# Clustered bourgueticrinid crinoid holdfasts on late Maastrichtian echinoids from northeast Belgium and southeast Netherlands*

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## Abstract

In general, holdfasts (including distalmost stalk plates) of bourgueticrinid crinoids (Comatulidina, Bourgueticrinina) are comparatively rare in Maastrichtian (Upper Cretaceous) strata in the extended type area (northeast Belgium, southeast Netherlands). Here we describe a number of examples of such holdfasts. Two of these are of note in comprising up to two dozen specimens in different size classes, with a predominance of juveniles, in close proximity to larger, 'fully grown' individuals. All specimens are of late Maastrichtian age and are found on tests of holasteroid echinoids of the genus *Echinocorys* Leske. The majority stem from the Lixhe 1 and 3 members (Gulpen Formation) at the former CPL SA quarry (Haccourt, Liège, Belgium), and at a disused quarry between Houtain-Saint-Siméon and Roclenge-sur-Geer (Liège). A single example is from the underlying Vijlen Member (Gulpen Formation) at the ENCI-Heidelberg Cement Group quarry (Maastricht). The clustering of juvenile and 'fully grown' holdfasts on two tests suggests at least three different spat falls. Settlement of crinoid larvae close to the tallest point of the test would have been conducive to further development, but the close proximity may also have had a detrimental effect on feeding, by interference from neighbours. Current action or probing by a predator or scavenger appears to have tumbled the echinoid tests, leading to the premature death of the recently settled crinoids by smothering.

