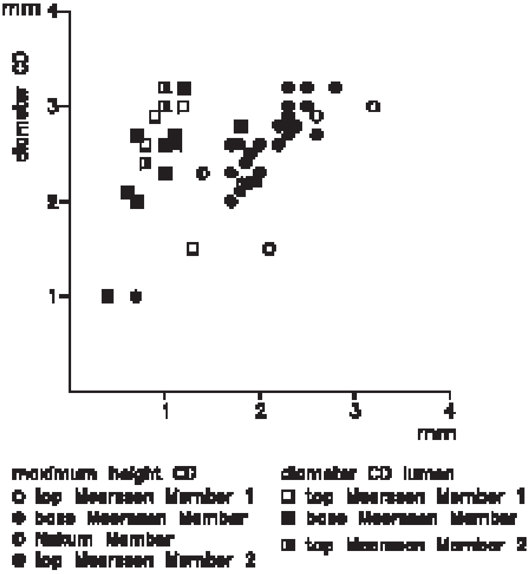

Fig. 14. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Amphorometra* gr. *conoidea* (Goldfuss, 1839) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

ing a subradial cleft. They are broadly triangular in plan view (Pl. 19, fig. 2), with dorsal ligament pit large and wide, interarticular ligament pits triangular and small, and ventral muscle pits tall and moderately deep. Body cavity relatively small (Pl. 19, fig. 2).

In the present material various 'morphotypes' may be distinguished mainly on the basis of centrodorsal outline and number and arrangement of cirral facets (compare Figs. 13, 15), but these are all connected by 'intermediate' morphologies. The general type, corresponding to Goldfuss's original (RFWUIP Goldfuss Colln, no. 1038), is here called 'Type 1' (Pl. 18, figs. 11-12). 'Type 2' (Pl. 18, figs. 9-10) comprises (high) conical forms in which cirral facet arrangement is much less regular. Facets tend to alternate, and a third row intercalates, resulting in a higher number of cirral facets (Fig. 15). Juvenile specimens generally have pronounced interradial edges, comparatively large central body cavities, and cirral facets may either be arranged regularly or alternate ('Type 1' and 'Type 2' morphologies). It may prove possible to separate these forms in future, but for now they are here considered as a group.

Discussion — Rasmussen (1961) considered *A. brydonei*, a species based on a single specimen (BMNH E 25421) to be distinct. Jäger (1982, pl. 2, figs. 1-2) illustrated a specimen from the Early Campanian of Höver (Hannover area, Germany) which is similar to the type of that 'species', and shows concave, (near)circular cirral facets with pronounced rims, and strong interradial processes. Awaiting detailed analyses of 'populations', and from the Early Maastrichtian of Rügen in particular, these forms are here considered to belong to *A. conoidea*.

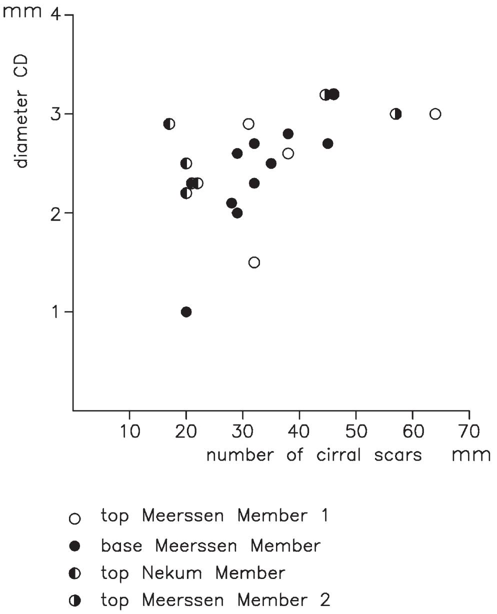

Fig. 15. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Amphorometra* gr. *conoidea* (Goldfuss, 1839) from the Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

A number of isolated proximal brachials may belong to the present species, e.g. those illustrated in Pl. 24, figs. 3-4. These are both IBr2, with a proximal synarthry and two asymmetrical muscular facets distally. In their proximal articulation type they clearly differ from Pl. 24, figs. 1-2, which show an axillary primibrachial with proximal (crypto)syzygial articulation, of unknown affinity. More distal brachials of the type illustrated in Pl. 26, figs. 8-9 and 11, with well-developed, typically comatulid, syzygial articulations facets and granulate latera, may also belong here.

Occurrence — Currently known from the Late Campanian to Late Maastrichtian of Liège-Limburg and southern Limburg (Figs. 4, 43, 46-47, 49).

Superfamily Notocrinacea Mortensen, 1918
Family Notocrinidae Mortensen, 1918
Genus *Semiometra* Gislén, 1924

Type species — *Antedon impressa* Carpenter, 1881, by original designation.

Semiometra impressa (Carpenter, 1881)
Fig. 51a-c; Pl. 25, figs. 1-2.

*1881 *Antedon impressa* Carpenter, p. 135, pl. 6, figs. 8-9.

1961 *Semiometra impressa* (Carpenter, 1881) — Rasmussen, p. 309 (partim), pl. 45, fig. 1, non fig. 2 (cum syn.).

1995c *Semiometra impressa* — Jagt, p. 189, figs. 4, 7.

Type — Lectotype, designated by Rasmussen (1961, p. 309), is the specimen illustrated by Carpenter (1881, pl. 6, fig. 9) from the Campanian of Balsberg (southern Sweden), now missing from the Lund University collections.

Material — Several dozens of centrodorsals and cups, as well as isolated primi- and secundibrachials, including RGM 396 265-396 266 (ex Jagt Colln); NHMM JJ 6482, 9480a/b; NHMM MB 619-11, 770-12, 808-10, 865-23, 1044-13b.

Description — Centrodorsal low (Fig. 16) to almost discoidal, slightly arched or with flat dorsal pole (Pl. 25, fig. 1), and very thin near the edges. Outline (sub)pentagonal with more or less irregular sides (Pl. 25, figs. 1-2). Dorsal star generally prominent and consisting of narrow deep, slit-like or comma-shaped pits (Pl. 25, fig. 1; Fig. 51b). Surrounding the dorsal star is a cirrus-free area of variable diameter (Pl. 25, fig. 1), and bounded irregularly by obsolete cirral scars, the remainder of the dorsal surface being covered with cirral facets, numbering 40-90 in total (Fig. 17). Facets are closely spaced, moderately to deeply concave, transversely oval in outline and have small cirral pores. With the exception of weak, round to elliptical, articular tubercles there is no other ornament.

The ventral surface of centrodorsal is concave to varying degrees, with subpentagonal central body cavity (Pl. 25, fig. 2; Fig. 51a) corresponding to 25-40 % of total centrodorsal diameter, depending on growth stage (Fig. 16). Grooves for rod-like basals narrow with slightly raised edges (Pl. 25, fig. 2; Fig. 51a); radial areas uneven. Radial pits distinct in well-preserved specimens (Pl. 25, fig. 2); in worn specimens

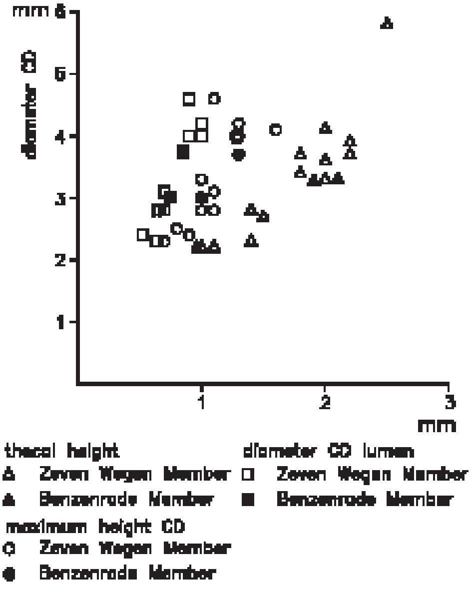

Fig. 16. Relationship between centrodorsal diameter (CD), thecal height, maximum centrodorsal height and diameter of centrodorsal lumen in *Semiometra impressa* (Carpenter, 1881) from the Benzenrade Member (Vaals Formation, Late Campanian) and the Zeven Wegen Member (Gulpen Formation, Late Campanian).

continuing into a furrow-like extension (Fig. 51a). Basals are generally not exposed, but their fused proximal ends form a collar around the central cavity (Pl. 25, fig. 2).

Thecal height (Fig. 16) corresponds to up to c. 45% (generally less) of centrodorsal diameter, and radials are of about the same height as the centrodorsal. They lack free lateral surfaces, and were apparently rather fragile, being compressed to varying degrees in all available specimens. Articular facets are concave and reach centrodorsal edge only interradially, leaving large free areas of ventral centrodorsal surface (compare Rasmussen, 1961, pl. 45, fig. 1a). The dorsal ligament pit is low and wide, and comparatively shallow. The interarticular ligament pits are broadly triangular and shallow and are separated from the ventral muscle pits (roughly as tall as wide) by oblique ridges forming an obtuse angle. The body cavity is narrow.

Discussion — Rasmussen (1961) considered *S. impressa* to be a long-ranging (Cenomanian to Maastrichtian) and widely distributed species with records from Sweden, England, The Netherlands, Belgium, and possibly Germany and the Czech Republic. Here it is preferred to restrict use of the name *impressa* (sensu Carpenter, 1881) to forms conforming to those from the Campanian of southern Sweden, from which the species was originally described. Rasmussen (1961) listed the following localities there: Båstad, Ivö Klack and Köpinge. Reference is here made to Christensen (1975, 1986, 1993) for proper age assignments (based on coleoid cephalopods) of the various outcrops in southern Sweden. Late Maastrichtian forms, assigned to *S. impressa* by Rasmussen (1961), appear to represent a separate species, of which large 'populations' are available (see below).

Isolated cirrals (Pl. 25, figs. 6-8, 10-11) co-occurring with the above centrodorsals and cups appear far too large to belong to the present species. This holds especially true for very large, massive cirrals with distinct synathrial ridges and deeply excavat-

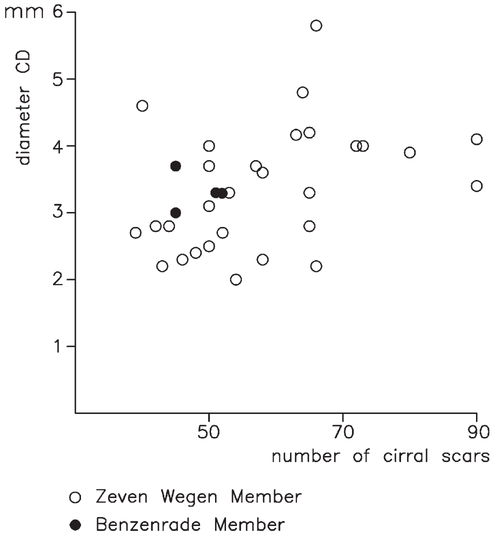

Fig. 17. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Semiometra impressa* (Carpenter, 1881) from the Benzenrade Member (Vaals Formation, Late Campanian) and the Zeven Wegen Member (Gulpen Formation, Late Campanian).

ed ligament pits (Pl. 25, figs. 6, 8, 10-11) for which still no match has been found amongst the centrodorsals/cups known from the Zeven Wegen Member.

Occurrence — Known to date exclusively from the Zeven Wegen Member (Gulpen Formation) in Liège (CPL SA quarry) and its lateral time equivalent of the Benzenrade Member (Vaals Formation) in the Benzenrade area (Figs. 4, 43).

Semiometra lenticularis (Schlüter, 1878)
Pl. 23.

*1878 *Antedon lenticularis* Schlüter, p. 46, pl. 3, figs. 1-3.
1961 *Semiometra lenticularis* (Schlüter, 1878) — Rasmussen, p. 311, pl. 46, figs. 1-2.
1995c *Semiometra lenticularis* — Jagt, p. 190, figs. 4, 7.

Type — Type specimen is RFWUIP Schlüter Colln, no. 302.

Material — Several dozens of centrodorsals and cups (one preserving IBrr1), including RGM 396 259 (ex Jagt Colln); NHMM MK 1186 (W.M. Felder Colln); NHMM K1018b, 1073, 1123b, 1412, 1642a, 2287b, 2438a; NHMM MB 108-12, 234-11, 377-3a/b, 601-5b, 768, 798.

Description — Centrodorsals large (exceeding 10 mm in diameter, Fig. 18), low and irregularly discoidal (Pl. 23, figs. 2, 8), with height corresponding to 20-25% of diameter (Fig. 18), of (sub)pentagonal to subcircular outline (Pl. 23, figs. 1, 4, 6, 9-10) and with concave cirrus-free dorsal area and distinct dorsal star (Pl. 23, figs. 1, 4, 6, 10). The depth and extent of the cirrus-free area varies considerably (compare e.g. Pl. 23, figs. 4, 10). The total number of cirral facets is also variable (Fig. 19; 50-70 accord-

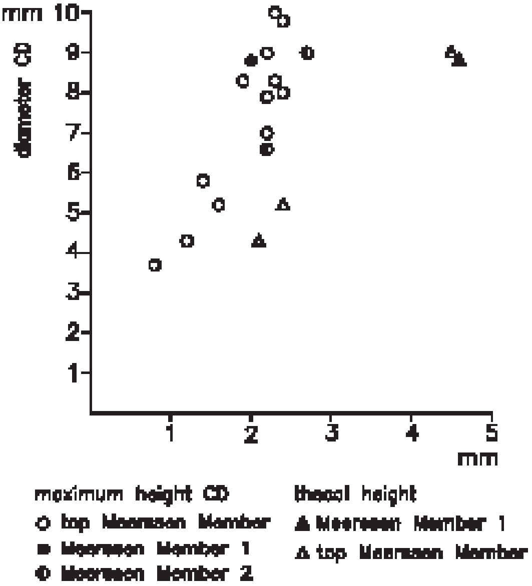

Fig. 18. Relationship between centrodorsal diameter (CD), thecal height and maximum centrodorsal height in *Semiometra lenticularis* (Schlüter, 1878) from the Meerssen Member (Maastricht Formation, Late Maastrichtian).

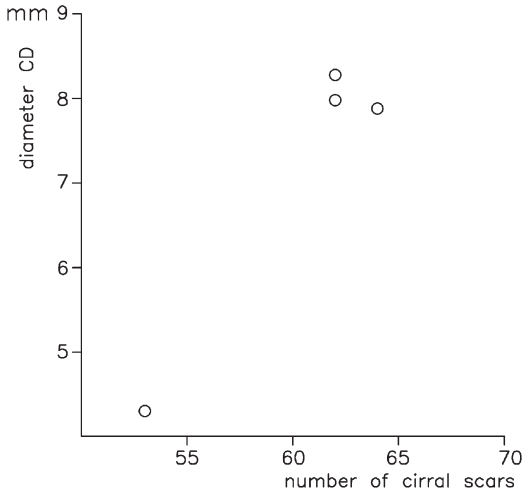

Fig. 19. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Semiometra lenticularis* (Schlüter, 1878) from the Meerssen Member (Maastricht Formation, Late Maastrichtian).

ing to Rasmussen, 1961) depending largely on the height of the centrodorsal and the width of the cirrus-free dorsal area. Facets are generally strongly concave, closely spaced and arranged in a number of circlets but not in vertical columns. Facets are subcircular to oval, with narrow oval-elongate pores and distinct articular tubercles. Other ornament lacking.

The ventral surface of the centrodorsal is nearly flat (Pl. 23, fig. 9) to (slightly) concave with narrow grooves for basals, with raised edges and club-shaped, raised adoral ends (Pl. 23, fig. 3). Radial pits are relatively small but distinct (Pl. 23, figs. 3, 9), the comparatively small central cavity being rather shallow. Thecal height varies considerably (Fig. 18). Radials lack a free lateral surface and reach the centrodorsal margin only interradially (Pl. 23, fig. 7), leaving wide free areas on the ventral surface. Articular facets of radials have wide, and (very) deep dorsal ligament pits (Pl. 23, fig. 8), and comparatively small, broadly triangular interarticular ligament pits and ventral muscle pits. Body cavity relatively narrow.

A single specimen (Pl. 23, fig. 5) preserves IBrr1, with synarthrial distal articular facet, and of a structure closely comparable to that seen in *S. saskiae* sp. nov. (see below, and Pl. 22, fig. 3).

Occurrence — Comparatively rare in Nekum Member, commoner in Meerssen Member (Maastricht Formation) (Figs. 4, 46-49).

Semiometra saskiae sp. nov.
Pl. 21, figs. ? 4, 5-11; Pl. 22.

1961 *Semiometra impressa* (Carpenter, 1881) — Rasmussen, p. 309 (partim), pl. 45, fig. 2, non fig. 1.
1965 *Semiometra impressa* — Rasmussen, table 1.
1995c *Semiometra* n. sp. — Jagt, p. 190, figs. 4, 7.

Type — Holotype is NHMM MB 377-4a (Pl. 21, figs. 6-7, 9); paratypes are NHMM K1018a (Pl. 21, figs. 5, 8) and RGM 396 251-396 252 (Pl. 21, figs. 10, 11; ex Jagt Colln).

Type locality and horizon — Blom quarry (Berg en Terblijt, southern Limburg, The Netherlands), Maastricht Formation, base Meerssen Member, Late Maastrichtian (*Belemnitella junior* Zone of authors).

Derivation of name — Named after Mrs Saskia M. Kars (Vrije Universiteit Amsterdam), as a small token of thanks for all the SEM work she did for the present paper.

Diagnosis — A notocrinid with discoidal to hemispherical centrodorsal of (sub)-pentagonal to subcircular outline, distinct dorsal star, cirrus-free dorsal area of varying extent, closely spaced cirral facets, tall radials and synarthrial articulations between IBr1-2 and IIBr1-2.

Material — Several hundreds of centrodorsals, cups (one preserving IBrr1-2), proximal and distal brachials, cirrals and pinnulars, including NHMM K1014, 1016, 1018, 1123c, 1157, 1347, 1413, 1642b, 1766, 2287a, 2438b, 2617, 2696, 2754-7 (?), 3833; RGM 396 253-396 258 (all ex Jagt Colln); NHMM JJ 10842a, 2784-2788, 9524(?); NHMM MB 95-2b, 108-11/15a, 234-2, 322c (?), 377-1b/4, 385-12, 506-Fa (?), 542-10 (?), 601-5a, 649-19, 655-4a, 754d (?), 866-6/11a; GM 1997.8 (ex Jagt Colln).

Description — Centrodorsals low-discoidal to almost hemispherical/bowl-shaped in profile, diameter more than twice the maximum height (Fig. 21), and irregularly pentagonal in outline (Pl. 21, figs. 6-7, 10-11). Dorsal surface mostly flattened, with cirrus-free area of varying diameter, sometimes clearly delimited, and with distinct dorsal star (Pl. 21, figs. 7, 10-11), of variable structure. The ventral surface is moder-

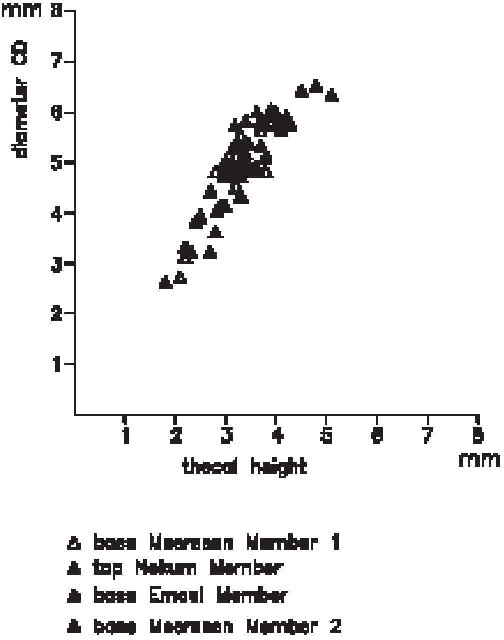

Fig. 20. Relationship between centrodorsal diameter (CD) and thecal height in *Semiometra saskiae* sp. nov. from the Emael, Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

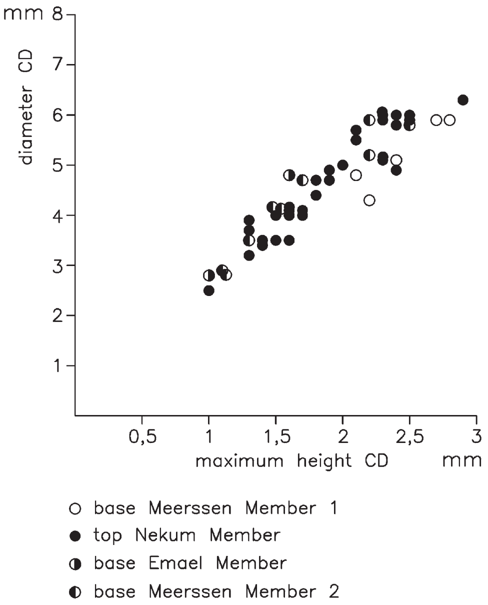

Fig. 21. Relationship between centrodorsal diameter (CD) and maximum centrodorsal height in *Semiometra saskiae* sp. nov. from the Emael, Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

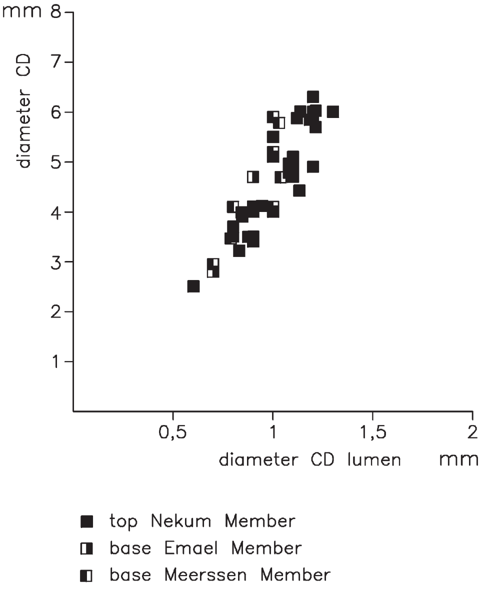

Fig. 22. Relationship between centrodorsal diameter (CD) and diameter of centrodorsal lumen in *Semiometra saskiae* sp. nov. from the Emael, Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

ately to deeply concave with narrow grooves for the rod-like basals. Basal troughs curve up at the periphery and form the highest parts of the centrodorsal. Radial areas are irregular and often concave. Central cavity corresponds to up to 20% of centrodorsal diameter (Fig. 22). Separate radial pits are developed.

