

The youngest pelagic crinoids (latest Maastrichtian, the Netherlands)

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The roveacrinid *Birgelenocrinus degraafi* Jagt, 1999b, the youngest pelagic crinoid known to date, appears to be confined to the Maastricht Formation in the southeast Netherlands, ranging from the Kunrade Limestone facies (ecozone V, lower part) to within two metres below the K/T boundary (= Meerssen Member, top subunit IVf-6, 'tuffaceous' biocalcarenic facies). Its disjunct distribution within this formation, *i.e.* occurring directly above omission surfaces or hardgrounds, suggests this is linked to local sea-level changes, which produced optimum feeding habitats. The morphology of theca and brachials show this species to have been truly pelagic; the collapse of the planktonic food chain at the end of the Cretaceous would explain the demise of this and other roveacrinids.

Key words: Crinoids, Maastrichtian, the Netherlands, palaeobiology.

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The most recent account of crinoid faunas from the type Maastrichtian (Jagt 1999b) recorded at least fourteen species from the Maastricht Formation. In the lower part of this unit (Valkenburg and Gronsvelt members; Fig. 1), the bourgueticrinid *Dunnocrinus aequalis* dominates assemblages, while comatulids, particularly species of *Amphorometra*, *Jaekelometra* (see also Messing 2003) and *Semiometra*, are commonest in the upper part (Emael, Nekum and Meerssen members). Isocrinids, holopodids, saccocomids and roveacrinids are rare, the latter group being represented by just two species, *Birgelenocrinus degraafi* and *Veugelersia diana* Jagt, 1999b. The last-named taxon does not appear to range higher than the base of the Emael Member.

The type material of *B. degraafi* (Fig. 2) is from 2 m below the top of the section exposed along motorway RW 76 near Benzenrade (Kunrade, southern Limburg, the Netherlands). This occurrence is within ecozone V of Felder & Bless (1989), the top of which equates with the base of the Emael Member in the Maastricht area (ENCI-HeidelbergCement Group quarry). To date, there are records of *B. degraafi* from the basal portions of the Schiepersberg and Emael members, and from various levels within the Meerssen Member (Fig. 1), from where several dozens of

thecae are now known. Thus, its distribution is disjunct; in addition, where the species is encountered, it usually occurs fairly commonly, including brachials. Puzzling is the near-absence of (axillary) primibrachials; the few ossicles that are available are fragmentary and generally poorly preserved. Secundi-brachials are much commoner, despite their fragility, and several hundreds of specimens have been collected. Whether or not this might be a function of selective cropping is difficult to determine.

Birgelenocrinus degraafi is thus an endemic species with a short range. Following Vonhof & Smit (1996), who on the basis of strontium isotope values estimated the depositional rate in the upper Maastricht Formation to have been *c.* 10 cm/ka, this yields a range of less than 400,000 years. The coleoid *Belemnella* gr. *junior* ranges throughout the Maastricht Formation; co-occurring with this in the upper third of the Meerssen Member is *Belemnella* (*Neobelemnella*) gr. *kazimiroviensis*, demonstrating the latest Maastrichtian age of this portion of the sequence (Christensen 1997a, b; see also Brinkhuis & Schiøler 1996).

Material described and illustrated is contained in the collections of the Natuurhistorisch Museum Maastricht (NHMM).

Maastricht Formation	Meerssen Member	+	
	Nekum Member		
	Emael Member	+	late Maastrichtian
	Schiepersberg Member	+	
	Gronsveld Member		
Gulpen Formation	Valkenburg Member		
	Lanaye Member		
	Lixhe 1-3 members		late Maastrichtian
	Vijlen Member, units 4-6		
	Vijlen Member, units 0-3		early Maastrichtian
	Beutenaken Member		late Campanian
	Zeven Wegen Member		

Fig. 1. Lithostratigraphic terminology of Campanian–Maastrichtian strata in the extended type area of the Maastrichtian Stage (southern Limburg, the Netherlands and contiguous areas; after Jagt 1999a), and indication of provenance (+) of *Birgelenocrinus degraafi* Jagt, 1999b.