**Key words:** Crinoidea, Bourgueticrinina, holdfasts, Cretaceous, Belgium, the Netherlands

## Introduction

Amongst articulate crinoids, bourgueticrinids predominate at many levels within the Campanian-Maastrichtian of the extended type area of the Maastrichtian Stage (Jagt 1999b). Usually, these have radix-type attachment, which at times can be highly intricate and extensive (see *e.g.*, Brünnich Nielsen 1913: Pl. 1, Fig. 15; Rasmussen 1961: Pl. 60, Fig. 2; Klikushin 1982: Fig. 1G–I; Jagt *et al.* 1998: Pls 1–2, 7); attachment by holdfasts, or terminal discs, is comparatively rare. In extant taxa, the distal stalk is attached either by 'roots' penetrating soft sediment (see *e.g.*, Clark 1977: Fig. 3; Roux 1977: Pl. 2, Fig. 5; Donovan 1997: Pl. 10, Figs. 1–3, 7; Mironov 2000: Fig. 4; Mironov & Pawson 2010: Fig. 5), or by encrusting discs on hard substrates (Clark 1973: Fig. 6; 1977: Fig. 2; Roux 1977: Pl. 2, Fig. 5; Donovan & Pawson 1994: Figs. 2, 4; Messing 2007: Fig. 5). The two types of attachment are occasionally found in the same genus, such as in *Democrinus* (Clark 1977). Until recently, only a
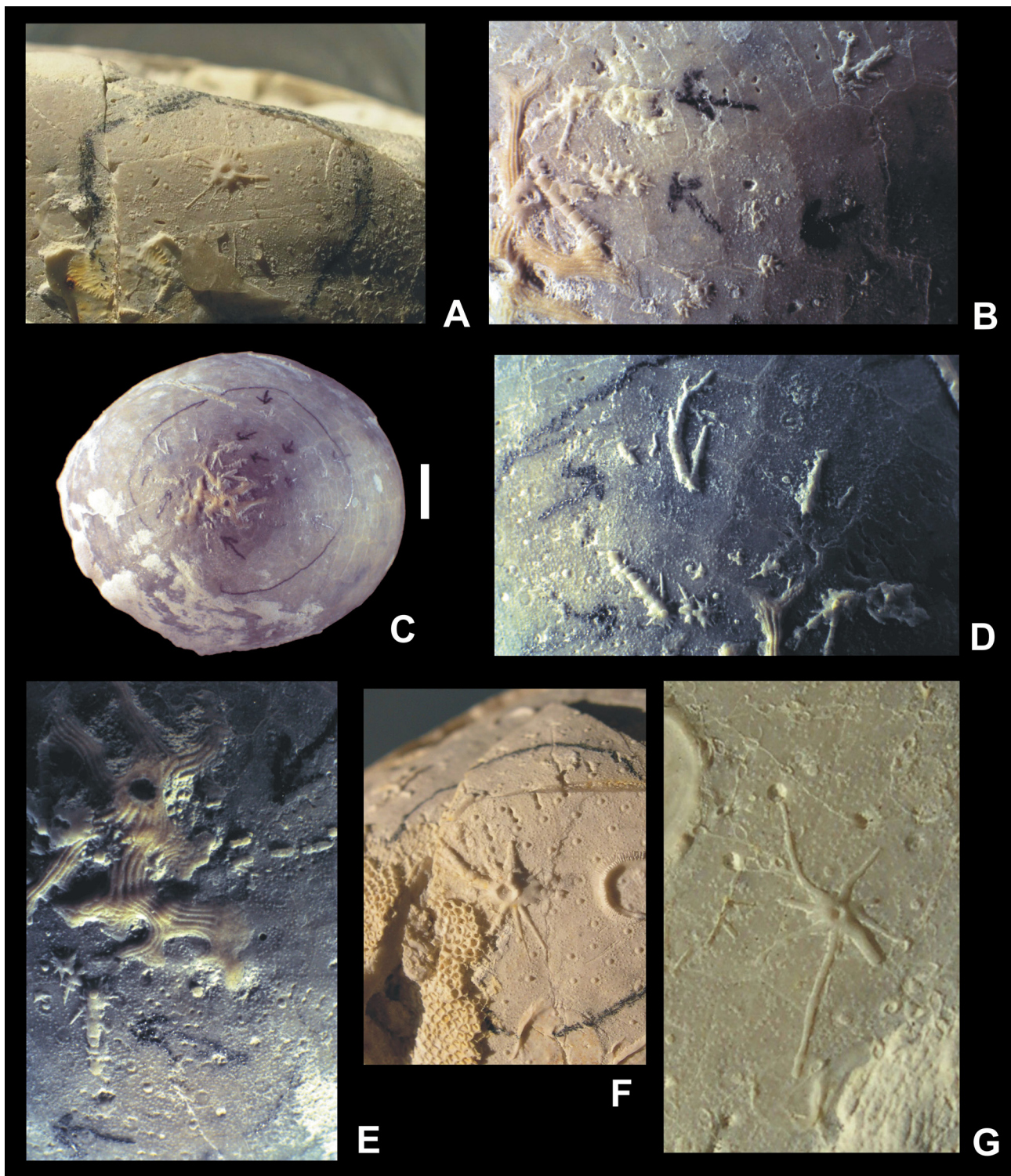
**FIGURE 1.** Bourgueticrinid holdfasts on *Echinocorys* gr. *conoidea* (A, F, G) and on *E.* gr. *limburgica/duponti* (B–E); A. NHMM 2010 166; B–E. NHMM 2010 167; F. NHMM 2010 169; G. NHMM 2010 168. Scale bar represents 10 mm (C); for other figures the image width is 30 mm (A), 28 mm (B), 18 mm (D, F), 12 mm (E) and 9 mm (G).

handful of examples of such terminal plates were known from the study area (compare Jagt 1999b). Here, we add three additional records of single, medium- to large-sized individuals, all on echinoid tests, as well as two spectacular instances of sets of a single, large-sized holdfast with up to two dozen juveniles, some barely 1 mm across, in close proximity. In both cases, other episkeletozoans (*sensu* Taylor & Wilson 2002) are associated, such as cheilostome and cyclostome bryozoans, pycnodon-

teine and dimyid bivalves, and adhering benthic foraminifera. As Schmid (1949) and Nestler (1965) have amply demonstrated, patterns in the settlement of bivalves, in particular, can be discerned on echinoid tests. Bourgueticrinids apparently also favoured the tallest point, that is, the highest elevation above the seafloor, of tests, enabling them to lift their crown even further into the water column for feeding. Despite successful settlement, some disturbance (either current or predator/scavenger action) led to the demise of the newly settled, third spat fall by smothering. In any case, the close proximity of the holdfasts would certainly have meant some interference from neighbours and, thus, a detrimental effect upon feeding.

## Geographic and stratigraphic setting

The material originates from three levels within the Gulpen Formation and is of late Maastrichtian age (*Belemnitella junior* Zone of authors; compare Christensen *et al.* 2004). The Lixhe 1 Member is well exposed at the former Ciments Portland Liégeois (CPL SA) quarry (Haccourt, province of Liège, Belgium), and at a disused quarry between Houtain-Saint-Siméon and Roclenge-sur-Geer (Liège), *c.* 4 km west of Haccourt. The Lixhe 3 Member, from which NHMM 2010 169 probably originates, is easily accessible at the CBR-Lixhe quarry which, in the south, is directly adjacent to the former CPL SA pit. Until recently, the upper portion of the Vijlen Member (Gulpen Formation) could be sampled at the ENCI-Heidelberg Cement Group quarry (Maastricht, southern Limburg, the Netherlands); this part of the quarry is now being refilled. For details, including a locality map, and lithologs, see Jagt (1999a, 1999b).