Cirral facets or scars are arranged in several circlets (up to 5 or 6), but not in vertical rows, their overall number depending largely on centrodorsal size (Fig. 23). Facets are generally closely packed (Pl. 21, figs. 7, 11), slightly increase in size upwards, are deeply concave and polygonal (rhombic) in outline and, with exception of very weak articular tubercles on opposite sides of tiny cirral pores, lack any ornament. Specimens in which cirral facets appear less deeply concave are generally poorly preserved and have suffered from (extensive) recrystallisation.

The radials (Pl. 21, figs. 6, 9; Pl. 22, figs. 1-2) are relatively large plates broadly triangular in plan view and in elevation. They lack a free lateral surface, reach the periphery only interradially, leaving a wide area on the ventral surface of the centrodorsal (Pl. 21, fig. 6). The dorsal ligament pit is large and very deep centrally below the (sub)circular to oval nerve canal. The triangular interarticular ligament pits (Pl. 22, fig. 1) are triangular and moderately deep to relatively shallow. The ventral muscle pits are much taller (Pl. 21, fig. 9; Pl. 22, fig. 1), fairly deep with a low, blunt groove between them. They are separated from the interarticular ligament pits by ridges which, in well-preserved specimens, form an acute angle.

Associated arm fragments (Pl. 21, fig. 4), preserving pinnules, show muscular and sygyzial brachial articulations and finely granulate latera. These may either belong to the present species or to its congener *S. lenticularis*, and are similar to brachials

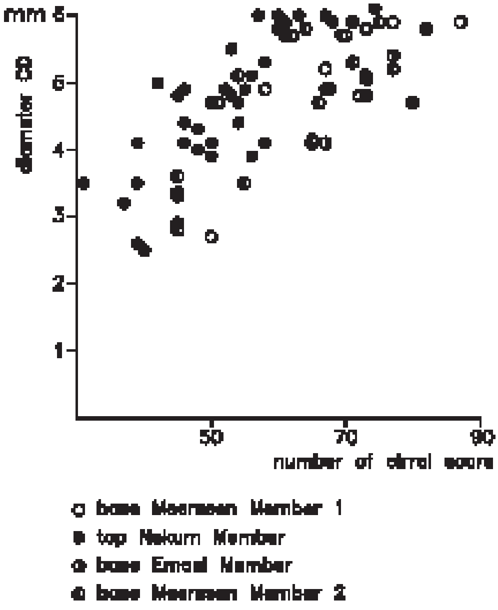

Fig. 23. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Semiometra saskiae* sp. nov. from the Emael, Nekum and Meerssen members (Maastricht Formation, Late Maastrichtian).

recorded in *Semiometra minuta* Peck & Watkins, 1972 (p. 413, pl. 1, figs. 13-15, 19-20) from the Early Cretaceous of Texas. Isolated proximal brachials that can be assigned to *S. saskiae* without any doubt include those illustrated in Pl. 22. IBr1 shows a proximal muscular articulation (fig. 2) and a distal synarthrial articulation (fig. 3), corresponding to the proximal facet of IBr2 (fig. 8), which is axillary and has two asymmetrical muscular articulations distally (fig. 6). Articulation IBr1-2 is synarthrial (Pl. 27, figs. 1-2). There is no indication of more distal arm divisions.

Discussion — The present species is here differentiated from *S. impressa*, to which Rasmussen (1961) assigned material from the Meerssen Member of the Maastricht area (NHMM M. Meijer Colln), on account of constant differences in thecal height (reflecting both maximum height of centrodorsal as well as radial height) (compare Figs. 16, 20-21); differences in total number of cirral facets and their outline (compare Figs. 17, 23) and differences in articular facet of radials (acute vs obtuse angle) and robustness of associated primibrachials. Some specimens, especially those from the Kunrade Limestone facies, differ in some respects from 'true' *S. saskiae* and are closer to *S. impressa*. These (see Material, those with a question mark) are here referred to as *S.* cf. *saskiae* for the time being.

Occurrence — 'Populations' of the present species are fairly common in the Nekum and Meerssen members in Liège and southern Limburg (Figs. 4, 45-49). Rare specimens from the Emael Member (Fig. 46) at the CBR-Romontbos quarry may also belong here.

Remarks — In all samples that have yielded the present species, in addition to *Amphorometra* gr. *conoidea* and *S. lenticularis*, occur isolated comatulid brachials and cirrals (Pl. 25, figs. 4-5, 9; Pl. 26, figs. 1, 4-7; Pl. 27, figs. 6-7, 9-10). These include relatively many syzygial articulations as well as oblique muscular articulations, but cannot be assigned to species with certainty. In some cases details of ornament are particularly well preserved (Pl. 26, figs. 4, 7, 10) and comparable to those of the extant comasterid *Alloeocomatella polycladia* Messing, 1995a (p. 438, fig. 2c).

Genus *Loriolometra* Gislén, 1924

Type species — *Comaster retzii* Lundgren, 1875, by original designation.

Loriolometra retzii (Lundgren, 1875)

Fig. 51d-l; Pl. 25, fig. 3.

*1875 *Comaster Retzii* Lundgren, p. 66, pl. 3, figs. 1-13.
*1878 *Antedon sulcatus* Schlüter, p. 47, pl. 2, figs. 8-9.
*1894 *Antedon arnaudi* de Loriol, p. 479, pl. 24, figs. 1-2.
1961 *Loriolometra retzii* (Lundgren, 1875) — Rasmussen, p. 302, pl. 43, figs. 1-3 (cum syn.).
1995c *Loriolometra retzii* — Jagt, p. 189, figs. 4, 7.

Type — Lectotype, designated by Rasmussen (1961, p. 302), is the specimen illustrated by Lundgren (1875, pl. 3, figs. 1-2), which is in the collections of Lund University.

Material — A dozen centrodorsals and isolated proximal brachials (Pl. 27, fig. 4) and cirrals, including NHMM MB 865-21/24, 619-15/15a/18; and a number of unregistered specimens in the Arpot Colln (Ulestraten, ex Prins Colln).

Description — Centrodorsal large, bluntly conical, with irregular or rounded dorsal end (Fig. 51e-f, h-i, k, l), and (sub)pentagonal to subcircular in outline. The dorsal side mostly comprises a cirrus-free area, which may be excavated and pit like (Fig. 51h) and which may bear an interradial stellate impression (Fig. 51h, k). Large, polygonal, deeply concave cirral facets are arranged in ten vertical columns of 3-5 facets each (Fig. 51f, i, l). Nerve canals are either small and inconspicuous or have a raised rim (Fig. 51f); articular tubercles are generally distinct, in contrast to the marginal crenellae which are well developed (Fig. 51f, l). Interradial edges are prominent, and at the periphery correspond to the outer ends of the fairly wide troughs for the basals.

The ventral surface of the centrodorsal is uneven and irregular (Pl. 25, fig. 3), with prominent, elliptical and concave furrows for basals (Pl. 25, fig. 3; Fig. 51d, g), which have raised edges. Central cavity is (sub)pentagonal to irregular in outline. The radial areas of the ventral surface show five elongated, keyhole-shaped or rounded triangular radial pits (Pl. 25, fig. 3; compare Fig. 51d, g). The very thin wall which separates these deep pits from the central cavity is occasionally not preserved (Fig. 51j).

The present material includes a single radial plate and a number of comparatively large proximal brachials which may belong to this species (see e.g. Pl. 27, fig. 4). According to Rasmussen (1961) radials are lower than centrodorsal, their free lateral surface being laterally contiguous, fairly low, and slightly overhanging. The articular facet is wide and almost vertical, the body cavity therefore large. He also noted that large brachials found associated showed a synarthrial IBr1-2 articulation, IBr2 being axillary, and that more distally, oblique muscular and syzygial brachial articulations occurred. A similar brachial arrangement was postulated for the Albian *Loriolometra marilynae* Nestell & Tenery (1988, p. 185, fig. 2) from north-central Texas.

Occurrence — Known to date only from the Benzenrade Member (Vaals Formation, Late Campanian) as exposed in the Benzenrade area (Fig. 4). Rasmussen (1961) recorded specimens from the Campanian of southern Sweden and France.

Comatulidina gen. et sp. indet.
Pl. 13, figs. 6-8.

Material — A single centrodorsal, RGM 396 224 (ex Jagt Colln, no. 7691).

Description and discussion — Although generally poorly preserved, the present specimen differs from co-occurring *Amphorometra* gr. *conoidea* (see above) not only in size, but also in having a much smaller, subpentagonal central cavity, less discrete troughs for basals on the ventral surface of the centrodorsal (Pl. 13, fig. 7), and marginal crenellae on cirral facets (Pl. 13, fig. 8). In the absence of radial pits it cannot be assigned to the genus *Loriolometra* (see above), nor to *Schlueterometra*, although the overall similarity with its type species *S. voigti* Rasmussen, 1961 (p. 319, pl. 43, fig. 4) is remarkable (see also Gasse & Hilpert, 1985). Not until more, and better preserved material is available can this form be characterised more fully.

Occurrence — Only known from the Late Campanian Zeven Wegen Member (Gulpen Formation) at the CBR-Lixhe quarry.

Superfamily Antedonacea Norman, 1865
Family Antedonidae Norman, 1865
Subfamily Heliometrinae A.H. Clark, 1909
Genus *Hertha* von Hagenow, 1840

Type species — *Hertha mystica* von Hagenow, 1840, by monotypy.

Remarks — Rasmussen (1978, p. T915) placed this genus, with reservation, in the Heliometrinae. It may have to be reassigned; moreover, species currently referred to this genus (Rasmussen, 1961) seem to constitute a heterogeneous lot, with *H. pygmea* Gislén, 1924 apparently more closely related to the Heliometrinae than its 'congeners'.

Hertha gr. *plana* (Brünnich Nielsen, 1913)
Pl. 20, figs. 1-7, 9.

*1913 *Antedon plana* Brünnich Nielsen, p. 106, pl. 12, figs. 54-56.
1961 *Hertha plana* (Nielsen, 1913) — Rasmussen, p. 348, pl. 51, figs. 6-8 (cum syn.).
1993 *Hertha plana* (Nielsen, 1913) — Kjaer, p. 152, pl. 6, figs. 1-2 (non figs. 3-4 = *H. mystica* von Hagenow, 1840).

Material — A few centrodorsals and cups, including RGM 396 246-396 250 (ex Jagt Colln); NHMM MB 387-6a, 414-4e, 754e, 867-10(?). NHMM MB 284-8a (Pl. 20, fig. 8) may also belong here; it is indicated as *Hertha*? sp. in Fig. 43.

Description — Centrodorsal low, subconical to almost discoidal in profile (Pl. 20, figs. 3-5; Fig. 26 - Vijlen Member 1 and 2 samples), and irregularly pentagonal in outline (Pl. 20, figs. 1-2, 7, 9), with cirrus-free area of varying width on dorsal pole (Pl. 20, figs. 2, 7), but lacking a dorsal star. Remainder of dorsal side with 35-55 closely packed cirral facets (Pl. 20, figs. 2, 7; Fig. 27). Facets are small, but increase in size upwards, are deeply concave, and relatively narrow. Pores are distinct and elliptical, with articular tubercles varying considerably in prominence (Pl. 20, fig. 8). The edges separating the cirral facets are generally more protruding along the dorsal edge of the facets (Pl. 20, figs. 2, 7-8).

The ventral surface of the centrodorsal slightly concave (Pl. 20, figs. 3-4, 9) with narrow, shallow grooves for basals with raised edges (Pl. 20, fig. 9), and indistinct radial pits. Radial areas are uneven (Pl. 20, fig. 9). Centrodorsal lumen or cavity almost circular and corresponding to c. 30 % of total diameter (Fig. 26, Vijlen Member 1 and 2 samples).

Basals are not exposed; radials (Pl. 20, figs. 3-4) are of comparable height to centrodorsal and lack a free lateral surface. The articular facet either reaches the edge of the centrodorsal only interradially (Pl. 20, fig. 1) leaving wide areas of the ventral surface of the centrodorsal uncovered, or closely approaches its edge (Pl. 20, figs. 4, 6). The dorsal ligament pit is low and wide, and very deep medially (Pl. 20, fig. 4). The interarticular ligament pits, which are broadly triangular and moderately deep, are separated from the ventral muscle pits by a slightly oblique ridge. The ventral muscle pits are poorly preserved in the specimens in hand (Pl. 20, figs. 3-4). Body cavity rather narrow (Pl. 20, fig. 1).

Discussion — First described from the Middle Danian of Denmark (Brünnich Nielsen, 1913), Rasmussen (1961) subsequently referred to this species (holotype is MGUH no. 1252) a number of forms previously assigned to the notocrinid *Semiometra*, of Early and Late Maastrichtian age (e.g. *Semiometra pommerania* Gislén, 1924 and *S. minuta* Gislén, 1925). This course of action is followed here, but it should be stressed that at times it is difficult to distinguish this form from poorly preserved specimens of *S. impressa* or of *S.* cf. *saskiae* (material from Kunrade Limestone facies). This is especially true when the dorsal star cannot be seen. Typical *S. saskiae* is easily distinguished on the basis of centrodorsal profile and structure and arrangement of cirral facets.

Occurrence — Leaving doubtful records from the Kunrade Limestone facies out of consideration, the present group is known only from the Vijlen Member (Gulpen Formation) of Liège, southern Limburg and the environs of Aachen (Fig. 2). Keutgen (1996, p. 195) recorded *Hertha* gr. *plana* and *H. pygmea* from interval 4 (= upper *sumensis* Zone) of the Vijlen Member at Aachen (Hans-Böckler-Allee). Whittlesea (1996a) recorded as *Hertha plana* Nielsen a single centrodorsal from Whitlingham (Norfolk, England) from the youngest beds of the Paramoudra-1 division (*mucronata* Zone, Late Campanian). This would thus constitute the first Campanian record of the group.

Hertha gr. *pygmea* Gislén, 1924
Pl. 21, figs. 1-3.

*1924 *Hertha pygmea* Gislén, p. 176, figs. 253-256.
1961 *Hertha pygmea* Gislén, 1924 — Rasmussen, p. 350, pl. 51, figs. 4-5.
?1993 *Hertha pygmea* Gislén, 1924 — Kjaer, p. 153, pl. 6, figs. 5-8.

Material — A few centrodorsals, including NHMM MB 414-4d, 506.Fb, 506.Hb, 590-3, 655-4c, 865-20, 1044-21, 1239; NHMM JJ 10421.

Description — For now, under this heading are grouped a few isolated centrodorsals of diminutive to small size, and of Late Campanian (Benzenrade and Zeven Wegen members) to Late Maastrichtian (Kunrade Limestone facies, Maastricht Formation) age (Figs. 24-25). Preservation varies, but is generally poor, which is why a well-preserved topotypical specimen displaying features typical of *H. pygmea* (Pl. 21, figs. 1-3) (holotype is BMNH E 21390), is here illustrated.

Centrodorsals are conical in profile with pointed dorsal end, height equalling 40-60% of diameter (Fig. 24), outline (sub)pentagonal to subcircular (Pl. 21, figs. 2-3). Dorsal surface with 45-85 closely packed cirral facets or scars (Fig. 25). Facets are (sub)circular near the dorsal pole, which is cirrus-free (Pl. 21, fig. 3), and polygonal-elliptical elsewhere, taller than wide and deeply concave, with an indistinct pore and lacking ornament (Pl. 21, figs. 1, 3). Facets are separated by protruding edges (Pl. 21, figs. 1, 3). Scars increase in size towards ventral margin of centrodorsal. There is no dorsal star (Pl. 21, fig. 3). The ventral surface of the centrodorsal is almost flat (Pl. 21, fig. 2) or slightly concave. Grooves for the basals are narrow, elliptical and have raised edges (Pl. 21, fig. 2). Radial areas of ventral surface are undulate; there are no radial pits (Pl. 21, fig. 2). The (sub)circular central cavity is large (Fig. 26) and deep (Pl. 21, fig. 2), its diameter corresponding to 30-50% of total centrodorsal diameter.

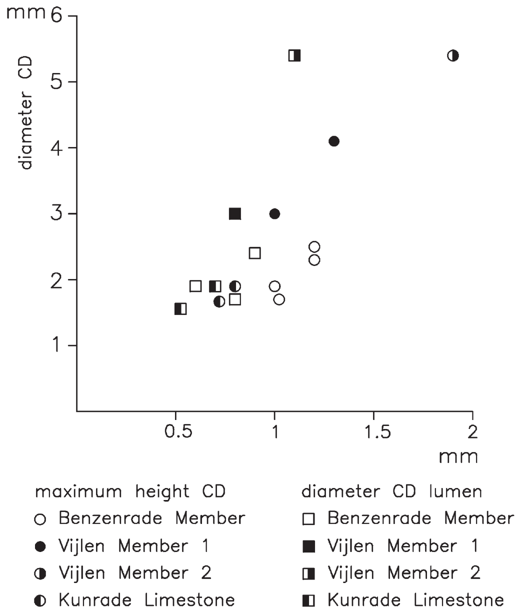

Fig. 24. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Hertha* spp. [*H.* gr. *pygmea* Gislén, 1924 and *H.* gr. *plana* (Brünnich Nielsen, 1913)] from the Benzenrade Member (Vaals Formation, Late Campanian), the Vijlen Member (Gulpen Formation, Early Maastrichtian) and the Kunrade Limestone facies of the Maastricht Formation (Late Maastrichtian).

Basals, which are not exposed, nor radials are known in material from the Maastrichtian type area. The specimen illustrated here (Pl. 21, fig. 1) has an extremely narrow free rim; the radials being of about the same height as the centrodorsal. The dorsal ligament pit is low, wide and concave and lacks depth (Pl. 21, fig. 1). The articular ridge is prominent and the nerve canal large and transversely oval (Pl. 21, fig. 1). The interarticular ligament pits are small and separated from ventral muscle pits by a prominent, near-horizontal ridge. The muscle pits are large and tall and deeply concave.

Discussion — Material here grouped under *H.* gr. *pygmea* (samples Benzenrade Member and Kunrade Limestone in Figs. 24-25) is closely comparable to the Rügen specimens here illustrated, but it cannot be ruled out that it represents more than one species. Rasmussen (1961) considered *H. pygmea* to be confined to the Early Maastrichtian of Germany and Denmark. Kjaer (1993), however, also recorded this species from the Late Maastrichtian of Denmark.

Occurrence — Currently known from the Late Campanian of Liège and southern Limburg, the Early Maastrichtian of southern Limburg (Mamelis-Selzerbeek sections) and the Late Maastrichtian of Liège (Eben Emael) and southern Limburg (Kunrade-Benzenrade area) (Figs. 4, 43).

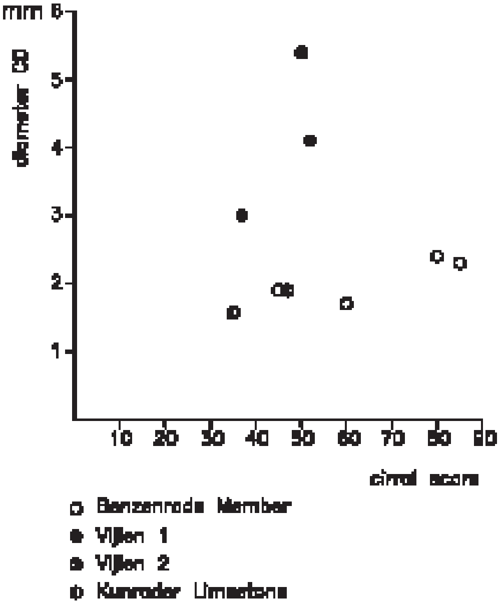

Fig. 25. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Hertha* spp. [*H.* gr. *pygmea* Gislén, 1924 and *H.* gr. *plana* (Brünnich Nielsen, 1913)] from the Benzenrade Member (Vaals Formation, Late Campanian), the Vijlen Member (Gulpen Formation, Early Maastrichtian) and the Kunrade Limestone facies of the Maastricht Formation (Late Maastrichtian).