Brief description

The best preserved material of *Birgelenocrinus degraafi* is from ecozone V of the Kunrade Limestone facies as exposed along motorway RW 76 near Benzenrade (Kunrade area). Thecae (Fig. 2) are small, yet tall (height to 1.7 mm), broadly conical in profile and (sub)pentagonal in outline. Interradii are concave, radii near-straight; thecae consist of elongate radials and much smaller, compact and exposed basals, forming a dorsal pointed end (Fig. 2C–D). Interradial areas show prominent extensions of the thecal margin, rising well above the articular facets, perforations separating the extensions consisting of an irregular arrangement of longitudinal ridges; the ridges corresponding to the sutures between radial plates are the best developed. The diameter of the thecae across these extensions equals or slightly exceeds that (to c. 1.2 mm) across the articular facets of the radials. Radial articular facets are well developed (Fig. 2A, D) and are almost vertical to sloping slightly outwards, showing a rather narrow, semicircular dorsal ligament pit that is deep medially, a prominent articular ridge and a large, deep nerve canal of much the same width. Distally, articular facets continue as elongate extensions, on opposite sides of a deep median notch, carrying prominent, relatively deep elongate interarticular ligament pits and a deep ventral muscle pit. Radial articular facets 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 (Fig. 2C–D). In many specimens, this spike appears to fuse, but this is due to recrystallisation. Extending from the distal margin of the radial articular facets are two prominent longitudinal ridges of variable width (Fig. 2C–D) which enclose a keyhole-shaped void in the theca. 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. Here the basals appear to join in, marking a dorsal cavity of variable diameter. In well-preserved specimens, it is extremely difficult to determine where the basal plates start, but specimens having undergone recrystallisation (Fig. 2B) present fewer problems. Basals are compact, elongate triangular ossicles, separated by distinct sutures and forming the dorsal pointed end of the theca, which resembles a central plate in some specimens (Fig. 2B–C). The entire theca shows many slit-like and key-hole shaped voids.

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Fig. 2. Thecae of *Birgelenocrinus degraafi* Jagt, 1999b, all (except specimen B, which is from the basal Emael Member (Maastricht Formation) at the ENCI-HeidelbergCement Group quarry, Maastricht) from the RW 76 motorway exposures near Benzenrade (Kunrade, southern Limburg); Maastricht Formation, Kunrade Limestone facies; A. NHMM MB 506-15j (paratype), × 65; B. NHMM JJ 9543 (paratype), × 100; C, D. NHMM MB 506-15i (holotype), × 120 and × 85, respectively; E. NHMM MB 506-15h (paratype), × 65.