**Institutional abbreviation.** NHMM, Natuurhistorisch Museum Maastricht (PK = P. van Knippenberg) (see Table 1).

**Note on terminology.** Motile cirri are only known from comatulid and isocrinid crinoids (Donovan 1993). We prefer to limit the terms cirral and cirrus to the attachment structures of these groups. The branching attachments described herein are correctly termed radices (Donovan 1997: 2–3).

## Description of holdfasts

Three specimens in the present lot comprise single, small- to medium-sized terminal plates; these will be described first. NHMM 2010 166 (Fig. 1A) represents a medium-sized holdfast, located on the anterior row of plates in interambulacrum I, just above the ambitus, of an average-sized individual (test length and width: 86 and 71 mm, respectively) of *Echinocorys* gr. *conoidea* (Goldfuss, 1829) *sensu* Jagt (2000). The disc has an irregular outline, measuring *c.* 2.5 mm in diameter, the central pit being rather shallow (equalling *c.* 50 per cent of disc height), smooth, with the elongate, slit-like lumen (1 mm in length) surrounded by a horseshoe-shaped wall; sutured sections of branches between 0.4 and 0.9 mm in length; the thinnest radice branch (lower left-hand side in Fig. 1A) is 0.1 mm, or less, in width; one comparably thin branch extends across the ambitus to the lower test surface, while another appears more or less 'unattached' and is 3 mm in length; the longest branch, 6 mm, extends adapically, but is partly hidden by a calcitic overgrowth; the thickest radice is 0.6 mm at the base and

thins out to 0.2–0.3 mm wide distally.

NHMM 2010 169 (Fig. 1F) is closely comparable, situated in the upper half of the test, in the anterior row of plates of interambulacrum V and in part extending onto ambulacrum 1. It is close to cheilostome and cyclostome bryozoan colonies and a dimyid bivalve, *Atreta costata* (Grönwall, 1900), is seen nearby (right-hand side in Fig. 1F). The substrate is again a specimen of *E*. gr. *conoidea*, which suffered sediment compaction and is laterally strongly compressed and cracked; test length is approximately 88 mm. One cheilostome bryozoan colony overgrows portions of the holdfast and thus post-dates the death of the crinoid. The basal plate measures *c*. 2.5 mm in diameter, the central pit is 1.5 mm in diameter and a slit-like, eroded lumen is *c*. 0.5 mm long. The width of the largest branch is 1.0 mm at the base and it thins out to 0.5 mm; two thin branches are 3.7 and 4.5 mm long, and constricted sections are visible only in the short branches to the right-hand side in Fig. 1F.

NHMM 2010 168 (Fig. 1G) represents the smallest example of this general type, the central pit being 0.5 mm across and circular, but no lumen is visible. The longest branch measures 3.7 mm, has feeble constrictions, and, in part, overgrows a juvenile oyster(?) and a cyclostome bryozoan (probably *Pyripora laxata* d'Orbigny, 1852; see Thomas & Larwood 1960). In addition, there are up to seven roots of variable thickness and length, with the thickest appearing rather solid at 0.3 mm wide and with no constrictions. This example also occurs on a large-sized test (length and width: 94 and 75 mm, respectively) of *E*. gr. *conoidea*, in the posterior row of plates in interambulacrum II and extending just onto ambulacrum 2, very close to the apical disc (*c*. 15 mm removed from it).

Two other examples illustrated here (Figs. 1B–E, 2) comprise sets of associated holdfasts, in which juveniles predominate. This character alone sets them apart from the examples discussed above; as far as we are aware, no similar examples have ever been recorded in the literature.