Hertha gr. *mystica* von Hagenow, 1840 (?)

*1840 *Hertha mystica* von Hagenow, p. 665, pl. 9, fig. 8.
1961 *Hertha mystica* Hagenow, 1840 — Rasmussen, p. 345, pl. 51, figs. 1-3 (cum syn.).
1993 *Hertha mystica* — Kjaer, pl. 6, figs. 3-4 (non figs. 1-2 = *H. plana* (Brünnich Nielsen, 1913)).
1995c *Hertha*? sp. — Jagt, figs. 4, 7.

Material — Some sixty centrodorsals, one preserving basals, and a few axillary primibrachials, including NHMM MB 339-3, 432.OO; NHMM 1996010, 1996012 (ex van der Ham Colln).

Description and discussion — The assignment of these specimens has presented quite some problems. Preservation is generally poor, with a few exceptions. A suite of centrodorsals and two IBrr2 have now been selected for SEM photography. These illustrations will be included, together with a more detailed description, in a sequel to the present paper. Figs. 26 and 27 suggest this to be a heterogeneous lot, with considerable variation in total number of cirral facets and in centrodorsal height vs diameter.

At first, most of these specimens were thought to be assignable to the genus *Bruennichometra*. Upon closer examination of the original material of Rasmussen's (1961) illustrations of *B. danica* (Brünnich Nielsen, 1913), *B. granulata* (Brünnich Nielsen, 1913) and *B. parvicava* (Gislén, 1924) it became clear that these differed considerably in cirral facet arrangement and structure of primibrachials. Danian species of the

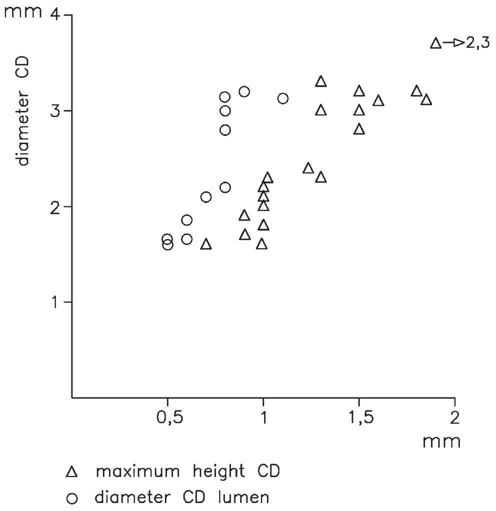

Fig. 26. Relationship between centrodorsal diameter (CD), maximum centrodorsal height and diameter of centrodorsal lumen in *Hertha* gr. *mystica* von Hagenow, 1840 (?) from the Geulhem Member (Houthem Formation, Middle Danian).

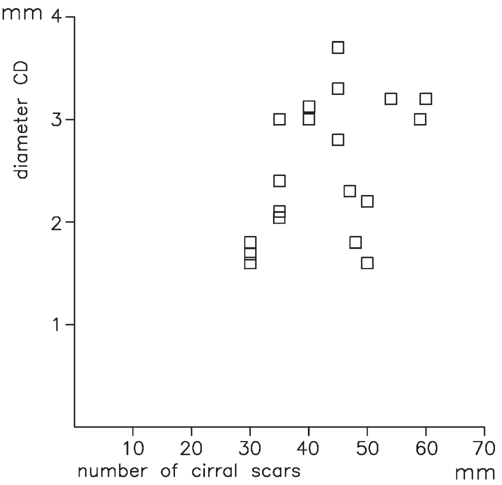

Fig. 27. Relationship between centrodorsal diameter (CD) and number of cirral scars in *Hertha* gr. *mystica* von Hagenow, 1840 (?) from the Geulhem Member (Houthem Formation, Middle Danian).

genera *Jaekelometra* (e.g. *J. faxensis* (Brünnich Nielsen, 1913); see Rasmussen, 1961, p. 324, pl. 47, fig. 8) and *Amphorometra* (e.g. *A. bruennichi* (Rosenkrantz, 1945), see Rasmussen, 1961, p. 330, pl. 48, fig. 1; and *A. semiglobularis* (Brünnich Nielsen, 1913), see Rasmussen, 1961, p. 337, pl. 49, fig. 1) also differ principally in cirral facet arrangement. The arrangement seen in the present specimens, at least in some of these, corresponds fairly well to that seen in *H. mystica*. In addition, the proximal synarthrial articulum of IBr2 associated with the centrodorsals is closely comparable to that of specimen MGUH no. 8995 (see Rasmussen, 1961, pl. 51, fig. 1a), despite the fact that the distal articular facet differs slightly from that illustrated by Rasmussen.

For the time being, the Limburg material is assigned to the group of *Hertha mystica*, albeit with a query.

Occurrence — Apparently confined to the upper Geulhem Member (Houthem Formation) of Middle Danian (*bruennichi* Zone equivalents) age.

Suborder Bourgueticrinina Sieverts-Doreck, in G. Ubaghs, 1953

Family Bourgueticrinidae de Loriol, 1882

Remarks — Simms et al. (1993, p. 503) are followed here in uniting the Bourgueticrinidae and Bathycrinidae in a single family, as these are undoubtedly paraphyletic taxa. Two groups of bourgueticrinids without fossil record, Phrynocrinidae and Porphyrocrinidae, are also included in the Bourgueticrinidae.

On the basis of analyses of large 'populations' from the Maastrichtian and Danian of Denmark, Kjaer & Thomsen (in prep.) concludes that many species of bourgueticrinid are in fact artificial entities, based on ontogenetic stages. This will have far-reaching implications for the classification of bourgueticrinids and bathycrinids, at the family and genus level.

The phylogenetic relationships of the family Bathycrinidae Bather, 1899 are still a matter of debate, having been triggered by the discovery of an extant species of archaic type in shallower water settings (see Améziane-Cominardi et al., 1987, 1990).

A rather conventional view is adopted in the present paper, although it is accepted that many, if not all, representatives of this suborder are characterised by a wide range of morphological variation (see e.g. Roux, 1976, 1977a, 1978a-c, 1987; Roux & Plaziat, 1978). New species recently described on the basis of single specimens only, or small numbers of specimens at best, include those introduced by Klikushin (1975b, 1982c) and Lee (1989). There can be no doubt that many species will turn out to be no more than morphotypes or ecophenotypes. Detailed biometric analyses of 'populations' are needed to determine the relationships of many of these forms.

Genus *Dunnicrinus* Moore, 1967

Type species — *Dunnicrinus mississippiensis* Moore, 1967, by monotypy.

Dunnicrinus aequalis (d'Orbigny, 1841)

Figs. 28-29; Pl. 34, figs. 3, 6; Pl. 35, figs. 2-3, 5-11; Pl. 36, figs. 1, 3, 9; Pl. 37, figs. 1-3; Pl. 38, figs. 1-4.

1831 *Apiocrinites ellipticus* Miller — Goldfuss, p. 186, pl. 57, fig. 3 (partim).

*1841 *Bourgueticrinus aequalis* d'Orbigny, p. 96, pl. 17, figs. 10-12.
1961 *Bourgueticrinus aequalis* Orbigny, 1841 — Rasmussen, p. 170, pl. 28, figs. 11-14.
?1980 *Bourgueticrinus suedicus* (Carpenter) — Klikushin, p. 83, pl. 1, fig. 4.
?1982c *Bourgueticrinus aequalis* d'Orbigny, 1840 — Klikushin, p. 812, fig. 1a-i, pl. 1, figs. 1-5.
1986b *Bourgueticrinus aequalis* d'Orbigny, 1841 — Jagt, p. 232, figs. 1, 4c, d, 10.
1994 *Bourgueticrinus aequalis* d'Orbigny, 1841 — Jagt et al., p. 221, fig. 1.
1995c *Dunnicrinus*? *aequalis* — Jagt, p. 192, figs. 5, 7.

Type — Lectotype, designated by Rasmussen (1961), is specimen RFWUIP Goldfuss Colln, no. 396a, illustrated by Goldfuss (1831, pl. 57, fig. 3) and d'Orbigny (1841, pl. 17, figs. 10-12). The state of preservation suggests this specimen to have been collected from the upper Lanaye Member (Gulpen Formation) or, more likely, the basal Valkenburg Member (Maastricht Formation) in the type area of the Maastrichtian Stage.

Material — In addition to a number of well-preserved, near-complete specimens in the Deckers, Dortangs, Jagt, Kuypers, and van Neer collections (see Jagt et al., 1998), many thousands of columnals, radicular cirri, proximal and distal brachials, proximalia, cups, isolated basals and radials, and pinnulars, including RGM 396 263-396 264 (ex Jagt Colln); NHMM MB 210, 369-371, 375-376, 417-3, 523, 590-1, 649-2, 655-3, 678-2, 728-1, 730, 737, 1120-3; NHMM JJ 3113, 4780, 8479a, 8622, 9138, 9721-9722; NHMM K3383; GM 1997.7 (ex Jagt Colln).

Discussion — This species is by far the commonest crinoid in the area, displaying a wide range of variation. A suite of well-preserved, articulated specimens with extensive radicular cirri networks for anchorage (Brett, 1981) will be described in detail shortly (Jagt et al., 1998), to which paper reference is here made. This exceptional occurrence in the basal Gronsveld Member (Maastricht Formation) is comparable to other so-called 'Obrution-Lagerstätten' recorded in the literature (see e.g. Moore & Vokes, 1953; P.D. Taylor, 1983; Seilacher et al., 1985; C.A. Meyer, 1990; Donovan, 1991; and W.L. Taylor & Brett, 1996). It provides a fine opportunity to reconstruct post-mortem depositional processes along the lines documented by D.L. Meyer et al. (1990), and to determine whether or not scavenging of these specimens has taken place (Maples & Archer, 1989).

On the basis of the extensive material available for study, it is proposed to reassign *Bourgueticrinus aequalis* to the otherwise exclusively North American genus *Dunnicrinus*. Moore (1967, p. 8), in diagnosing *Dunnicrinus*, noted that, '.... first brachial quadrangular, equal in width and height to radial, invariably nonpinnulate, muscular articulation between radial and first brachial and between all brachials except between lower and upper elements of syzygial brachial .....'. On p. 15 in the same paper it reads, 'Articulations of the brachials, excepting that between the first and second and counting syzygially paired brachials as units, are all oblique muscular.' The ossicle figured in pl. 7, fig. 14a-e in Moore (1967), and interpreted to be, '.... brachial (possibly second)..' indeed appears to have a muscular articulation proximally. The specimen illustrated in pl. 8, fig. 8b shows, '.... first brachial (above), both showing distal articula of muscular type ...', but this is not entirely convincing. An attempt to study these 'key' ossicles for myself proved unsuccessful, since the specimens Moore illustrated could not be located. In '*B.*' *aequalis*, the articulation between the radial and first brachial is muscular, that between the first and second brachial cryptosynarthrial (comparable to Pl. 38, figs. 8-9), and that between all other brachials obliquely muscular (Pl. 38, figs. 1, 3-4) or cryptosyzygial (Pl. 38, fig. 2). Despite the degree of uncertainty outlined above, the similarities between both species are such that they may be considered closely related. Moore (1967) stressed that in his material 'genuine' proximalia were rare; in contrast, none of the numerous Maastricht specimens lack such a structure.

Occurring on both sides of the Atlantic, the genus *Dunnicrinus* may thus have biostratigraphic potential (Broadhead, 1980).

The occurrence of stalked crinoids in shallow-water settings of Late Cretaceous age, and that of *D. mississippiensis* in particular have led Améziane-Cominardi & Roux (1994, p. 189, fig. 5) to note that, '*Dunnicrinus* avec son pédoncule de faible niveau d'organisation et sa couronne très péramorphique à cinq bras uniramés et pinnulés dès I Br 2 (Moore, 1967) s'interprète comme un Bathycrinidae épibathyal (voire circalittoral) du Crétacé terminal.' In discussing Cretaceous shallow-water isocrinids, Oji (1985, p. 632) referred to *D. mississippiensis* and remarked that this was a

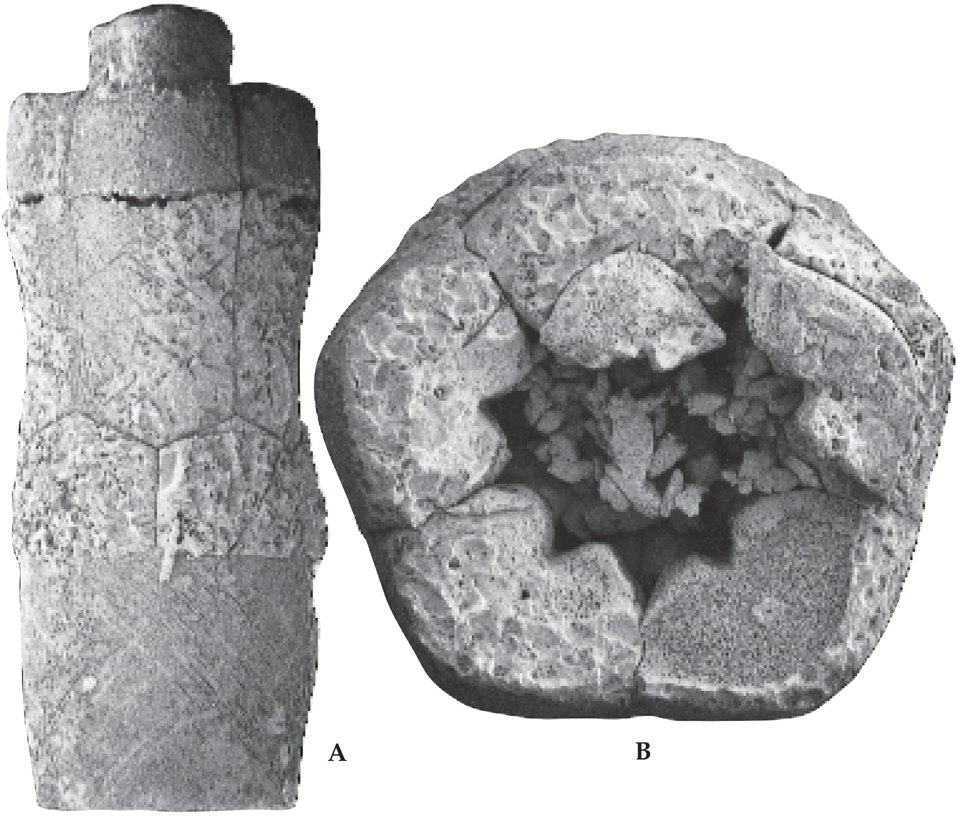

Fig. 28. Scanning electron micrograph of a subadult specimen of *Dunnicrinus aequalis* (d'Orbigny, 1841) [NHMM MD 0307], preserving ring of Brr1 and two Brr2, one of them regenerating. Maastricht Formation, base Gronsveld Member, ENCI-Maastricht BV quarry, Maastricht (Late Maastrichtian), a: × 15, b: × 34.

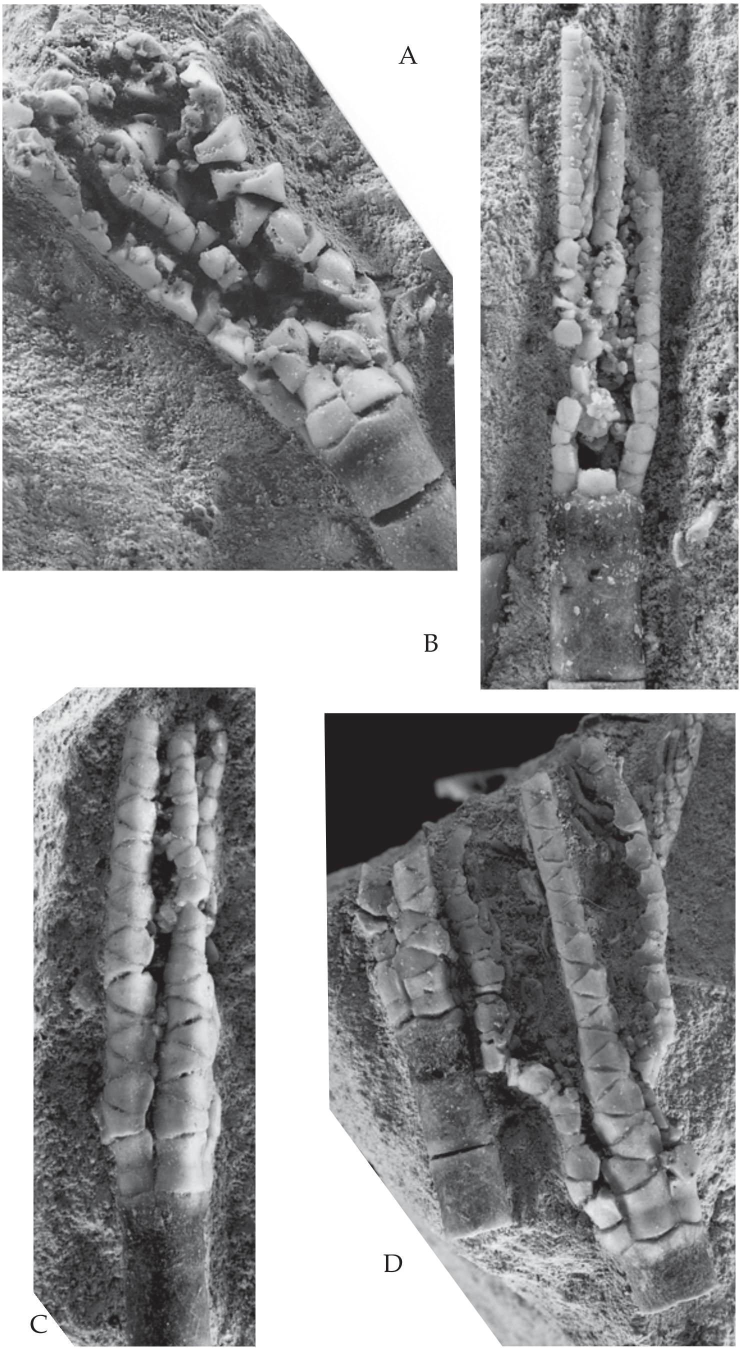

Fig. 29. *Dunnicrinus aequalis* (d'Orbigny, 1841), ENCI-Maastricht BV quarry, Maastricht; Maastricht Formation, base Gronsveld Member (Late Maastrichtian); a: NHMM MD 3380, b: NHMM JJ 9653, c: NHMM MD 3378, d: NHMM MD 3385, all × 3.

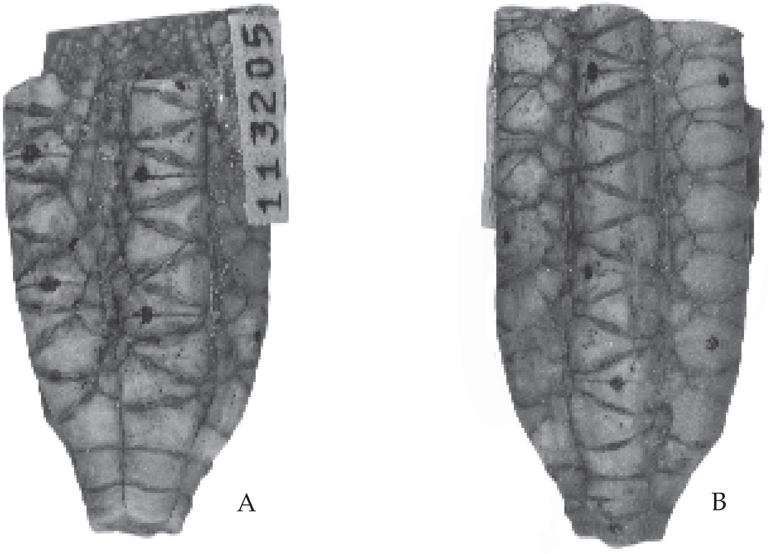

Fig. 30. *Dunnicrinus mississippiensis* Moore, 1967, paratype no. MNHUK 113205 (ex KJA-1; see Moore, 1967, pl. 3, fig. 7; pl. 8, fig. 10), Prairie Bluff Formation, Josey Creek (Oktibbeha Co., Mississippi), × 3. Black dots indicate syzygial brachial articulations.

bathycrinid known from 'apparently shallow-water facies of Maastrichtian age (Moore 1967). This may suggest that some bathycrinids persisted in shallow seas after the isocrinids had disappeared from such depths'.