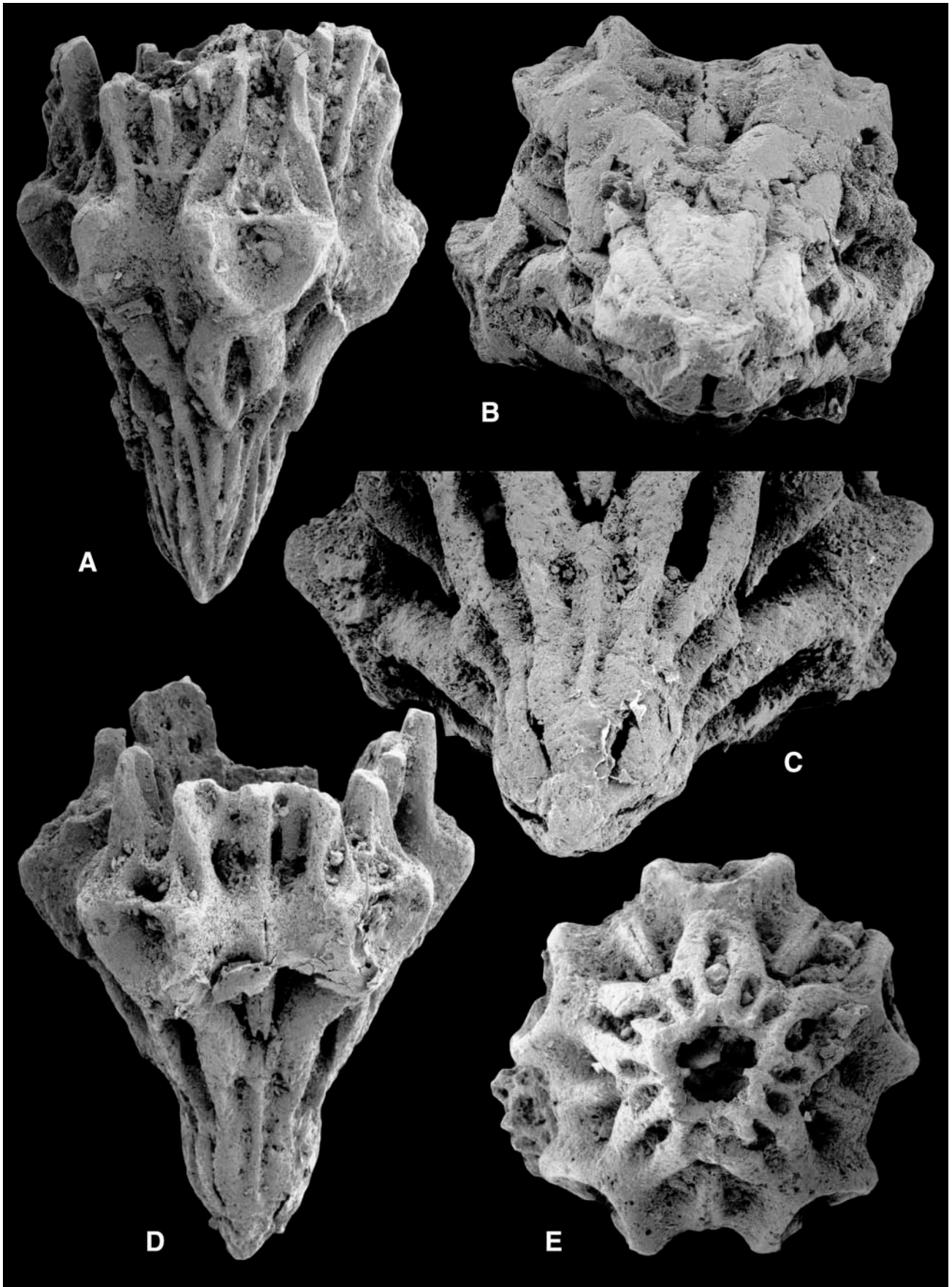




Fig. 3. Secundibrachials of *Birgelenocrinus degraafti* Jagt, 1999b, all from the RW 76 motorway exposures near Benzenrade (Kunrade, southern Limburg); Maastricht Formation, Kunrade Limestone facies; A. NHMM MB 506-15a, $\times 100$; B. NHMM MB 506-15c, $\times 95$; C. NHMM MB 506-15d, $\times 120$; D. NHMM MB 506-15e, $\times 100$.

Associated brachials comprise only very few, and poorly preserved, (axillary) primibrachials, but many more secundibrachials (Fig. 3). These are extremely flattened, have keeled and centrally constricted dorsal surfaces, prominent V-shaped ambulacral grooves bordered by prominent flanges towards both distal and proximal articular facets. Articular facets are muscular, dorsal ligament pits being elongate-triangular, and ventral muscle pits deep and transversely oval. Pinnular facets are small and rather inconspicuous.

Discussion

Morphological features of theca and brachials serve to distinguish the genus *Birgelenocrinus* from other members of the Roveacrinidae (see e.g. Peck 1943, 1955; Rasmussen 1961, 1971; Scott *et al.* 1977; Schneider 1987, 1989, 1995). The current classification of the Roveacrinida (Rasmussen 1978) is considered unsatisfactory, the order at present containing three families, Somphocrinidae, Saccocomidae and Roveacrinidae; it appears necessary to add a fourth (Table 1). Simms *et al.* (1993) noted that it is far from clear how these families are interrelated and what are their relationships to other articulate crinoids (see also Hess 2002). The family Roveacrinidae is fairly species-rich and ranges from the early Hauterivian (Ferré & Granier 1997) to the latest Maastrichtian.