NHMM 2010 167 (Fig. 1B–E) is an example of *E*. gr. *limburgica* Lambert, 1903/*duponti* Lambert, 1903 *sensu* Jagt (2000), of average size (length and width: 75 and 65 mm, respectively). At least thirteen individuals, maybe even more, can be counted, most of them with well-constricted branches; a single larger individual occurs. Juveniles measure between 1.2 and 1.8 mm across. One specimen shows a divided central pit (1.1 mm in diameter), while the basal plate is 1.5 mm across. A specimen with a longer, well-constricted branch (4.5 mm long, varying between 0.4 and 0.6 mm in width) has a calcitic bulge of 0.4 mm diameter, which may represent the first stalk element (Fig. 1D–E). All holdfasts cluster close to the echinoid's apical disc, where an octocoral base covers the test surface, and extend onto ambulacra 3, 4 and 5, and interambulacra II, IV and V (Fig. 1B–C, E). The octocoral base most probably is referable to either *Moltkia* Steenstrup, 1847 or *Isis* Linnaeus, 1758, and compares well to examples illustrated by Voigt (1958), Małecki (1982) and König (1991).

NHMM PK 1488 (Fig. 2A–F) is the most spectacular example in the present lot, occurring on a large-sized (length and width: 93 and 79 mm, respectively) test of *E*. gr. *conoidea*, which reveals the highest density of episkeletozoans on the anterior portion (ambulacra 3 and 4; interambulacra III, IV; see Fig. 2A–B). Crinoid holdfasts are restricted to a small area of 30 by 20 mm in ambulacrum 3 (Fig. 2A). The base of the largest specimen measures 0.8 mm across, has a slit-like, eroded lumen, the longest branch being 13 mm overall, 1.2 mm wide at the base and thinning out distally to 0.6 mm, but with four side branches. These are all well constricted, with portions measuring between 0.4 and 1.2 mm in length; this specimen partially overgrows a smaller example with well-developed, spiky branches (Fig. 2D), adjacent to the dimyid bivalve (see also Fig. 2E). Juveniles (Fig. 2E–F) measure between 0.6 and 1.4 mm across; all have circular lumens of between 0.1 and 0.2 mm in diameter.
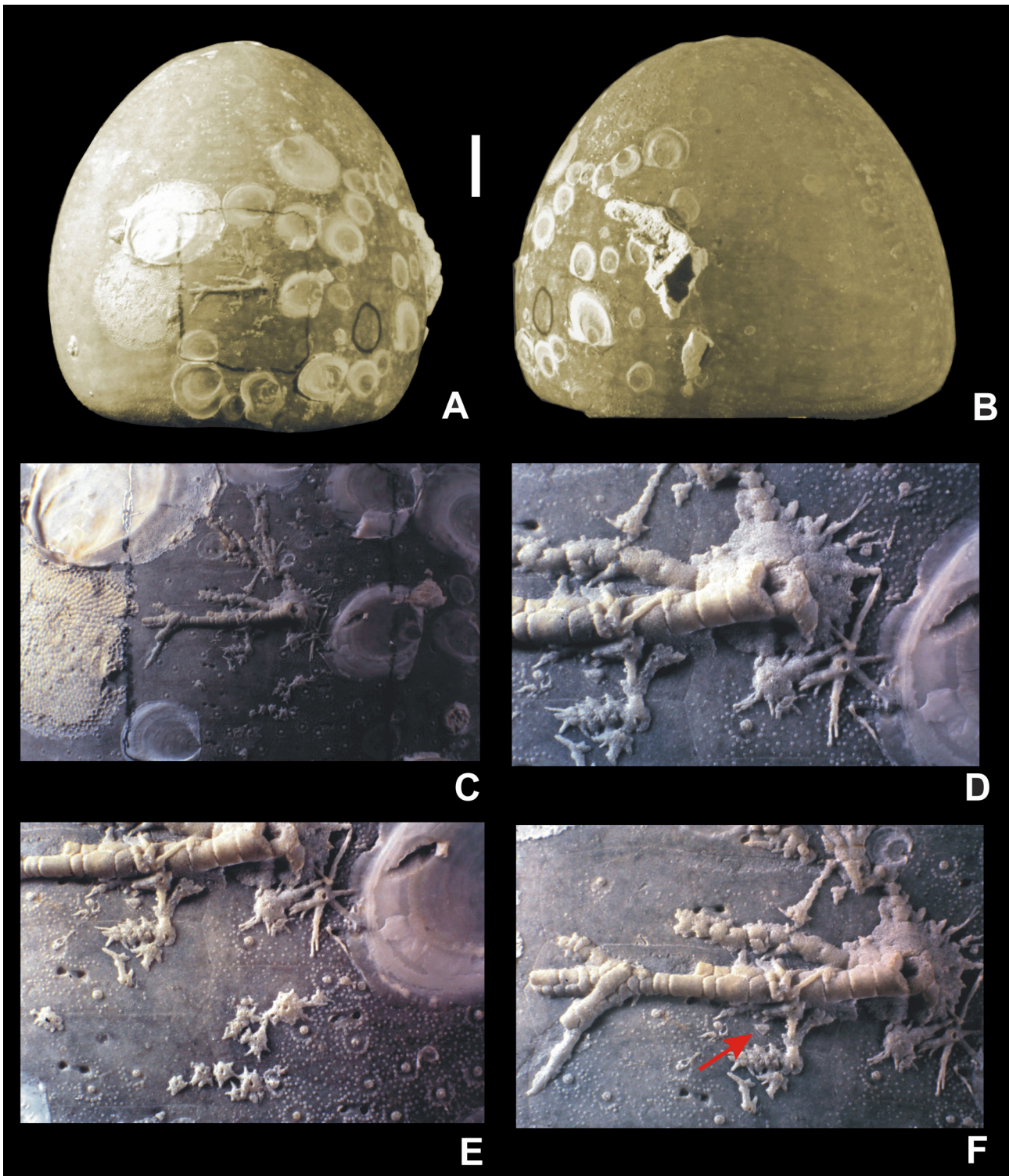
**FIGURE 2.** Bourgueticrinid holdfasts on a test of *Echinocorys* gr. *conoidea* (NHMM PK 1488); A. frontal view, ambulacrum 3 in the centre; B. left-lateral view, showing episkeletozoan growth on anterior portion of test; C. close association of crinoid terminal plates with cheilostome bryozoans, and pycnodonteine and dimyid bivalves; D. detail of largest specimen, partially overgrowing another, much smaller specimen with spike-like branches (lower right, adjacent to bivalve); E. detail of juveniles adorally of largest specimen, in a clear cluster; note irregular outline of basal plate and circular lumens; F. full view of the largest specimen, with long branch and several side branches (arrow). Scale bar represents 10 mm (A, B); for other figures the image width is 40 mm (C), 10 mm (D), 8.2 mm (E) and 15 mm (F).