Specimens selected for illustration in the present paper are intended to show:

- Various crowns, preserving pinnules (Fig. 29; see also Pl. 36, figs. 1, 3, 9), allowing articulations along the arms to be assessed, and confirming earlier observations that this species had but five arms (Jagt, 1986b, 1988). Syzygial articulations appear to be distributed rather randomly along the arms, and in a less regular pattern than in its closest relative, *D. mississippiensis* (Figs. 30-31).
- The occurrence of deviations from pentaradiate symmetry (4, 6 and even 8 rays; Pl. 35, figs. 3, 7), comparable to records in the literature (Jäger, 1979, 1980).
- The occurrence of specimens in which one or two of the radials extend above the others (Pl. 35, fig. 2; see also Pl. 31, fig. 11), which is considered to be the result of deformation caused by permanent direction of current flow (see Roux, 1987).
- Changes occurring during ontogeny in the relationship between various thecal/proximal measurements and the relationship height IBr1 vs height radial (compare Figs. 28, 32-35; Pl. 35, figs. 8-10).
- The occurrence of juvenile, articulated specimens (Pl. 35, figs. 8-9).
- The structure of the proximale, having resulted from the fusion of various proximal columnals (Pl. 35, fig. 5).
- The fairly common occurrence of specimens showing traces of predation (Pl. 35, figs. 6, 10-11), not to be confused with traces of bioerosion, possibly brought about by scraping of regular echinoids, of a type described by Breton et al. (1992). A few specimens were smothered by sudden sediment influx while in the process of regenerating

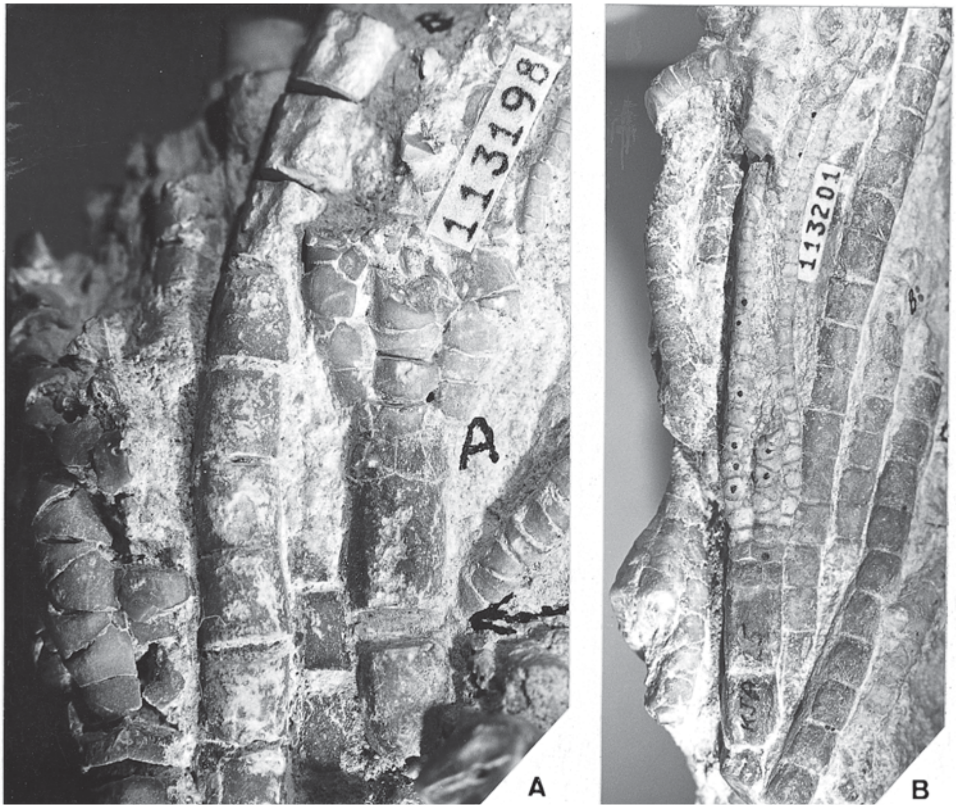

Fig. 31. *Dunnicrinus mississippiensis* Moore, 1967, a - paratypes nos MNHUK 113198 and 113197 (ex KJA-34 and 34a; see Moore, 1967, pl. 2, fig. 7); b - paratypes nos MNHUK 113201 and 113202 (ex KJA-25 and 25a; see Moore, 1967, pl. 3, fig. 3), Prairie Bluff Formation, Josey Creek (Oktibbeha Co., Mississippi), × 3 and × c. 2, respectively. Black dots indicate syzygial brachial articulations.

their crowns, allowing this process to be compared with data on extant bathycrinids (Donovan & Pawson, 1998) and isocrinids (Amemiya & Oji, 1992).

- The often exceptionally good preservation of dissociated thecal ossicles, allowing stereom structure (Macurda et al., 1978) and internal thecal organisation to be assessed (Pl. 37, figs. 1-3).

Other features, such as the occurrence in columnals of galls as a result of myzostomid infestation (compare Arendt, 1961, Lane, 1978; D.L. Meyer & Ausich, 1983; Eeckhaut & Améziane-Cominardi, 1994 and Klikushin, 1996) and the absence of epizoans on columnals, also deserve attention.

Occurrence — Widely distributed in Liège-Limburg and southern Limburg (Figs. 40, 43-47), with records from the Lanaye Member (acme) to the basal Emael Member (Maastricht Formation). In the Kunrade-Benzenrade area the species appears to be confined to the lower portion of the sequence, which P.J. Felder & Bless (1989) suggested to correspond to the Lanaye Member in the Maastricht-Lanaye-Eben Emael area. The record of *Bourgueticrinus aequalis* by Kristan-Tollmann (1987b) from the Early Maastrichtian of the Gosau Basin (Austria) is doubtful, that of Klikushin (1982c)

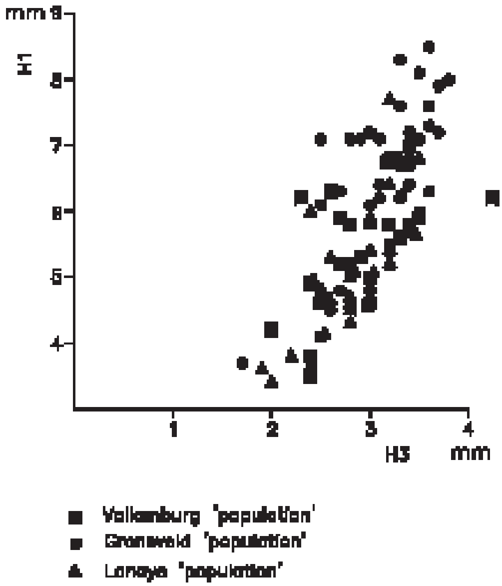

Fig. 32. Relationship between height of proximale + theca (H1) and height of theca (H3) in *Dunnicrinus aequalis* (d'Orbigny, 1841) from the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Valkenburg and Gronsveld members (Maastricht Formation, Late Maastrichtian).

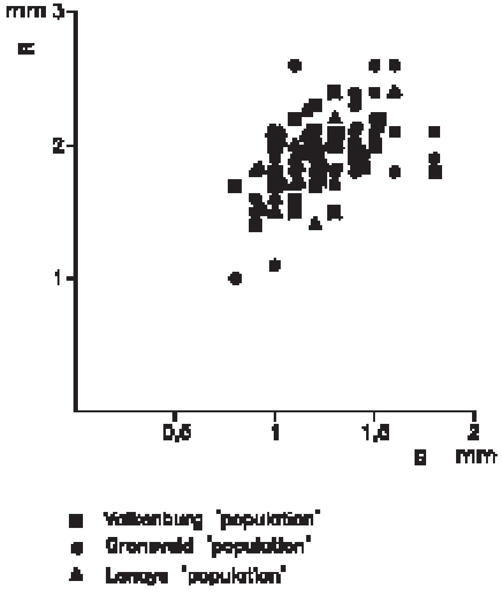

Fig. 33. Relationship between height of radials (R) and basals (B) in *Dunnicrinus aequalis* (d'Orbigny, 1841) from the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Valkenburg and Gronsveld members (Maastricht Formation, Late Maastrichtian).

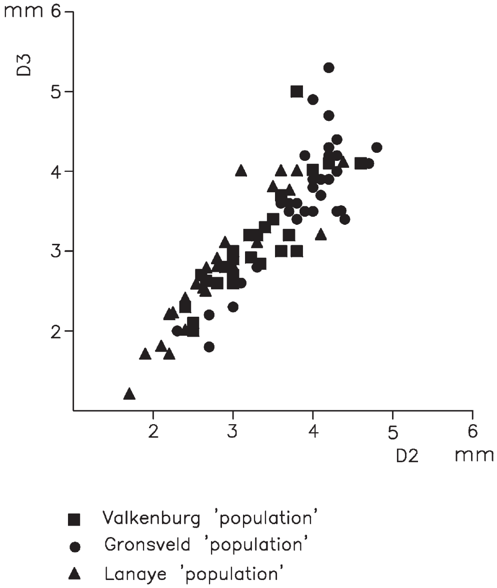

Fig. 34. Relationship between upper diameter of theca (radial ring) (D3) and lower diameter of theca (basal ring) (D2) in *Dunnicrinus aequalis* (d'Orbigny, 1841) from the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Valkenburg and Gronsveld members (Maastricht Formation, Late Maastrichtian).

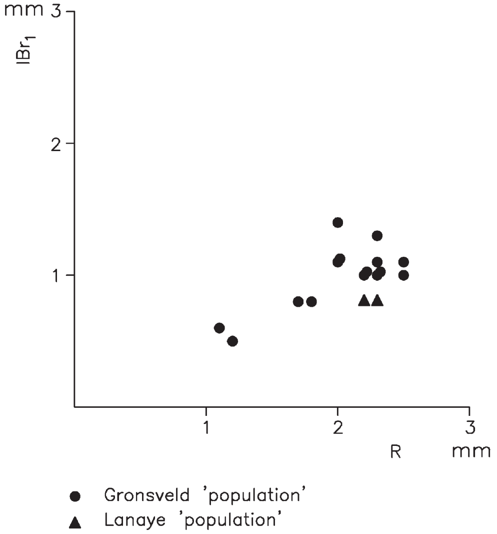

Fig. 35. Relationship between height of Br1 and radials (R) in *Dunnicrinus aequalis* (d'Orbigny, 1841) from the Lanaye Member (Gulpen Formation, Late Maastrichtian) and the Gronsveld Member (Maastricht Formation, Late Maastrichtian).

may indeed refer to the present species. Lauginiger's (1988, pl. 7, fig. 7) record of *Dunnicrinus* sp., based on dissociated columnals only, from the Mount Laurel Formation of Delaware cannot be assigned to species. It represents an indeterminate bourgueticrinid at best. Gallagher (1993) showed the Mount Laurel Formation (Monmouth Group) to be of (Late Campanian-) Early Maastrichtian age.

Genus *Bourgueticrinus* d'Orbigny, 1841

Type species — *Apiocrinites ellipticus* Miller, 1821, by original designation.

Remarks — With few exceptions, bourgueticrinids from the Late Campanian to Middle Danian strata in the study area can be assigned to previously described species or species groups without too many problems. Wright & Smith (1987) noted that in the Late Cretaceous white chalk facies of Great Britain many forms could be used as zonal indicators. From the literature it appears that many authors agree on the current status of a few distinctive forms amongst these bourgueticrinids, despite the fact that for most, if not all, of these biometric analyses of 'populations' are still lacking (see e.g. Merta, 1972; Jäger, 1979).

Bourgueticrinus sp. 1 (aff. *baculatus* Klikushin, 1982)
Pl. 31, figs. ? 1, 4, 8, 10; Pl. 32, fig. 10.

*1982c *Bourgueticrinus baculatus* Klikushin, p. 820, figs. 6d-i, 7a; pl. 4, figs. 7-11.
?1986b *Bourgueticrinus* sp. 1 — Jagt, p. 230, figs. 4b, 5.

Material — A dozen thecae, including NHMM MB 383, 761-39, 808-17, 1044-8.

Discussion — In having basals considerably taller than radials (Pl. 31, figs. 4, 8; Pl. 32, fig. 10), a slight constriction halfway the radial ring, and a moderate-sized proximale, the upper diameter of which exceeds the lower, the present specimens resemble *B. baculatus* of Klikushin (1982c, fig. 6d-i). Except for the outward projection of the radial articular facets, there is a good match. Klikushin considered this species (holotype: KT-8-1, Leningrad Mining Institute) to be closely related to *B. constrictus* (see below), *B. hagenowii* (Goldfuss, 1840) (see Rasmussen, 1961, p. 190, pl. 29, figs. 8-15) and *B. danicus* (see below), a conclusion with which I concur. *Bourgueticrinus baculatus* could even be part of the lineage leading to *B. constrictus* and *B. danicus*. The resemblance with certain forms of *B. constrictus* from the study area (see Pl. 32, figs. 5-7, 9) is such that they could be easily confused.

Occurrence — Known only from the Late Campanian Zeven Wegen Member (Gulpen Formation) as exposed at the Heure-le-Romain and CPL SA quarries (Figs. 40, 43).

Bourgueticrinus sp. 2
Pl. 31, figs. 6-7.

Material — Some thirty thecae, including NHMM MB 838-6b, 1044-8; NHMM JJ 4893(?).

Discussion — Specimens grouped under this heading are variable, but invariably are characterised by two constrictions, one occurring apparently at the base of the basal ring (Pl. 31, fig. 6), the other near or at the suture between the basals and radials (Pl. 31, figs. 6-7). The lower and diameter of the proximale are (near)equal or the lower diameter exceeds the upper. Basals are up to 1.5 times taller than the radials, which project outwards gradually. The greatest diameter of the theca is thus situated at the radial articular facets.

This form is best left in open nomenclature for now; I could find no match in the available literature on Late Cretaceous and Early Palaeogene bourgueticrinids.

Occurrence — Currently known only from the Late Campanian Zeven Wegen and Beutenaken members (Gulpen Formation) of the CPL SA and CBR-Lixhe quarries (Liège) and Pesaken (southern Limburg) (Figs. 40, 43-44).

Bourgueticrinus bruennichinielseni Ødum, in Jessen & Ødum, 1923
Pl. 28, figs. 3-4, 7.

*1923 *Bourgueticrinus Brünnichi Nielseni* Ødum in Jessen & Ødum, p. 18, fig. 8.
1961 *Bourgueticrinus bruennichinielseni* Ødum, 1923 — Rasmussen, p. 172, pl. 30, figs. 9-19.
1982c *Bourgueticrinus bruennichinielseni* Odum, 1923 [sic] — Klikushin, p. 816, fig. 3B.

Type — Holotype is the specimen illustrated by Ødum, from the Early Danian of Vokslev (Denmark), in the collections of the Geological Survey of Denmark (Rasmussen, 1961, p. 172).

Material — Seven thecae: NHMM MB 734-13, 734-14, 734-15.

Discussion — Amongst numerous thecae which are easily assigned to *B. danicus* (see below) and *Democrinus*? *maximus* (see below), there are a few specimens in which the basals are 2-3.5 times taller than the radials (Figs. 36-37) and in which a proximale

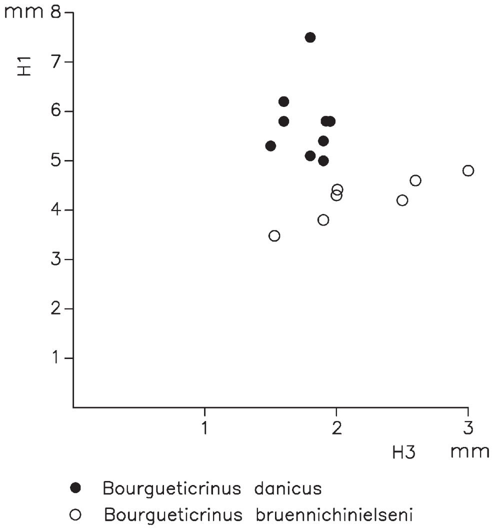

Fig. 36. Relationship between height of proximale + theca (H1) and height of theca (H3) in *Bourgueticrinus danicus* (Brünnich Nielsen, 1913) and *B. bruennichinielseni* Ødum, in Jessen & Ødum, 1923 from the Geulhem Member (Houthem Formation, Early/Middle Danian).

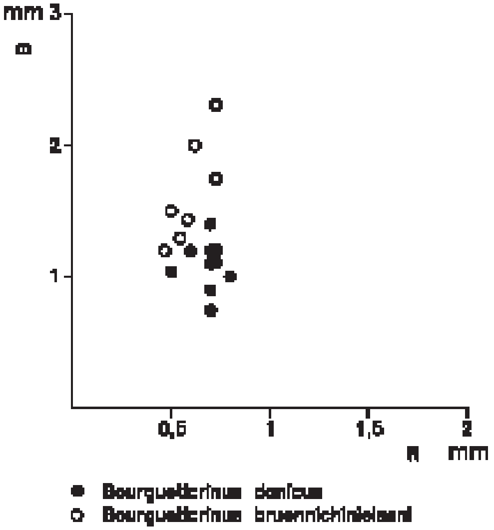

Fig. 37. Relationship between height of basals (B) and radials (R) in *Bourgueticrinus danicus* (Brünnich Nielsen, 1913) and *B. bruennichinielseni* Ødum, in Jessen & Ødum, 1923 from the Geulhem Member (Houthem Formation, Early/Middle Danian).

is incorporated. Structurally, this type constitutes an intermediate between *B. danicus* (Pl. 28, fig. 1) and *D.*? *maximus* (Pl. 28, figs. 2, 5-6).

Rasmussen (1961) noted the problems in distinguishing this 'species' from *B. constrictus* (see below), *B. danicus*, *Democrinus dubius* (Brünnich Nielsen, 1913), and *D. maximus*. His records of this form from the Maastrichtian of Denmark and Rügen (northeast Germany) are, according to Kjaer & Thomsen (in prep.), simply juvenile individuals of *B. constrictus*. Kjaer (1993) recorded *B. bruennichinielseni* from the Early Danian. On the basis of large collections from bulk samples with good stratigraphic control, Kjaer & Thomsen (in prep.) demonstrate the importance of heterochrony (neoteny/paedomorphosis) in the development of bourgueticrinids across the K/T boundary. This could then offer an explanation for the co-occurrence of the various thecal morphologies.

Associated columnals of the 'rhizocrinid' type with funnel-shaped axial canal (Pl. 28, figs. 8-9), which range throughout the Geulhem Member (Early/Middle Danian) cannot be assigned to species.

Occurrence — All available specimens are from the basal part of the Geulhem Member (Houthem Formation, Early Danian) of temporary Albertkanaal sections, Vroenhoven-Riemst (Limburg, Belgium) (Fig. 40).

Bourgueticrinus aff. *brydonei* Rasmussen, 1961
Pl. 32, figs. 1-4.

*1961 *Bourgueticrinus brydonei* Rasmussen, p. 174, pl. 28, figs. 1-2 (? 3-6).
?1982c *Bourgueticrinus brydonei* Rasmussen, 1961 — Klikushin, p. 816, fig. 3a.
1987 *Bourgueticrinus brydonei* Rasmussen — Wright & Smith, p. 205, pl. 45, fig. 11.
1995c *Bourgueticrinus brydonei* — Jagt, p. 191, figs. 5, 7.

Type — Holotype is B.78650 (Brydone Colln, Sedgwick Museum Cambridge), illustrated by Rasmussen (1961, pl. 28, fig. 2), from the latest Campanian or earliest Maastrichtian of Trimingham (Norfolk, England).

Material — Four proximalia: NHMM JJ 6983; NHMM MD 2736; NHMM K254a, b.

Discussion — The majority of bourgueticrinids from the Vijlen Member (? and Lixhe Member) of Liège-Limburg and southern Limburg are of small size and are characterised by a 'rhizocrinid' columnal type (Pl. 33, figs. 1, 3, 7-10). Isolated columnals of the 'bourgueticrinid' type (Pl. 34, figs. 1-2) are generally of a larger size, but even so cannot be assigned to *B.* aff. *brydonei*, which is larger still. Specimens before me, although differing considerably in overall height (varying from 6.5 to 23.4 mm), resemble forms illustrated by Rasmussen (1961). Since only proximalia are available this assignment is tentative at best.

Rasmussen (1961) recorded this species from the Early Maastrichtian of Denmark, the Late Campanian of Ahlten (Germany) and the latest Campanian-earliest Maastrichtian of Norfolk (see also Wright & Smith, 1987). Material referred to this species by Klikushin (1982c, 1983) is considerably older, being from the Late Santonian of Mangyshlak (Kazakhstan). At Trimingham (Norfolk), there are outcrops of Lower Maastrichtian strata, commonly referred to the 'pre-*Porosphaera* Beds' and '*Porosphaera* Beds' (Peake & Hancock, 1970). Johansen & Surlyk (1990) introduced the formal units, Sidestrand Chalk Member, Trimingham Sponge Beds Member, Little Marl Point Chalk Member and Beacon Hill Grey Chalk Member for these beds, and showed them to range from the *lanceolata* to upper *sumensis* zones (sensu Schulz, 1979, 1985; Early Maastrichtian). This suggests that *B. brydonei* is predominately (? exclusively) of Early Maastrichtian age.

Occurrence — The only specimen collected in situ is from the basal Vijlen Member at the CPL SA quarry (Figs. 40, 43); other specimens were collected loose, which means that it cannot be ruled out that the species ranges into the overlying Lixhe Member.

Bourgueticrinus constrictus (von Hagenow, in Quenstedt, 1876)
Pl. 32, figs. 5-9, 11; ? Pl. 33, figs. 7-10; Pl. 36, fig. 7.