As noted by Schneider (1987), although little is yet known about the function of the dorsal cavity in roveacrinids, this feature might be of great importance in determining ontogenetic patterns and phylogenetic relationships. Only in a handful of species are details regarding the formation of basals and radials known to date. Subsequently, Schneider (1989) demonstrated that in *Roveacrinus geinitzi* (upper Cenomanian, eastern Germany) the ventral (body) cavity reached its final size early in ontogeny; in contrast, the dorsal cavity was later modified, thus suggesting this to have had a function. Schneider noted that it is feasible that between these cavities there occurred gaseous exchange. To counter the weight increase of a growing crinoid, a larger reservoir for gases and fluids, whose intrinsic weight would be less than that of sea water, appears plausible. The dorsal cavity could thus have functioned as a hydrostatic organ, enabling the animal, by gas and/or fluid exchange, to move vertically using comparatively little muscle exertion. In this way, pelagic crinoids might ascend and/or descend so as to select sites where food availability and/or currents were optimal.

Additional skeletal details in the theca were sub-

Table 1. Current systematics of the order Roveacrinida (Rasmussen 1961, 1978; Simms *et al.* 1993; Hess and co-workers, research in progress).

Roveacrinidae
<i>Birgelenocrinus</i> Jagt, 1999b
<i>Discocrinus</i> Peck, 1943
<i>Hyalocrinus</i> Destombes, 1984
<i>Orthogonocrinus</i> Peck, 1943
<i>Poecilocrinus</i> Peck, 1943
<i>Plotocrinus</i> Peck, 1943
<i>Roveacrinus</i> Douglas, 1908 (= <i>Drepanocrinus</i> Jaekel, 1918)
<i>Roveacrinoides</i> Rasmussen, 1971
<i>Styracocrinus</i> Peck, 1943
<i>Veugelersia</i> Jagt, 1999b
Saccocomidae
<i>Applinocrinus</i> Peck, 1973
<i>Crassicoma</i> Sieverts-Doreck & Hess <i>in</i> Hess (2002)
<i>Saccocoma</i> Agassiz, 1836
Somphocrinidae
<i>Ossicrinus</i> Kristan-Tollmann, 1970
<i>Osteocrinus</i> Kristan-Tollmann, 1970 (= <i>Poculicrinus</i> Mostler, 1973)
<i>Somphocrinus</i> Peck, 1948 (= <i>Vasculicrinus</i> Donofrio & Mostler, 1975)
New family (Hess <i>in</i> Hess and co-workers, research in progress)
<i>Axicrinus</i> Kristan-Tollmann, 1977

sequently noted by Schneider (1995), who discovered diminutive axial dorsal canals in *Roveacrinus communis* (lowermost Turonian, northwest Germany), traceable into the dorsal cavity and used for gaseous exchange, thus allowing changes in position within the water column. Gaseous exchange through interradi- al voids also is conceivable; Schneider (1995) wondered what the function of lateral openings might have been. Perhaps, during life, a membrane sealed off these voids which, in conjunction with the hydrostatic organ, could have regulated gas pressure through balloon-like extensions or contractions.

Milsom (1994, 1999) noted that a pelagic mode of life has been postulated for members of the order Roveacrinida on account of small thecal size, absence of anchoring device and wide geographic distribution. She distinguished three ways in which these crinoids could have achieved this; passively through weight reduction of skeletal ossicles and construction of a buoyancy aid; actively by swimming to maintain lift or, possibly, through attachment to floating material. Based on analyses of functional morphology, Milsom (1999) opined that roveacrinids exploited two lifestyles, either benthic (coupled with ability to swim) or nektic. Forms living in or on the sea floor characteristically have flanges and spines on the theca and proximal brachials, and show limited arm mobility. Nektic species, on the other hand, have an enlarged dorsal cavity, extreme arm mobili-

ty and show little or no ornament, as well as evidence for lightening of the skeleton. Milsom (1999) also proposed that the crinoid sank passively through the water column during feeding. Stability of the animal during this process was dependent of arm length, which also determined the dimensions of the mucuous net used in feeding. Milsom was of the opinion that roveacrinids opted for increased stability at the expense of feeding net size.