*1876 *Apiocrinus constrictus* von Hagenow in Quenstedt, p. 368, pl. 104, figs. 64-66.
1961 *Bourgueticrinus constrictus* (Hagenow, 1876) — Rasmussen, p. 175, pl. 29, figs. 1-7.
*1961 *Bourgueticrinus tenuis* Rasmussen, p. 197, pl. 29, figs. 16-18.
?1982c *Bourgueticrinus constrictus* (Hagenow, 1876) — Klikushin, p. 817, fig. 3c; pl. 1, fig. 6.
?1982c *Bourgueticrinus tenuis* Rasmussen, 1961 — Klikushin, p. 820, fig. 5g.
1986b *Bourgueticrinus* sp. 2 (? nov.) — Jagt, p. 230, figs. 6a-c, 7-9.

Types — Lectotype of *B. constrictus*, designated by Rasmussen (1961, p. 176), is the columnal illustrated by Quenstedt (1876, pl. 104, fig. 65), from the Early Maastrichtian of Rügen (northeast Germany); present whereabouts unknown. Holotype of *B. tenuis* is MGUH no. 8939, from the Early Maastrichtian of Rørdal (Denmark).

Material — In addition to articulated and/or associated remains of a few individuals (thecae with columnals, arm fragments and dissociated brachials/pinnulars), several dozens of thecae, columnals and articulated arm fragments as well as isolated brachials/pinnulars, including NHMM MB 284-8, 522-7, 867-2a(?)/867-9, 1175, 1239;

NHMM K254c-d; NHMM JJ 3604, 3661, 5951; RGM 396 298-396 299 (ex Jagt Colln).

Discussion — This is the commonest species of bourgueticrinid in the Vijlen and Lixhe members, characterised by a 'rhizocrinid' type of columnals (Pl. 33, figs. 7-10) and, based on associated finds, an axillary primibrachial (Pl. 36, fig. 7; Pl. 37, figs. 5, 7, 9-10). It is often extremely difficult to make out the sutures between basals and radials; only in very few specimens are they clearly seen (Pl. 32, fig. 8). Thecal constriction usually situated near the basal/radial suture (Pl. 32, figs. 5-6, 8-9). Outline of proximale varies from slender conical to slightly claviform or more or less cylindrical. Basal height exceeds radial height (see also *Bourgueticrinus* sp. 1 above). Radial articular facets slope slightly outwards (Pl. 32, figs. 5-6, 8-9, 11).

From the Mamelis-Selzerbeek sections a single terminal holdfast, which probably belongs to this species, is known (Pl. 33, fig. 10). The crinoid encrusted a hard substrate; in this case, the rostrum of a coleoid cephalopod. Such finds are extremely rare, most bourgueticrinid species in the study area being characterised by (extensive) radicular cirri systems. For Early Jurassic eudesicrinids Manni et al. (1991) assumed these to have had the ability to actively explore the substrate before final settlement.

As noted above (under *B.* aff. *brydonei*), more than one species of bourgueticrinid is now known from the Vijlen Member. Assignment of arm fragments and dissociated brachials, however, is problematic. The present species appears to have had ten arms, the second primibrachial being axillary (Pl. 36, fig. 7; Pl. 37, figs. 5, 7, 9-10). Cooccurring in the same samples are arm fragments consisting of strongly wedge-shaped brachials with muscular and syzygial articulations (Pl. 36, figs. 2, 4) of much the same type as those of *Dunnicrinus aequalis* (Pl. 36, figs. 1, 3, 9) and of an indeterminate Late Campanian bourgueticrinid (Pl. 36, figs. 5-6; possibly *Bourgueticrinus*? *suedicus*, see below). The other type (Pl. 36, figs. 8, 10-11; Pl. 37, figs. 4, 6, 8) shows tall, irregularly quadrangular proximal brachials, with oblique muscular articula on Br2 (Pl. 37, figs. 4, 8) and higher (Pl. 36, fig. 10; Pl. 37, fig. 6). However, specimen RGM 396 299 (Pl. 36, fig. 7) shows that this type of brachial can be associated with an axillary primibrachial.

Rasmussen (1961) noted that his new species *B. tenuis* might in fact represent a pathological specimen of *B. constrictus* (see also Klikushin, 1982c, p. 820, fig. 5g; Jagt, 1995c, p. 192, figs. 5, 7), a view subscribed to here. It should be noted that Klikushin (1982c) recorded *B. tenuis* from the Late Campanian of the Crimea.

Occurrence — Unequivocal specimens are known to date from the Vijlen and Lixhe 1 members (Gulpen Formation) of Liège-Limburg and southern Limburg (Figs. 40, 43). Keutgen's (1996, pp. 195, 196) *Bourgueticrinus* sp. 1 probably refers to the present species, occurring in intervals 0, 4 and 6 of the Vijlen Member, and in the basal Lixhe Member.

Bourgueticrinus danicus Brünnich Nielsen, 1913
Pl. 28, fig. 1.

*1913 *Bourgueticrinus danicus* Brünnich Nielsen, p. 53, pl. 2, figs. 49-51; pl. 3, figs. 1-58.
1961 *Bourgueticrinus danicus* Nielsen, 1913 — Rasmussen, p. 178, pl. 30, figs. 1-8.
1982c *Bourgueticrinus danicus* Nielsen, 1913 — Klikushin, p. 818, fig. 4b, pl. 1, figs. 7-11.
1995c *Bourgueticrinus danicus* — Jagt, p. 192, figs. 5, 7.

Type — Lectotype, designated by Rasmussen (1953, p. 417), is the specimen (MGUH no. 1070) illustrated by Brünnich Nielsen (1913, pl. 3, figs. 3, 4).

Material — Some 90 thecae and isolated columnals, including NHMM MB 734-15/16; NHMM JJ 2446; NHMM K1697, 1713b.

Discussion — Thecae of this species are so similar to those of *Bourgueticrinus* sp. 1 (aff. *baculatus*, see above) and *B. constrictus* that they might easily be confused. Basal height exceeds radial height (Fig. 37). From co-occurring *Democrinus*? *maximus* and *B. bruennichinielseni*, it differs in that it does have a proximale, and in that it is taller, respectively (Fig. 36).

Also in brachial and columnal structure are there many similarities between the present species and *B. constrictus*, with a synostosial IBr1-2 articulation, and with IBr2 being axillary, having oblique muscular articular facets for secundibrachials. Proximal columnals are barrel shaped and elliptical and have synarthrial fulcra and an enlarged axial canal.

Occurrence — Confined to the Geulhem Member, apparently ranging throughout this unit but being commoner in the basal part, of temporary Albertkanaal sections (Vroenhoven-Riemst, Veldwezelt) and of Ankerpoort-Curfs quarry (Geulhem) (Figs. 40, 50).

Bourgueticrinus hureae (Valette, 1917)
Pl. 29.

*1917 *Volvola hureæ* Valette, p. 104, fig. 6/1-3 (? fig. 6/4-10).
1961 *Bourgueticrinus hureae* (Valette, 1917) — Rasmussen, p. 191, pl. 28, figs. 7-10.
1986b *Bourgueticrinus* aff. *hureae* (Valette, 1917) — Jagt, p. 229, fig. 4a.
1987 *Bourgueticrinus hureae* (Valette) — Wright & Smith, p. 206, pl. 45, fig. 2.
1995c *Bourgueticrinus hureae* — Jagt, p. 191, figs. 5, 7.

Type — Holotype is the specimen figured by Valette (1917, fig. 6/1), from the Santonian of Saint-Bond (Yonne, France); present whereabouts unknown.

Material — Several dozens of thecae, isolated basal and radial rings, proximalia, and columnals and brachials possibly belonging to the present species (Pl. 38, figs. 6-7), including NHMM MB 382, 581-4/5, 770, 811; NHMM JJ 2221.

Discussion — Amongst bourgueticrinids from the Late Campanian Zeven Wegen Member (Gulpen Formation) this is the commonest species. Thecae are medium sized, with tumid basals and radials separated by (deeply) depressed sutures (Pl. 29, figs. 1-4). The proximale is of variable height and outline (Pl. 29, figs. 1-2, 4, 8). Radials are (slightly) taller than basals (Fig. 38). Articular facets of radials project slightly outwards, with dorsal ligament pit wide and deep medially, interarticular ligament pits large and concave and ventral muscle pits continuing onto high, collar-like structure around a narrow radial cavity (Pl. 29, figs. 1, 5-7, 9-10).

Large muscular and syzygial brachials (Pl. 38, figs. 6-7) may belong to the present species.

Rasmussen (1961) recorded this species from the (Late) Santonian-Campanian of France, Germany and the United Kingdom.

Occurrence — Apparently confined to the Zeven Wegen Member (Gulpen Forma-

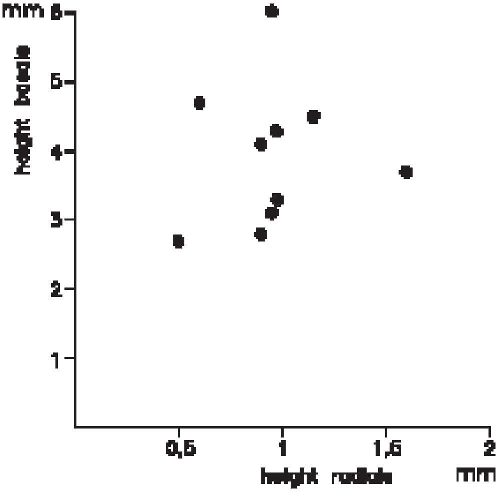

Fig. 38. Relationship between height of basals and height of radials in *Bourgueticrinus hureae* (Valette, 1917) from the Zeven Wegen Member (Gulpen Formation, Late Campanian).

tion, Late Campanian) of Liège (CPL SA and CBR-Lixhe quarries) (Figs. 40, 43-44). There is also a record from coeval strata in Belgium Brabant (Bless et al., 1991).

Bourgueticrinus? *suedicus* (Carpenter, 1881)
Pl. 31, figs. 2-3, 5, 9, 11; ? Pl. 36, figs. 5-6; ? Pl. 38, figs. 8-9.

*1881 *Mesocrinus suedicus* Carpenter, p. 130, pl. 6, fig. 7.
1961 *Bourgueticrinus suedicus* (Carpenter, 1881) — Rasmussen, p. 196, pl. 27, figs. 1-8.
1995c *Bourgueticrinus suedicus* — Jagt, p. 191, figs. 5, 7.

Type — Rasmussen (1961, p. 196) pointed out that the specimen illustrated by Carpenter (1881), from the Campanian of Köpinge (southern Sweden) could not be traced.

Material — About twenty thecae and dissociated proximal and distal brachials which may belong here, including RGM 396 293-396 296 (all ex Jagt Colln, nos 8631, 10607, 7884, and 4894, respectively); NHMM MB 761-1.

Discussion — The similarity between these thecae and those of the Late Maastrichtian *Dunnicrinus aequalis* (see above) is such that at first these specimens were assigned to that species. A closer examination revealed a number of, admittedly slight, differences. Apparently, the present specimens generally have longer proximalia (12 mm in NHMM MB 761-1) and proximal columnals than *D. aequalis*. That these species may be more closely related than previously assumed can also be deduced from the structure of the proximal brachials. Rasmussen (1961, pl. 27, fig. 8) illustrated a wedge-shaped proximal brachial which he assigned to *B. suedicus*. Although poorly preserved, it does show a synarthrial proximal articulum and oblique muscular distal articulum with pinnule facet. Similar proximal brachials are known from the Zeven Wegen Member (Pl. 36, fig. 5; Pl. 38, figs. 8-9), and suggest that Rasmussen's specimen is a Br3. The distal facet of Br1 (Pl. 38, fig. 8) shows a synarthrial articulation, which corresponds to that of the proximal facet of Br2 (Pl. 38, fig. 9), which also has a prominent pinnular facet (Pl. 38, fig. 5).

Should these brachials indeed belong to the thecae generally referred to as *B. suedicus*, this species is perhaps best reassigned and considered a precursor of *D. aequalis*. Unfortunately, little is yet known of the type of brachial articulation in most 'species' of the genus *Bourgueticrinus*. Rasmussen (1978, p. T842) indicated IBrr1-2 to be synostosial or synarthrial, IBr2 to be axillary, IIBrr1-2 flat synarthrial, and first pinnule abaxial on IIBr2, with non-muscular articulation on IIBrr4-5 and scattered through more distal part of arms. Data presented here show that this arrangement is not a uniform one within the family.

In thecal features, differences between the present species and *Bourgueticrinus fischeri* (Geinitz, 1872) are slight (see Rasmussen, 1961, p. 185, pl. 27, figs. 12-14; Klikushin, 1980, pl. 1, fig. 3; 1982c, p. 818, fig. 4d-f; Jäger, 1979, 1980), but according to Rasmussen (1961, p. 186) the latter species had divided arms.

Occurrence — At present, known only from the Zeven Wegen Member (Gulpen Formation) in Liège (Heure-le-Romain, CPL SA and CBR-Lixhe quarries) (Figs. 40, 43-44).

Genus *Democrinus* Perrier, 1883

Type species — *Democrinus parfaiti* Perrier, 1883, by monotypy.

Democrinus? *maximus* (Brünnich Nielsen, 1915)

Pl. 28, figs. 2, 5-6.

*1915 *Rhizocrinus maximus* Brünnich Nielsen, p. 392, fig. 1.
1961 *Democrinus maximus* (Nielsen, 1915) — Rasmussen, p. 207, pl. 31, figs. 1-8.
1982c *Democrinus maximus* (Nielsen, 1915) — Klikushin, p. 823, pl. 3, figs. 9-11.
1995c *Democrinus maximus* — Jagt, p. 192, figs. 5, 7.

Type — Lectotype, designated by Rasmussen (1953, p. 417), is the specimen (MGUH no. 1783) illustrated by Brünnich Nielsen (1915, fig. 1, larger specimen).

Material — Some seventy thecae and isolated columnals, including NHMM MB 432.QQ, 734-14/16; NHMM JJ 2448; NHMM 1996011 (ex van der Ham Colln); NHMM K1713a.

Discussion — Representatives of this species are easily differentiated from co-occurring *Bourgueticrinus danicus* and *B. bruennichinielseni* in lacking a proximale. The height of the basals considerably exceeds that of the radials (Fig. 39; Pl. 28, figs. 2, 5-6). Thecal outline varies and may or may not be constricted just above the suture between the basals and radials (Pl. 28, figs. 2, 6). A single specimen in the present lot preserves the proximalmost columnal and the first brachials (Pl. 28, fig. 5). Deformations in basal structure are relatively common, but extreme examples such as the ones here illustrated (Pl. 28, figs. 5-6) are rare in the material available.

Håkansson et al. (1996) assumed the genus *Democrinus* to have evolved directly from Late Maastrichtian *Bourgueticrinus* through neoteny, and to be a true crisis rep-

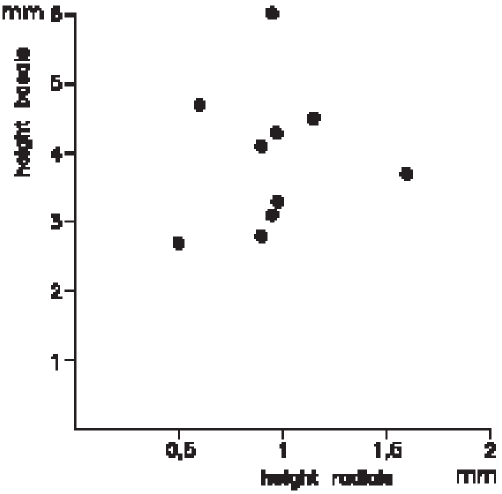

Fig. 39. Relationship between height of basals and height of radials in *Democrinus*? *maximus* (Brünnich Nielsen, 1915) from the Geulhem Member (Houthem Formation, Early/Middle Danian).

resentative. Kjaer's view (1993; also Kjaer & Thomsen, in prep.) that *Democrinus maximus* differs too much (ten arms !) from the type species of *Democrinus* to be confidently assigned to that genus (compare A.M. Clark, 1972, 1977; Messing & Dearborn, 1990), is here adopted. He also suggests that a number of diminutive 'species' (e.g. *Democrinus gisleni* Rasmussen, 1961 and *D. dubius*) are in fact juvenile bourgueticrinids. The *Democrinus* type did not occur until after the K/T boundary perturbations; it thus represents an important evolutionary phase in the Bourgueticrinina (Kjaer & Thomsen, in prep.).

Améziane-Cominardi & Roux (1994) noted that the fossil record comprised many examples of how important paedomorphic processes have been in crinoid evolution. In contrast, paedomorphosis is extremely rare in extant crinoids (Messing, 1984). Simms (1988a, 1990a, b) stressed the role of heterochrony (terminology following McNamara, 1986) in the evolution of post-Palaeozoic crinoids, and provided examples for Jurassic forms (Simms, 1988b).

Occurrence — Confined to the Geulhem Member (Houthem Formation) as exposed in Limburg (Belgium) and southern Limburg (The Netherlands), apparently commoner in the lower portion of that unit (Figs. 40, 50).

Genus *Monachocrinus* A.H. Clark, 1917

Type species — *Monachocrinus sexradiatus* A.H. Clark, 1917, by original designation.

Remarks — Rasmussen (1961) referred with a query a number of diminutive bourgueticrinid thecae to this extant genus. Of these, *M.*? aff. *regnelli* (sensu Rasmussen, 1975) was later described by Jäger (1987) under the name of *Bourgueticrinus pockrandti* (Late Santonian, northern Germany).

None of the species described by Rasmussen (1961) really belong in *Monachocri-*

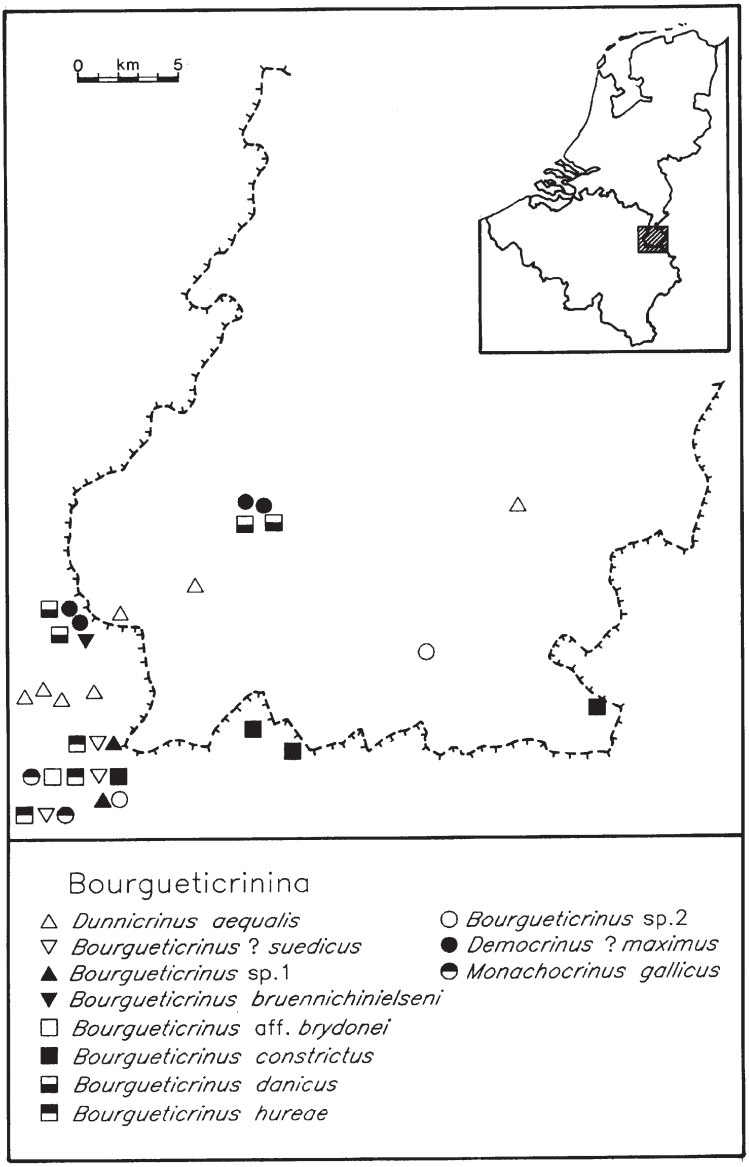

Fig. 40. Geographic distribution of Late Cretaceous-Early Palaeogene bourgueticrinids in the type area of the Maastrichtian Stage.

nus; even in samples with relatively numerous thecae there is no trace of any proximal columnals or brachials comparable to those of that genus (see Rasmussen, 1978, fig. 567/2f). Awaiting more detailed studies of bourgueticrinid ontogeny, and biometric analyses of fossil 'populations', the fairly numerous diminutive thecae are here referred to as '*M.*? *gallicus*'.

'*Monachocrinus*? *gallicus* Rasmussen, 1961'

Pl. 30, figs. 4-6,? 7, 8-13.

*1961 *Monachocrinus*? *gallicus* Rasmussen, p. 209, pl. 31, fig. 11.
1995c *Monachocrinus*? *gallicus* Rasmussen, 1961 — Jagt, p. 191, figs. 5, 7.

Type — Holotype is MGUH no. 8964, from the 'Upper Senonian' of Meudon (France), possibly referring to the Late Campanian (see Bignot, 1994; Bignot et al., 1993).

Material — About 65 thecae, including NHMM MB 761-39/40, 770-15, 808-11, 1044-8; RGM 396 291 (ex Jagt Colln, no. 6578).

Description and discussion — In specimens comparable to Rasmussen's type of the present species (Pl. 30, figs. 6, 9, 12) the basals appear to be fused, the radials showing discrete sutures. In these individuals, the proximal end of the theca (Pl. 30, figs. 4-5) either shows what appears to be a synostosial articulum, or a very faint indication of sutures on a concave facet. There are about equal numbers of thecae with six and with five radials; the present collection also comprises a single theca with four radials.

Co-occurring with these specimens are diminutive thecae with discrete basals (Pl. 30, figs. 1-3). These undoubtedly represent juvenile bourgueticrinids, and are closely comparable in details of radial articular facet to specimens that lack discrete basal sutures.

Occurrence — Known only from the Late Campanian (Zeven Wegen Member) of Liège (Heure-le-Romain and CPL SA quarries) (Figs. 40, 43).

Other bourgueticrinids

Material — Indeterminate bourgueticrinid ossicles are here recorded from the following localities and stratigraphic levels:

- de Wingerd quarry, Benzenrade Member (Vaals Formation): a few columnals (NHMM MB 865-18).
- Benzenrade ('kapelletje'), Benzenrade Member (Vaals Formation): a single proximale and two columnals (NHMM MB 619-16/18).
- CPL SA quarry, Vaals Formation: radicular cirri (NHMM 918-2, see Pl. 35, figs. 1, 4).
- Pesaken, Beutenaken Member (Gulpen Formation): a few dozens of columnals, a single proximale and a single, poorly preserved theca (NHMM MB 838-6).
- CPL SA quarry, Zeven Wegen Member (Gulpen Formation): a few columnals of 'rhizocrinid' type (see Pl. 33, figs. 2, 5-6).
- CPL SA quarry, Lanaye Member (Gulpen Formation): a single columnal of 'rhizocrinid' type (see Pl. 33, fig. 4).
- Kunrade, Kunrade Limestone facies (Maastricht Formation): two columnals, one of 'bourgueticrinid' (possibly *D. aequalis*), the other of 'rhizocrinid' type (NHMM MB 414-4f).
- CPL SA quarry, Zeven Wegen Member (Gulpen Formation): a few columnals (Pl. 34, figs. 5, 8) and articulated brachials/pinnules (RGM 396 305, 396 308, 396 314).

- Heure-le-Romain quarry, Zeven Wegen Member (Gulpen Formation): articulated columnals (Pl. 34, fig. 9; RGM 396 309).

- CBR-Lixhe quarry, Zeven Wegen Member (Gulpen Formation): a few columnals (Pl. 34, fig. 7; RGM 396 306).

Infraorder Holopodinidia Arendt, 1974
Family Holopodidae von Zittel, 1879
Genus *Cyathidium* Steenstrup, in Michaelis & Scherk, 1847

Type species — *Cyathidium holopus* Steenstrup, in Michaelis & Scherk, 1847, by monotypy.

Cyathidium vlieksi Jagt, 1986

*1986a *Cyathidium vlieksi* Jagt, p. 216, figs. 1-6.
1987 *Cy. vlieksi* Jagt, 1986 — Manni & Nicosia, p. 87.
1995c *Cyathidium vlieksi* — Jagt, p. 192, figs. 6-7.
1996 *Cyathidium vlieksi* (Jagt, 1986) [sic] — Heinzeller, Fricke et al., p. 81.

Type — Holotype is NHMM 1986017, paratypes are NHMM 1986018-1986019 and IRScNB no. 257 (Bosquet Colln, IG 4285).

Material — A few thecae and a single axillary primibrachial, including NHMM MB 272, 718, 763; NHMM BL 0477, 0484, 0485, 0545; NHMM JJ 10783.

Discussion — The material does not add anything substantial to the original description of this species, to which the reader is referred. In addition to *C. foresti* Cherbonnier & Guille, 1973 (p. 2194, pl. 1) (= *C. meteorensis* Fechter, 1973, p. 162, figs. 1-2; see A.M. Clark, 1980; Heinzeller & Fechter, 1995), a second extant species has recently been recorded, viz. *Cyathidium plantei* Heinzeller, in Heinzeller, Fricke et al., 1996. Of the other genus contained in the Holopodidae two modern species are now known, *H. rangii* d'Orbigny, 1837 (see Donovan, 1992) and *H. alidis* Bourseau et al., 1991 (p. 284, pls 12-13).

Baumiller & Gazdzicki's (1996) recent record of *Cyathidium holopus* considerably extends the stratigraphic and geographic range of the species, previously known only from the Middle Danian (*bruennichi* Zone) of Denmark and southwest Sweden. They list this species also for the Maastrichtian of The Netherlands, but this should be *C. vlieksi*. Kühn's (1930) record of *Cyathidium* from the Danian of Austria probably represents *C. holopus*, but this is in need of confirmation.

Lommerzheim (1991b) recorded but did not figure *Cyathidium* from Upper Campanian strata penetrated in borehole Metelen 1001 (Münsterland, northwest Germany).

Occurrence — Until recently, the present species was held to be confined to the Nekum or Meerssen Member and Kunrade Limestone facies (Maastricht Formation) (Figs. 41, 47, 50). However, from the Mamelis-Selzerbeek sections (Gulpen Formation, Vijlen Member; Early Maastrichtian), a single theca, six axillary primibrachials and a single secundibrachial assignable to *C. vlieksi* have recently been collected (NHMM MB 3639). These specimens will be illustrated and described elsewhere (Jagt & van Birgelen, in prep.).

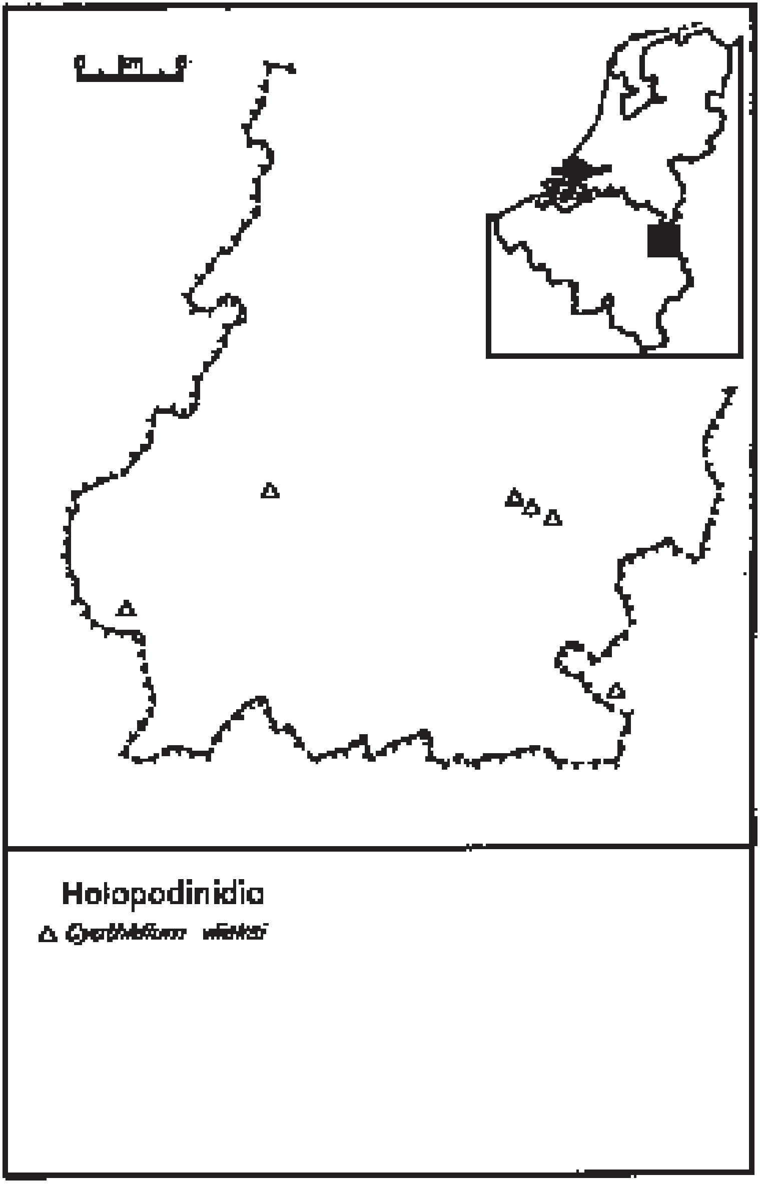

Fig. 41. Geographic distribution of Late Cretaceous holopodids in the type area of the Maastrichtian Stage.

Order Roveacrinida Sieverts-Doreck, in Moore et al., 1952
Family Saccocomidae d'Orbigny, 1852

Remarks — Current classifications of the Roveacrinida (Rasmussen, 1978) are considered unsatisfactory, the order containing three families, Somphocrinidae, Saccocomidae and Roveacrinidae. Simms et al. (1993) noted that it is far from clear how these families are interrelated and how they relate to other articulate crinoids. For reasons not given, Sepkoski (1992) added another family, the Ainigmacrinidae. This, however, comprises highly-adapted representatives of Late Triassic encrinids (see Hagdorn, 1988, 1995). Members of the Somphocrinidae have been shown to be excellent marker fossils on account of their wide geographic distribution during the Triassic (see Peck, 1948; Kristan-Tollmann, 1970, 1977, 1987a, 1988, 1991; Hagdorn, 1995).

Castellana et al. (1990) pointed out that it would be necessary to remove the Saccocomidae, and stressed the need for a thorough revision of this group. Saccocomid crinoids have been widely recorded from Jurassic-Early Cretaceous deposits worldwide, and are often recognised in thin sections of carbonate rocks. Generally these remains are assignable to the genus *Saccocoma*, which has well-developed arms with large, winglike brachials (see e.g. Verniory, 1960, 1961, 1962; Nekvasilová & Prokop, 1964; Pisera & Dzik, 1979; Manni & Nicosia, 1984, 1986, 1990; Nicosia, 1991; Roman, 1991; Manni et al., 1992).

Genus *Applinocrinus* Peck, 1973

Type species — *Saccocoma cretacea* Bather, 1924, by original designation.

Applinocrinus cretaceus (Bather, 1924)

Pl. 39; Pl. 40, figs. 1-4, 7-8.

*1924 *Saccocoma cretacea* Bather, p. 113, figs. 8-9.
1961 *Saccocoma (Saccocoma) cretacea* Bather, 1924 — Rasmussen, p. 390, pl. 57, fig. 9 (non fig. 10).
1973 *Applinocrinus cretaceus* (Bather) — Peck, p. 97, pl. 1, figs. 1-3, 6-12; text-fig. 1c, d.
*1973 *Applinocrinus texanus* Peck, p. 98, pl. 1, figs. 4-5; text-fig. 1a, b.
1987 *Saccocoma cretacea* Bather — Wright & Smith, p. 211, pl. 45, figs. 5-6.
1992 *Applinocrinus* n. sp. — Jagt, p. 157, fig. 2a-f, j-l, n-o.
1993 *Applinocrinus cretacea* (Bather, 1924) — Donovan et al., p. 127.
1995c *Applinocrinus* n. sp. — Jagt, p. 192, figs. 6-7.
1995c *Applinocrinus cretaceus* — Jagt, p. 193, figs. 6-7.
1996 *Applinocrinus cretacea* (Bather, 1924) — Donovan et al., p. 869, fig. 2.

Type — Holotype is BMNH E 24767, from the Early Campanian (*quadrata* Zone) of Durrington (Sussex, England) (see also Wright & Smith, 1987, pl. 45, figs. 5-6).

Material — Several hundreds of thecae, only few of them preserving ventral covering plates, including NHMM MB 95-9a, 284-6, 415, 517-5, 591-2, 619-32/33, 649-3, 655-4d, 672, 708a, 814-5, 815-3, 867-2a, 1044-18, 1175a-c; NHMM JJ 3082, 5573, 9380-5, 10482, 10503a, 10533, 10600/1, 10845-10847a.

Description and discussion — Selected specimens from Liège-Limburg (Belgium) (Pl. 39, figs. 1-2, 4-5, 7-8, 11), southern Limburg (The Netherlands) (Pl. 39, figs. 3, 6), Jasmund/Rügen (Pl. 39, fig. 9; Pl. 40, figs. 1-4, 7-8) illustrate the wide range of morphological variation. Peck's (1973) description of *A. cretaceus* is the most detailed published so far; it is here adapted to characterise the present material.

The small thecae (diameter up to 3.8 mm) are evenly arched (Pl. 39, fig. 2), dorsally pointed to varying degrees (Pl. 39, figs. 4-5, 7-9, 11; Pl. 40, figs. 2-3), (sub)pentagonal to (sub)circular in outline (Pl. 39, figs. 1, 7-8) and mitriform in profile (Pl. 39, figs. 5, 9, 11; Pl. 40, figs. 2-3), thecal width more or less equalling height or height exceeding width. Ornament is either absent (in part undoubtedly due to recrystallisation, Pl. 39, figs. 4-5) or prominent (Pl. 39, figs. 2, 9; Pl. 40, figs. 1-4). Basal circlet is pentagonal (Pl. 39, figs. 7-8) or (sub)circular and varies in size and prominence (Pl. 40, figs. 1, 4), individual basals being rhombic. Sutures between basals almost straight and with raised edges (Pl. 39, figs. 7-8), sutures between basals and radials denticulate, comparable to sutures between radials (Pl. 39, figs. 2, 7-8, 11; compare Peck, 1973, pl. 1, fig. 6). Distal point of basals raised and knob- or spikelike, concealing the central plate or surrounding it (Pl. 39, figs. 7-8, 11; compare Peck, 1973, pl. 1, figs. 8, 12). As the Rügen material shows, this feature is highly variable: the central plate may grow out to considerable lengths, being coarsely ornamented by twisted, longitudinal ridges, separated by concave interspaces of variable width (Pl. 39, figs. 9-10; Pl. 40, figs. 7-8). Dorsal outgrowths in some of the Rügen specimens (Pl. 40, figs. 1, 4) are so prominent as to conceal basal/radial sutures. Prominent ridges mark basal/basal sutures and apparently continue onto the radials. On the central plate (Pl. 40, fig. 4) these ridges develop into protuberances which apparently could develop into the spikes. These spikes may have greatly facilitated (by friction) anchorage in the substrate, thus suggesting these saccocomids to have been benthic rather than pelagic animals (compare Ettensohn, 1980, 1984; Milsom, 1994, 1995). This is in accord with Donovan et al.'s (1996) interpretation of the present species.

Radials are shield shaped, bearing an ornament consisting of longitudinal ridges of varying length and prominence. The ventral surface is evenly convex (Pl. 39, fig. 6) or rises well above the distal edge of the radials (Pl. 39, fig. 11). Ventral covering plates (Pl. 39, figs. 1-3, 5-6, 9, 11) have a slightly raised, flattened area (Pl. 39, figs. 1-2) adorally leads to a shallow central furrow. Broadhead & Russell (1985) assumed the oral covering plates of *Applinocrinus* to be modified arms formed from single ossicles. Donovan et al. (1996) again addressed the problem of brachial attachment in this genus, if present at all. In well-preserved specimens (Pl. 39, figs. 2, 11) a raised median area can be seen on the upper radial margin (compare Peck, 1973, text-fig. 1c; pl. 1, fig. 7; Wright & Smith, 1987, pl. 45, figs. 5-6). Donovan et al. (1996, p. 870) suggested that there could have been an articular facet (?) on this median prominence, with a central depression. The general absence of brachials which would be assignable to this genus, these authors would explain as the result of taphonomic processes such as current sorting. The specimen here illustrated in Pl. 39 (fig. 2) also shows a central depression, but no facet of any kind. Ventral covering plates tend in some specimens (Pl. 39, fig. 11) to encroach on this median prominence, which suggest that, if brachials were attached to this raised area, they could only have been tiny. In the specimen illustrated in Pl. 39 (figs. 3, 6) the radials have been displaced by compaction, causing the ventral covering plates to overhang the theca. This, and the fact that the majority of specimens from the study area lack these covering plates, suggests articulation between these plates and the distal margin of the radials to have been (extremely) weak.

Peck (1973, text-fig. 1a, b; pl. 1, figs. 4-5) differentiated a new species, *A. texanus*, on height/width ratio, the high-domed ventral cover and the elongated longitudinally ribbed basal circlet open at the proximal end. This form is here considered to represent no more than an extreme morphology, with morphologies shown by Rügen material here illustrated linking it to 'typical' *A. cretaceus*.

The present species appears to be widely distributed, with records from England, North America, Mexico, Jamaica, Belgium, and The Netherlands (Bather, 1924; Applin & Applin, 1967; Peck, 1973; Broadhead & Russell, 1985; Donovan et al., 1993, 1996). Additional records include southern Sweden (Ivö Klack, in a regressional sequence of Early Campanian age; see Gabrielson & Holland, 1984) and northeast Germany (Jasmund/Rügen, Early Maastrichtian).

Jagt's (1992) *Applinocrinus* n. sp., based on comparatively large thecae from the Meerssen Member (Maastricht Formation, Late Maastrichtian) with well-developed basal circlets and a relatively large central plate, are now considered conspecific with *A. cretaceus*.

Occurrence — Known to date from the Late Campanian to latest Maastrichtian (Zeven Wegen, Benzenrade, Vijlen, Lixhe 1, Lanaye, Gronsveld, Schiepersberg, Emael, Nekum, and Meerssen members) of Liège-Limburg and southern Limburg (Figs. 42-43, 45-48).

Family Roveacrinidae Sieverts-Doreck, in Moore et al., 1952

Remarks — Until recently, roveacrinids were considered to range from the Early/Middle Albian to the latest Maastrichtian (Destombes, 1984; Pisera, 1983; Simms, 1990; Jagt, 1992, and the present paper). However, Ferré & Granier (1997) have subsequently recorded species of Early Hauterivian age from Spain. Note that the roveacrinid brachials collected from erratic boulders in northern Germany as described by Sieverts-Doreck (1943) may be of Late Maastrichtian age too, but this seems to have escaped attention in the subsequent literature.

Roveacrinids in fact turn out to be commoner than previously assumed (Lommerzheim, 1991b; Ferré & Berthou, 1993; Ferré, work in progress; Frenzel et al., 1996; Reich & Frenzel, 1996). Liebau (1984) recorded the common occurrence of planktonic crinoids (saccocomids or roveacrinids?) in the Maastrichtian of northern Spain, and noted that their ecological distribution apparently differed from that of planktonic foraminifera.

Future studies of roveacrinids should concentrate on developing a sound taxonomic framework, and on determining the phylogenetic relationships of the various genera. During the 5th International Cretaceous Symposium (Freiberg/Sachsen, 1996), Bruno Ferré proposed forming a working group, to comprise people from all continents, in order to do just that.

In the extended type area of the Maastrichtian Stage, quite a number of lithostratigraphic units have now been shown to yield isolated brachial ossicles of roveacrinids. With the exception of a single radial (Pl. 40, fig. 10), so far no thecae have been collected from the Zeven Wegen Member (Gulpen Formation) as exposed at the CPL SA and CBR-Lixhe quarries. The Benzenrade Member (Vaals Formation) as exposed near Benzenrade and at de Wingerd quarry, however, has yielded comparatively many thecae, associated with comparable brachial ossicles. As these strata have been shown to be lateral time equivalents on micro- and macrofossil evidence, it seems reasonable to assign the majority of the Zeven Wegen Member brachials to the same species (see

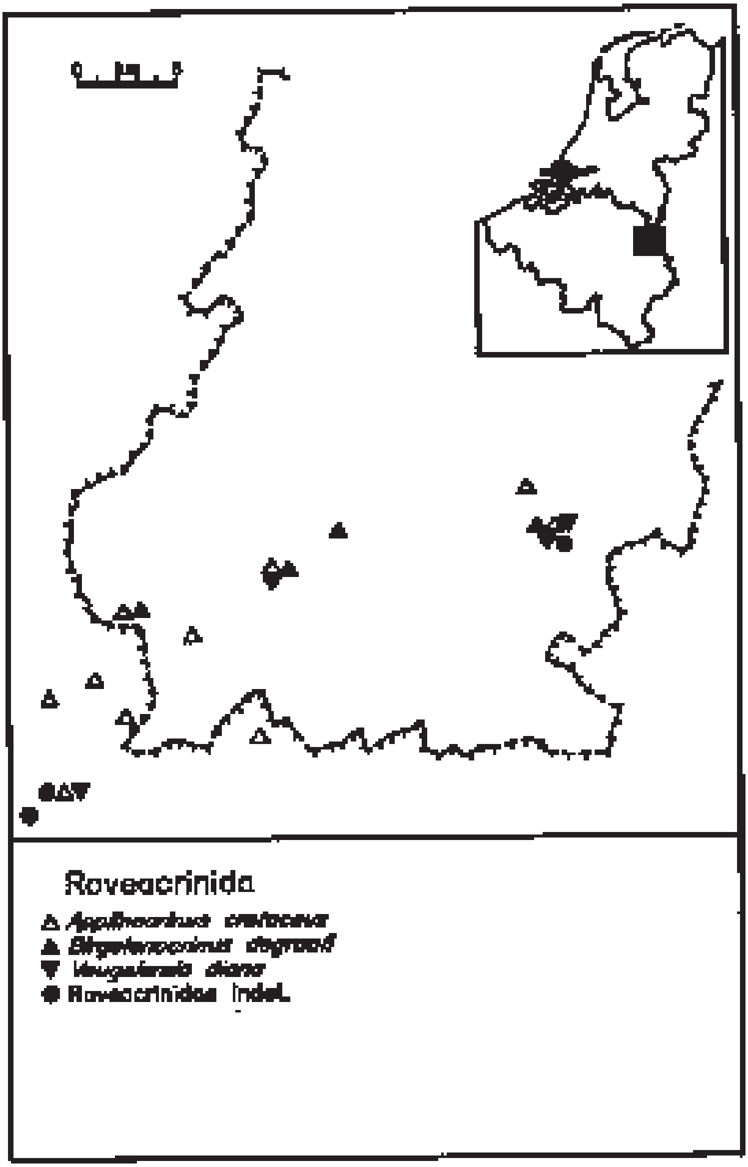

Fig. 42. Geographic distribution of Late Cretaceous roveacrinids and saccocomids in the type area of the Maastrichtian Stage.