It should be borne in mind that the above assumptions should be tested on more or less completely preserved roveacrinids. Unfortunately, such specimens are exceedingly rare. Ferré & Bengtson (1997) described, but failed to illustrate, an articulated individual of *Roveacrinus spinosus* from the upper Turonian of Sergipe, Brazil. They noted that overall shape is reminiscent of comatulids, but arms are more incurved, with raised arms forming a basket-like feeding net, reinforced by pinnular extensions. These authors indicated that a pelagic mode of life for this form could be excluded, on the basis of taphonomic setting of this find, the morphology of the arms and the brachial articulation with the theca. Adults must have been able to swim actively, albeit for a short period, to search for food or escape from predators. Ferré & Bengtson (1997) also considered that the ratio between ventral and dorsal cavities may be a possible bathymetric indicator, thus following Schneider (1995).

There are several abundance horizons (acmes) in roveacrinid distribution (Ferré *et al.* 1997, in press) in Brazil and southern England (in their example), linked to acmes in ostracod and foraminiferal ranges, and apparently related to sea level changes. These authors suggested that roveacrinids may have thrived in hypoxic conditions, commonly leading to the generation of opportunistic populations, feeding on calcisphere blooms.

Recently, Hess (2002) noted that the Jurassic saccocomid genus *Saccocoma* comprises pelagic forms which fed while actively moving through the water column, and which have light skeletons and floating devices. Hess remarked that saccocomids share with other Roveacrinida the sloping cryptosynarthries between primibrachials 1–2 and secundibrachials 1–2. This type of cryptosynarthry appears typical of small or very lightly built, partially or fully pelagic crinoids and must thus have had a special function. The comparatively large surface of sloping articular faces may have stabilised the proximalmost arm portions, protecting the cup with the exposed soft parts.

Although studies on roveacrinid phylogeny, palaeobiology and palaeobiogeography are still limited in scope and extent, the data above clearly show promising results. More data are needed, in particu-

lar on ontogeny, and more taxa should be examined following the work of Schneider (1987, 1989, 1995). In addition, the few more or less complete specimens that are available should be described in detail. For *Birgelenocrinus degraafi*, the lack of well-preserved primibrachials is unfortunate. However, thecal structure and features of secundibrachials show this to be have been a truly pelagic form, with the voids in the theca probably used for gaseous exchange (in compensation of a relatively small dorsal cavity?) and prominent flanges on secundibrachials. This species is perhaps best considered a K-strategist (equilibrium species), since it occurs near the end of a radiation, is specialised to an ecological niche and highly vulnerable to new crises. Further, it is relatively restricted (revealing a trend towards endemism) and shows low variability of morphological characters.

Birgelenocrinus degraafi appears confined to levels directly overlying omission surfaces and/or hardgrounds, where it is comparatively common and with thecae associated with brachials, suggesting very limited *post mortem* transport. This may indicate that the species exploited food-rich niches generated by local sea level fluctuations. Strata directly overlying hardgrounds in the area are particularly fossiliferous, and hardground surfaces (plus associated crustacean burrows) often are covered in cheilostome bryozoan colonies, thecideid and craniid brachiopods and verrucid cirripedes. The base of the following sedimentary cycle yields abundant benthic faunas of foraminifera, ostracods, bryozoans, echinoderms and even more numerous microfaunal groups. It needs to be determined if roveacrinid acmes can be tied in with abundance levels for other microfaunal groups. At present, the disjunct distribution favours interpretation of *B. degraafi* as a local (regional) species that only frequented the Maastricht area during periods of increased food availability. Being directly dependent on suspended material in the (upper) water column, this type of crinoid is expected to have been hard hit by the food chain collapse postulated for the latest Maastrichtian/earliest Paleogene interval. In fact, all roveacrinids became extinct, *B. degraafi* being the last representative of this order.

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