Veugelersia diana below). However, so long as no thecae or thecal fragments are known from this member, it is preferred to refer to these ossicles as Roveacrinidae indet. (Fig. 42).

The stratigraphically oldest record in the study area of roveacrinids is a proximal IIBr (?) from the Early Campanian Vaals Formation as exposed at the CPL SA quarry

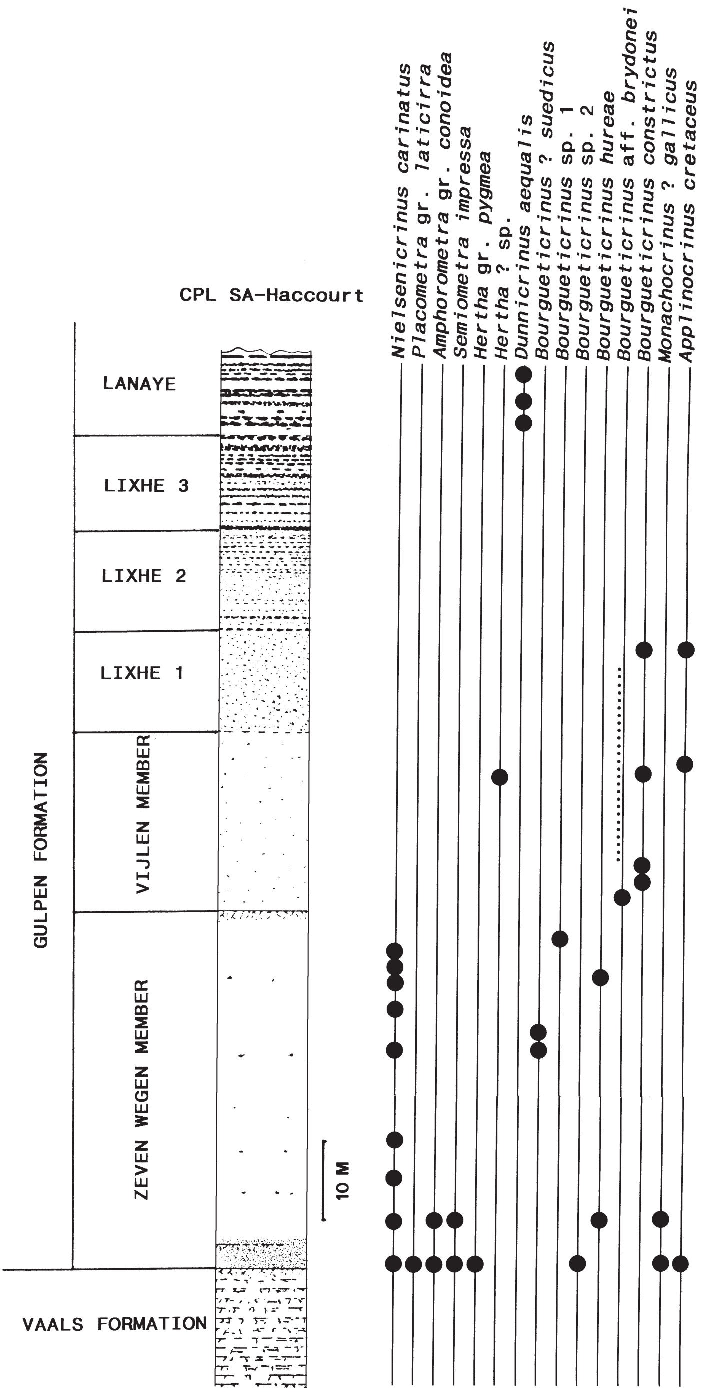

Fig. 43. Lithostratigraphy of section exposed at Ciments Portland Liégeois SA quarry (Haccourt, Liège) and stratigraphic provenance of crinoid material studied herein.

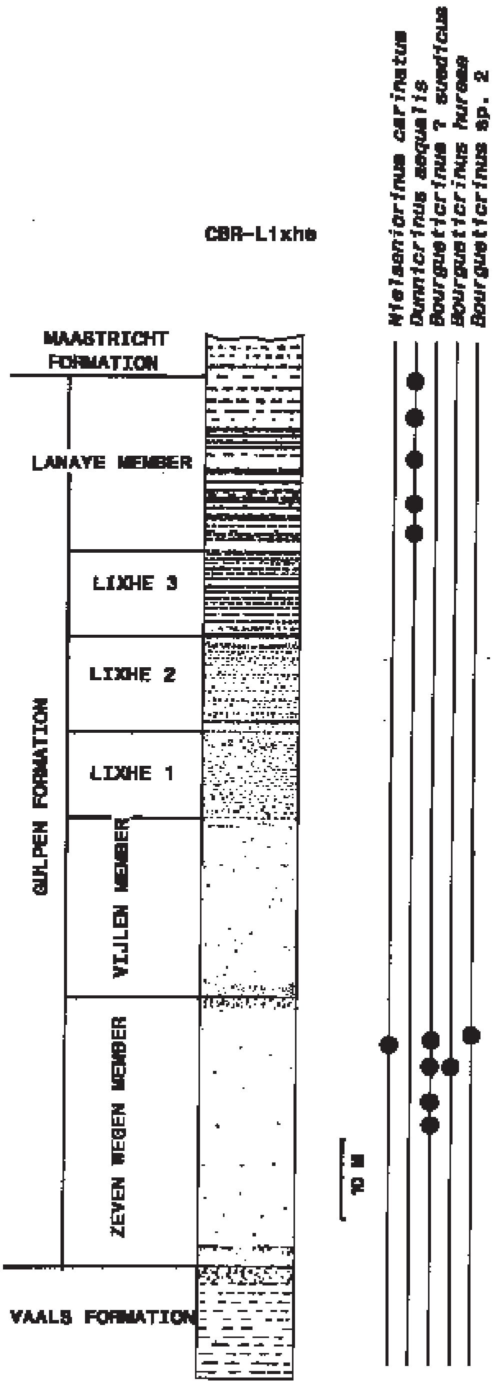

Fig. 44. Lithostratigraphy of section exposed at Cimenterie Briqueterie Réunie-Lixhe quarry (Lixhe, Liège) and stratigraphic provenance of crinoid material studied herein.

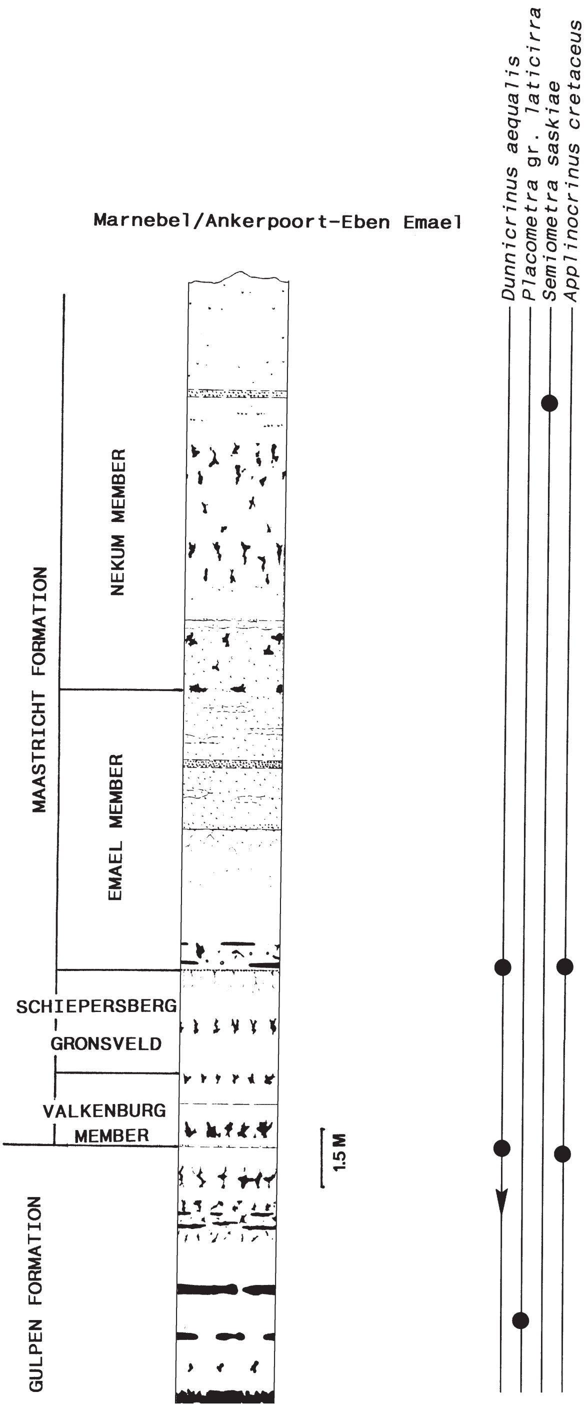

Fig. 45. Lithostratigraphy of section exposed at Ankerpoort-Marnebel quarry complex (Eben Emael, Liège) and stratigraphic provenance of crinoid material studied herein.

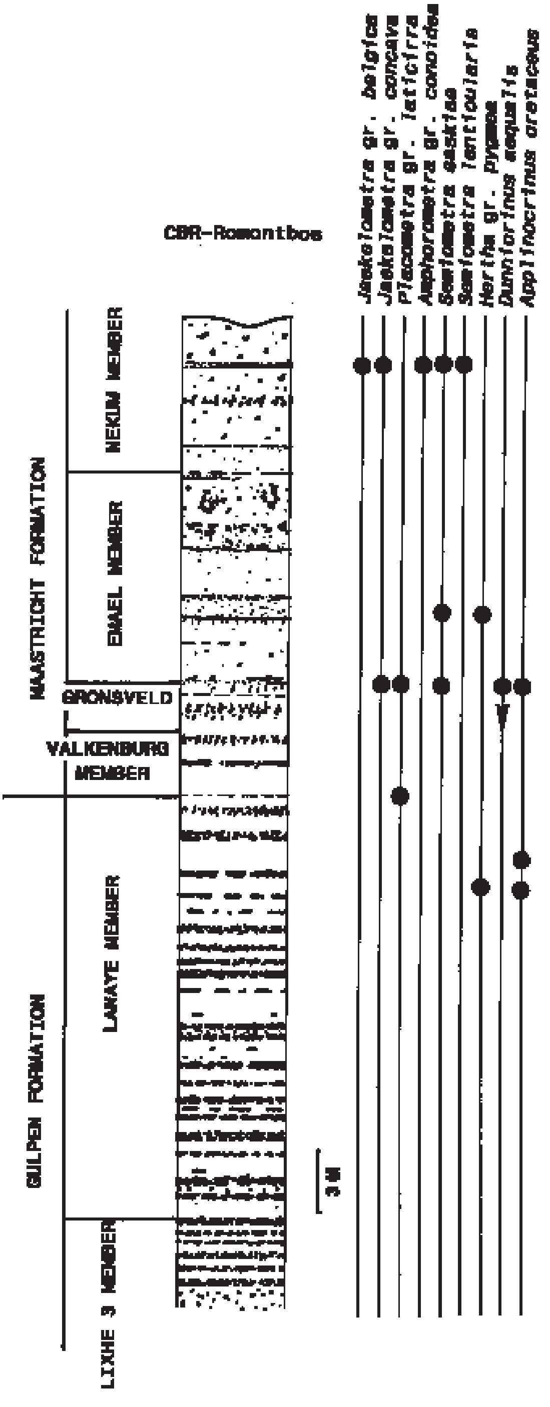

Fig. 46. Lithostratigraphy of section exposed at Cimenterie Briqueterie Réunie-Romontbos quarry (Eben Emael, Liège) and stratigraphic provenance of crinoid material studied herein.

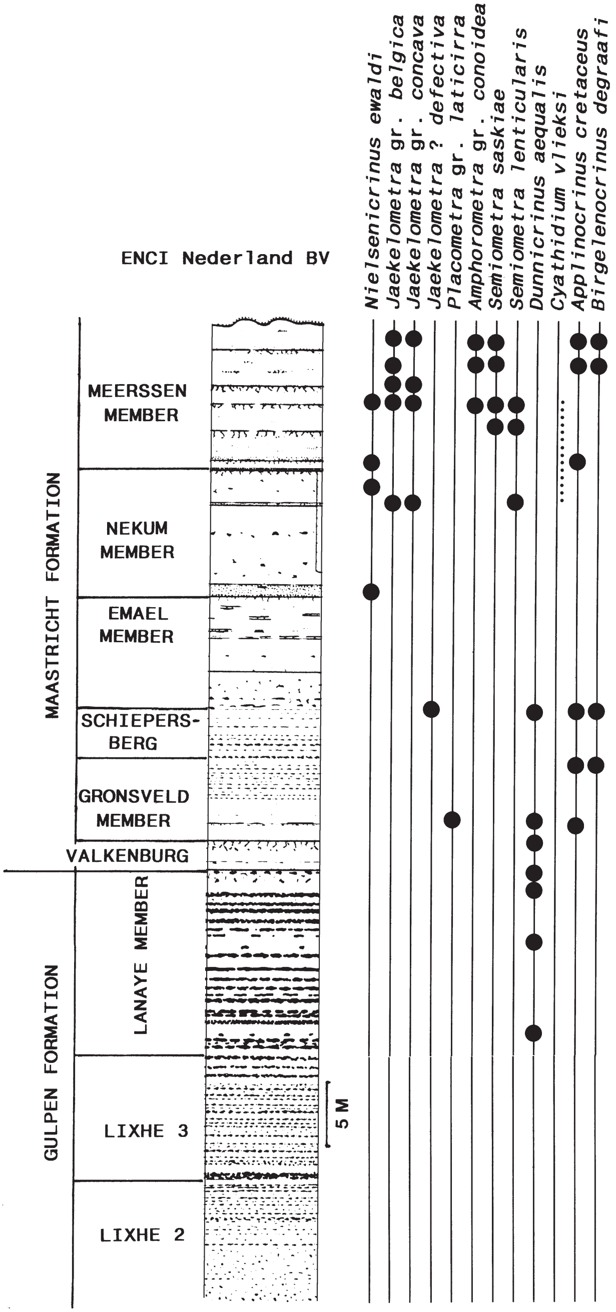

Fig. 47. Lithostratigraphy of section exposed at ENCI-Maastricht BV quarry (Maastricht) and stratigraphic provenance of crinoid material studied herein.

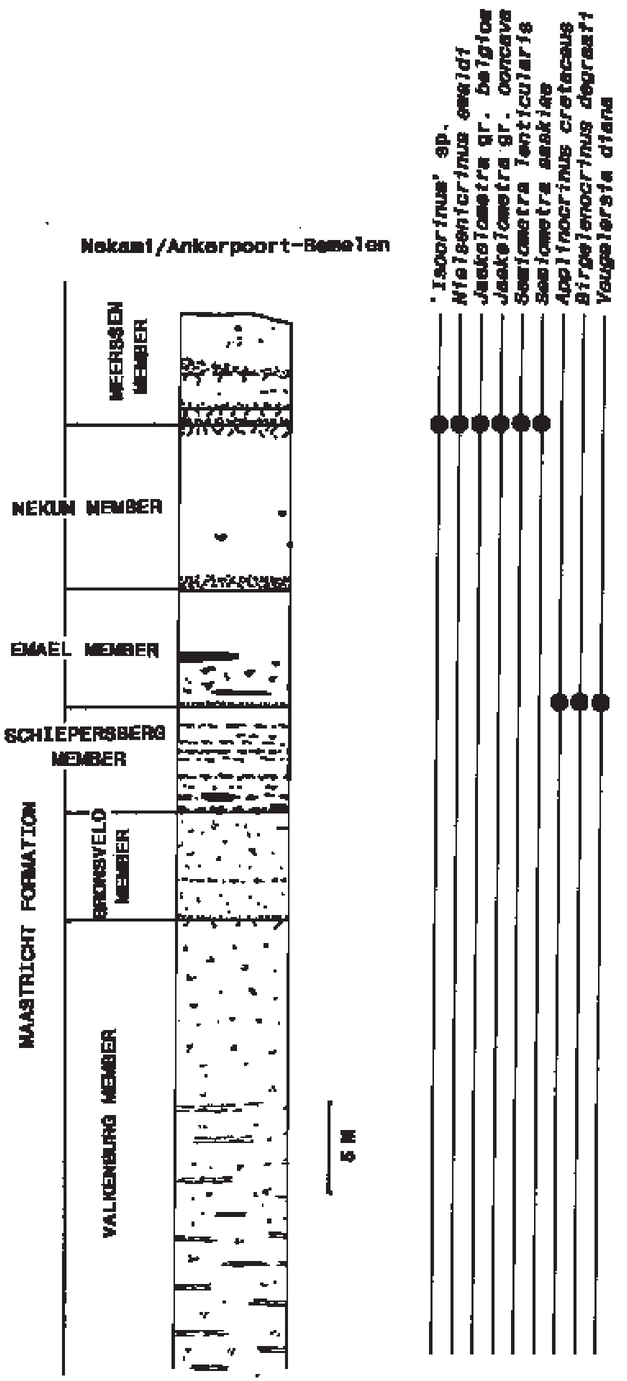

Fig. 48. Lithostratigraphy of section exposed at Ankerpoort-Nekami quarry (Bemelen, Limburg) and stratigraphic provenance of crinoid material studied herein.

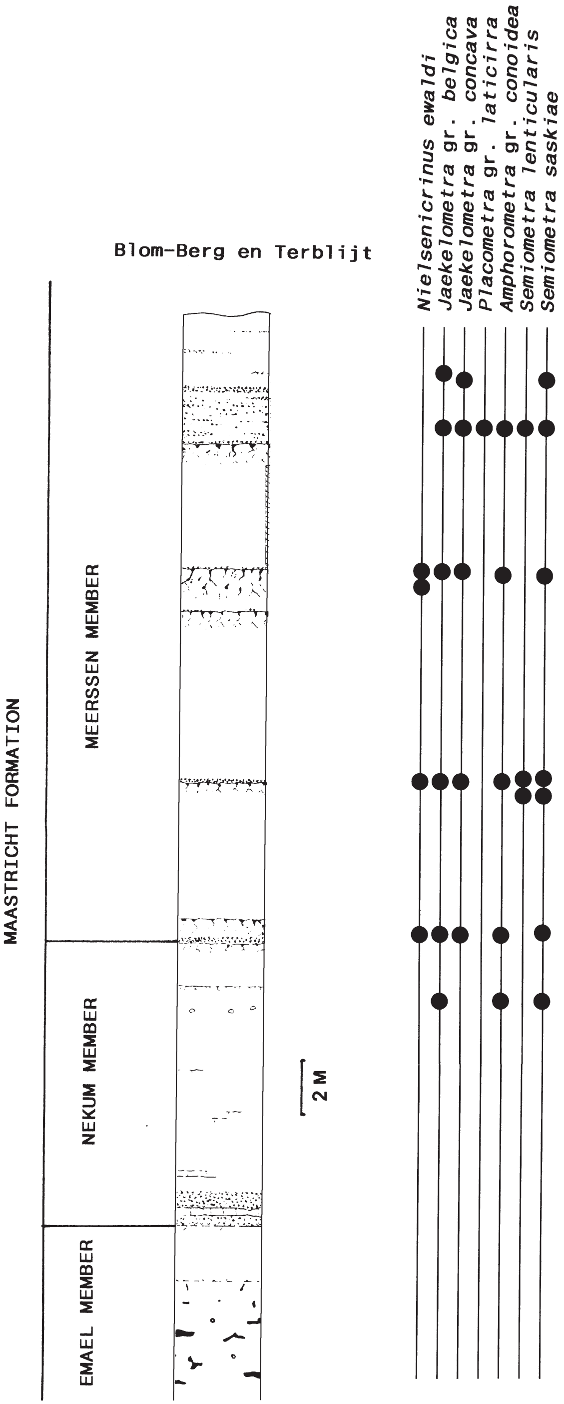

Fig. 49. Lithostratigraphy of section exposed at Blom quarry (Berg en Terblijt, Limburg) and stratigraphic provenance of crinoid material studied herein.

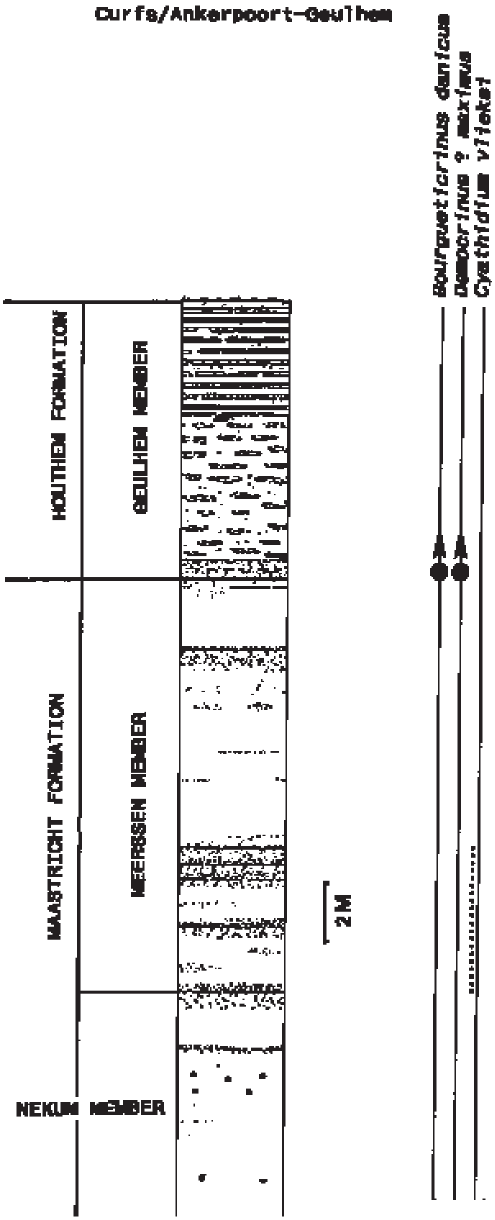

Fig. 50. Lithostratigraphy of section exposed at Ankerpoort-Curfs quarry (Geulhem, Limburg) and stratigraphic provenance of crinoid material studied herein.

(Pl. 42, fig. 2). Similar ossicles are known from the overlying Zeven Wegen Member (Pl. 40, fig. 5; Pl. 41, fig. 10; Pl. 42, fig. 4), where they are associated with IBrr1 (Pl. 40, figs. 6, 9), axillary primibrachials (Pl. 41, figs. 7-8) and more distal (?) secundibrachials (Pl. 41, fig. 9). A rare find, preserving IBr1, IBr2, IIBr1-4 in anatomical connection, is illustrated in Pl. 42, fig. 4. Closely comparable ossicles are known from the Benzenrade Member of correlative age (Pl. 41, figs. 1-6; Pl. 42, fig. 1).

Roveacrinid brachials of a peculiar type (Pl. 42, figs. 3, 5-10) occur sporadically throughout most of the Maastricht Formation and in the Kunrade Limestone facies. These are here interpreted as secundibrachials, but near-absence (only one or two poorly preserved ossicles available) of, in particular, axillary primibrachials precludes reconstruction of brachial arrangement in this taxon, introduced below as a new genus and species.

Genus *Birgelenocrinus* gen. nov.

1992 Roveacrinidae n. gen. (?), n. sp. — Jagt, p. 159, fig. 2g-i.
1995c roveacrinid n. gen. 2 — Jagt, p. 192, figs. 6-7.

Type species — *Birgelenocrinus degraafi* sp. nov., by monotypy.

Derivation of name — Named after Marcel J. van Birgelen (Voerendaal-Ubachsberg), on whose extensive echinoderm collections a considerable portion of the present work is based.

Diagnosis — Roveacrinid with high, broadly conical theca consisting of large elongate radials with prominent interradial, perforate extensions, and well-developed, almost flat articular facets, and of much smaller, but compact exposed basals forming the dorsal end and enclosing a dorsal cavity. Base of body cavity apparently enclosed by (sub)pentagonal basal ring. Many voids along the entire theca. (Secundi)brachials probably belonging here have keeled dorsal surfaces, v-shaped ambulacral grooves, are constricted in the centre and bear prominent flanges.

Birgelenocrinus degraafi gen. et sp. nov.

Pl. 42, figs. 3, 5-10; Pls 43, 44.

1992 Roveacrinidae n. gen. (?), n. sp. — Jagt, p. 159, fig. 2g-i.

Type — Holotype is NHMM MB 506-15i (Pl. 43, figs. 2, 5), paratypes are NHMM MB 506-15g/15h/15j/15k; NHMM JJ 5152a, b, 9543/a, b; and RGM 396 336 (ex Jagt Colln, no. 9335b).

Type locality and horizon — RW 76 motorway outcrops near Benzenrade (southern Limburg, The Netherlands), Maastricht Formation, Kunrade Limestone facies, 2 m below top of section; Late Maastrichtian, *Belemnitella junior* Zone of authors.

Derivation of name — Named after Douwe Th. de Graaf (Natuurhistorisch Museum Maastricht) for support and assistance in every possible way during recent years.

Diagnosis — See genus (monotypy).

Material — Several dozens of thecae and isolated (? secundi)brachials possibly belonging to this species, including NHMM JJ 10503b, 10519, 10847b; NHMM 1997045 (van Birgelen Colln), NHMM MB 95-9b, 506-15, 517-6a.

Description and discussion — The state of preservation of specimens available differs considerably; the best preserved material is from the type locality and type horizon. Thecae are small and high (up to 1.7 mm in height), broadly conical (Pl. 43, figs. 1-3, 5-7; Pl. 44, figs. 1-4) in profile, and (sub)pentagonal in outline with concave interradii and near-straight radii (Pl. 43, figs. 4, 8), and consist of elongate radials and much smaller, exposed and compact basals which form the dorsal pointed end (Pl. 43, figs. 4, 9; Pl. 44, figs. 6-7). Interradial areas show prominent extensions of the thecal distal margin, rising well above the articular facets (Pl. 43, figs. 1-2, 5-6; Pl. 44, figs. 1-3). The extensions consist of an irregular arrangement of longitudinal ridges (the one corresponding to the suture between radial plates being the best developed, Pl. 43, figs. 2, 5; Pl. 44, fig. 3) separated by perforations. The diameter of the thecae across these extensions equals or slightly exceeds that (up to c. 1.2 mm) across the articular facets of the radials (Pl. 43, figs. 1-2, 5-6; Pl. 44, figs. 1, 3). Radial articular facets are well developed, and are almost vertical to sloping slightly outwards, showing a rather narrow, semicircular dorsal ligament pit, deep medially, prominent articular ridge and a large, deep nerve canal of much the same width (Pl. 43, figs. 1-2, 5, 7; Pl. 44, fig. 1). Articular facets are continued as elongate extensions distally, on opposite sides of a deep median notch, carrying prominent, relatively deep elongate interarticular ligament pits and deep ventral muscle pit (Pl. 43, figs. 1-2, 5; Pl. 44, fig. 1). Radial articula are separated by concave interradii processes; characteristically, a spike is developed here along the suture of abutting radial plates, which extends downwards but never fuses with the dorsal extensions of the radials (Pl. 43, figs. 1-2, 5; Pl. 44, fig. 7). In many specimens it appears to fuse, but this is due to recrystallisation (e.g. Pl. 43, figs. 3, 6). Extending from the distal margin of the articular facet of the radials are two prominent longitudinal ridges of variable width which enclose a keyhole-shaped void in the theca (Pl. 43, figs. 1-2, 6, 8; Pl. 44, fig. 7). These appear to fuse into a ring at the bottom of the body cavity with the interradii, which are characterised by two smaller teardrop-shaped voids separated by a longitudinal ridge (Pl. 43, figs. 2, 4-5, 8). Here the basals appear to join in, marking a dorsal cavity of variable diameter (Pl. 43, figs. 1-2, 6-7; Pl. 44, figs. 1-5, 7). In well-preserved specimens (Pl. 43, figs. 1-2, 5, 7; Pl. 44, figs. 1, 5, 7) it is extremely difficult to determine where the basal plates start, but specimens having undergone recrystallisation (Pl. 43, figs. 4, 9; Pl. 44, fig. 6) present fewer problems. Basals are compact, elongate triangular ossicles, separated by distinct sutures (Pl. 43, fig. 9; Pl. 44, fig. 6), and forming the dorsal pointed end of the theca, which occasionally resembles a central plate (Pl. 43, fig. 9; Pl. 44, fig. 6). The entire theca shows many slit-like and keyhole-shaped voids (Pl. 43, figs. 1-2, 5, 8; Pl. 44, figs. 5, 7).

As noted above, associated brachials which are here considered to probably belong to the present species comprise only very few, and poorly preserved axillary primibrachials, but many more secundibrachials. These are extremely flattened (Pl. 42, figs. 7-10), have keeled and centrally constricted dorsal surfaces (Pl. 42, figs. 5-6, 8), prominent v-shaped ambulacral grooves (Pl. 42, figs. 7-10) bordered by prominent flanges towards both the distal and proximal articula (Pl. 42, figs. 3, 5-10). Articular facets are muscular (Pl. 42, fig. 8), dorsal ligament pits being elongate-triangular, and ventral muscle pits deep and transversely oval. Villain (1977, fig. 15: 'spicule «en forme de cheval», d'origine échinodermique (?)') illustrated an isolated brachial of this species. Some of these ossicles superficially resemble saccocomid brachs as illustrated by Manni & Nicosia (1984).

The above suite of characters serves to distinguish the new genus from all other roveacrinids known to date (see also next species).

Occurrence — Together with the saccocomid *Applinocrinus cretaceus* (see above), this species extends to the top of the Meerssen Member (IVf-5/6) to slightly below the K/T boundary, and thus is the youngest roveacrinid known to date. Current records include the Schiepersberg, Emael and Meerssen members (Maastricht Formation) of various outcrops and quarries in southern Limburg (Figs. 42, 47-48).

Genus *Veugelersia* gen. nov.

1992 Roveacrinidae n. gen., n. sp. — Jagt, p. 159, fig. 2m.
1995c roveacrinid n. gen. 1 — Jagt, p. 192, figs. 6-7.

Diagnosis — Roveacrinid with broadly conical theca, bearing prominent interradial flanges united into a stellate base, and with high, distally rounded and perforate interradial extensions, rising well above radial articular facets. Facets oblique with distal flange-like continuation. Bottom of body cavity apparently formed by stellate basal ring from which the interradial flanges proceed. Associated brachials include axillary primibrachials and highly ornamented, spiny secundibrachials of porous structure.

Type species — *Veugelersia diana* sp. nov., by monotypy.

Derivation of name — Named after my former secondary school teacher Sef Veugelers (deceased), for introducing me to palaeontology many years ago.

Description and discussion — On account of its highly distinctive thecal structure, none of the other roveacrinid genera and species known to date (e.g. Sieverts-Doreck, 1933a, b; Peck, 1943, 1955; Rasmussen, 1971; Scott et al., 1977; Destombes, 1984; Gasse & Werkmann-Hügel, 1985; Schneider, 1987, 1988, 1989a, b, 1995) are likely to be confused with the present genus. There is a superficial similarity to a number of representatives of the genus *Roveacrinus* Douglas, 1908 (p. 358, pl. 17), e.g. *R. carinatus* Nekvasilová & Prokop, 1963 (pl. 1, figs. 1, 3).

Veugelersia diana gen. et sp. nov.
Pl. 40, fig. 10?; Pls 45-46.

Type — Holotype is NHMM MB 517-1a (Pl. 45, figs. 1-2); paratypes are NHMM MB 517-1b, 619-9a, b, 865-17a/c, and 865-25a/c.

Type locality and horizon — Ankerpoort-Nekami quarry, Bemelen (southern Limburg, The Netherlands), Maastricht Formation, base Emael Member; Late Maastrichtian, *Belemnitella junior* Zone of authors.

Derivation of name — Lat. Diana = goddess of the hunt, with reference to Manfred Jäger, who entrusted roveacrinid thecae to me for description, many years ago.

Diagnosis — See genus (monotypy).

Material — Some thirty thecae and many dissociated primi- and secundibrachials, possibly belonging to this species, including NITG/TNO Vergoossen Colln, no. 11430; NHMM MB 517-6b, 865-17, 865-25.

Description and discussion — Material before me differs considerably in preservation and size, specimens from the glauconitic-sandy Benzenrade Member being larger and generally lacking the basal ring and interradial processes (Pl. 45, figs. 7-8; Pl. 46, figs. 1-5).

Complete thecae are small (up to 2.7 mm in height), broadly conical in profile and have prominent interradial flanges which are united into a stellate base as outgrowths of basals (Pl. 45, figs. 1-6). Thecae are (sub)pentagonal in outline with concave interradii and low-triangular radii with prominent spines (Pl. 46, figs. 1-5). Tall, distally rounded and perforate interradial extensions rise well above the articular facets of the radials (Pl. 45, figs. 1-2), but are broken off in most specimens. Articular facets of radials are oblique, details of which are hidden in the holotype, but other specimens (Pl. 46, fig. 2) show it to have a medially deep semicircular dorsal ligament pit, prominent articular ridge and a large, deep nerve canal. Interarticular ligament pits and ventral muscle pits are apparently shallow and small. Radials have triangular spine or flange-like continuations dorsally (Pl. 45, figs. 1-3; Pl. 46, figs. 1-4). To the left and right of these two additional obliquely placed ‘spines’ are seen in the material from the Benzenrade Member (Pl. 45, figs. 6-8; Pl. 46, figs. 1-5), but lacking in specimens from the Emael Member (Pl. 45, figs. 1-3). The radials continue as two extensions diverging slightly distally (Pl. 46, fig. 4) and running obliquely towards body cavity. These radial extensions are separated by voids on all sides (Pl. 46, fig. 4). Where they are broken off (Pl. 46, figs. 2-3) a star-shaped opening is visible, and where they meet interradially they are thickened (Pl. 46, fig. 3). The bottom of body cavity is apparently formed by the stellate basal ring (Pl. 45, fig. 7; Pl. 46, figs. 1, 4-5) from which the interradial flanges proceed. Illustrated specimens (Pl. 45, fig. 7; Pl. 46, figs. 1-5) demonstrate various states of preservation and show the basals to be comparatively stout polygonal ossicles separated by obvious sutures (Pl. 46, fig. 1). The structure and size of the flanges that proceed from the basal plates vary, but invariably meet distally to form a prominent stellate distal end of the theca (Pl. 45, figs. 1-6). Associated brachials include axillary primibrachials and highly ornamented, spiny secundibrachials of porous structure.

Despite small differences in structure of radials and interradial flanges, specimens from the Upper Maastrichtian Emael Member and the Upper Campanian Benzenrade Member are considered conspecific, at least for the time being. Currently only two complete theca are known from the former member, in which the distal end of the radials and the structure of the basal ring cannot be seen satisfactorily. In view of their extreme rarity it was decided not to damage them to reveal these features. However, material from both localities and units seems to lack a dorsal cavity of the type that is seen in many other roveacrinid taxa. Radials do not continue into a dorsally pointed end, thus concealing the basals to varying extent, as in many other roveacrinids.

Occurrence — Known to date from two stratigraphically highly disjunct occurrences, one in the Benzenrade Member (Vaals Formation, Late Campanian) as exposed in the Benzenrade area (including de Wingerd quarry) and possibly Zeven

Wegen Member of Liège (CPL SA quarry), and the other in the Emael Member (Late Maastrichtian) of Bemelen (Ankerpoort-Nekami quarry) (Figs. 42, 48).

Acknowledgements

I wish to thank the following people and companies for donation or loan of material, for preparation of scanning electron micrographs, photographs and line drawings, for allowing access to quarries and/or outcrops, for supply of literature, for constructive comments on earlier versions of the typescript, and for any other help received, in alphabetical order: Ankerpoort NV (Maastricht, NL), L. Arpot (Ulestraten, NL), F. Bergsteyn (Geulhem, NL), M.J. van Birgelen (Voerendaal-Ubachsberg, NL), Dr M.J.M. Bless (Gulpen, NL), M. Blom (Berg en Terblijt, NL), Professor G.J. Boekschoten (Vrije Universiteit, Amsterdam), H.L. Bongaerts (Posterholt, NL), Professor W.K. Christensen (Geologisk Museum, København, DK), E. Croimans (Maaseik, B), M.J.M. Deckers (Tegelen, NL), Dr A.V. Dhondt (Institut royal des Sciences naturelles de Belgique, Bruxelles), Professor S.K. Donovan (Natural History Museum, London), R.W. Dortangs (Amstenrade, NL), Professor F.R. Ettensohn (University of Kentucky, USA), D. Eysermans (Vosselaar, B), P.J. Felder (Cadier en Keer, NL), W.M. Felder (Vijlen, NL), Dr B. Ferré (Université P. & M. Curie, Paris), Dr R.H.B. Fraaye (Geo Centrum Brabant, Boxtel, NL), Professor A.S. Gale (University of Greenwich, Chatham, UK), D.Th. de Graaf (Natuurhistorisch Museum Maastricht), Dr H. Hagdorn (Muschelkalkmuseum, Ingelfingen, D), Dr R.W.J.M. van der Ham (Delft, NL), Dr T. Heinzeller (Ludwig-Maximilians-Universität, München), Dr H. Hess (Binningen, CH), K. Hoedemakers (Mortsel, B), L. Indeherberge (Zonhoven, B), Dr M. Jäger (Rohrbach Zement, Dotternhausen, D), S.L. Jakobsen (Geologisk Museum, København, DK), A.W. Janssen (Gozo, Malta, formerly Nationaal Natuurhistorisch Museum, Leiden), Dr A.H. Kamb (deceased), S.M. Kars (Vrije Universiteit, Amsterdam), P.H. Kessels (Linne, NL), Dr N. Keutgen (Aachen, D), C.R. Kjaer (Aarhus, DK), Dr V.G. Klikushin (St Petersburg, Russia), P.H.M. van Knippenberg (Kessel, NL), I. Krause (Wennigsen-Bredenbeck, D), M. Kutscher (Sassnitz-Lancken, D), M.M.M. Kuypers (Ittervoort, NL), Dr J.M. Lawrence (University of South Florida, USA), D.N. Lewis (Natural History Museum, London), R. Malherbe (Nationaal Natuurhistorisch Museum, Leiden), K. Mattelé (Bochum, D), Dr C.G. Messing (Nova University, Dania, USA), R. Meuris (Beerzel, B), G. Michels (Venlo, NL), W. Miseur (Institut royal des Sciences naturelles de Belgique, Bruxelles), R. van Neer (Sittard, NL), Dr U. Nicosia (Università degli Studi di Roma), Dr T. Oji (University of Tokyo), Dr C.R.C. Paul (University of Liverpool, UK), Dr D.L. Pawson (National Museum of Natural History, Smithsonian Institution, Washington DC), J.H.G. Peeters (Natuurhistorisch Museum Maastricht), R. Pieters (Geel, B), P. Pletzers (ENCI-Maastricht BV, Maastricht), S. Prins (Hoensbroek, NL), Dr U. Radwanska (Uniwersytet Warszawski, PL), I. Regtien (Nationaal Natuurhistorisch Museum, Leiden), E. Reijnaers (Roosendaal, NL), J.P.H. Reynders (Houthalen-Helchteren, B), Dr W. Riegraf (Münster, D), Professor M. Roux (Université de Reims, F), Dr P.M. Sander (Rheinische Friedrich-Wilhelms Universität, Bonn, D), Dr H.L. Schneider (Düsseldorf-Oberkassel, D), J. Severijns (Maastricht, NL), Dr M.J. Simms (Ulster Museum, Belfast), Dr E. Simon (Bruxelles), Dr A.B. Smith (Natural History Museum, London), J.W.M. Thompson (National Museum of Natural

History, Smithsonian Institution, Washington DC, USA), H. Vlieks (deceased), C. Vlieks-Rademakers and I. Schols-Vlieks (Simpelveld-Molsberg, NL), Professor E. Voigt (Geologisch-paläontologisches Institut, Universität Hamburg), H. van Weele (ENCI-Maastricht BV, Maastricht), F.P. Wesselingh (Nationaal Natuurhistorisch Museum, Leiden), Dr C. Winkler Prins (Nationaal Natuurhistorisch Museum, Leiden), and G.L. Wingard (US Geological Survey, Reston, USA).

This research was supported (in part) by the Geosciences Foundation (GOA) with financial aid from the Netherlands Organisation for Scientific Research (NWO). This is contribution No. 6 of the 'Vijlen Werkgroep'.

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[For additional references see also Part 1 of the current series]

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Manuscript received 9 May 1997.