## Discussion

There can be no doubt that these holdfasts are assignable to the Bourgueticrinina, because in associated skeletal material, recovered from bulk sampling, only these crinoids have been identified. However, identification at the species level is impossible. From the Vijlen and Lixhe members in the Haccourt-Lixhe area, Jagt (1999b) recorded only two species, *Bourgueticrinus* aff. *brydonei* Rasmussen, 1961, and *B. constrictus* (von Hagenow *in* Quenstedt, 1876), mostly on the basis of thecae, columnals and dissociated brachials. The latter has 'rhizocrinid' columnals, that is, the lumen is shaped like the figure '8'. The holdfast illustrated by Jagt (1999b: Pl. 33, Fig. 10), fixed to the guard of a belemnitellid coleoid and originating from the Vijlen Member at Mamelis-Selzerbeek (southern Limburg, the Netherlands), shows exactly this and may thus be attributed to that species.

Although much rarer than radicular attachments (see, for example, Fig. 3), holdfasts of Late Cretaceous bourgueticrinids have so far been recorded from the Santonian of Sussex (southern England; Rasmussen 1961: Pl. 24, Fig. 1; on an echinoid), the lower Campanian of the Münsterland Basin and the Hannover area (northern Germany; Wittler 1998: Figs 3–5; on *Echinocorys* gr. *humilis* Lambert, 1903; Wittler 2001: Figs 1–2; on *Echinocorys* sp.; Amme 2005: 42, upper row of pictures; on ?sponges), the upper lower Campanian of southern Sweden (Rasmussen 1961: Pl. 24, Fig. 2; unidentified substrate) and the lower Maastrichtian of Rügen, northeast Germany (Nestler 1965: Pl. 5, Fig. 10; on *Echinocorys* sp.).

Some typical examples of bourgueticrinid holdfasts have previously been misidentified as bases of octocorals. Such is the case with what Małecki (1982: 70, Pl. 23, Figs 5, 6; Pl. 28, Figs 10, 11) referred to as *Octobasis spinosa* Małecki, 1982 from the Campanian of southern Poland. This 'parataxon' was defined as follows: 'Bases nodular, with radially arranged, sharp spines. Bases attached to flat surfaces are very irregular, while those fused to the sides of echinoids have spines varying in length. Spines usually single, rarely ramifying. Spines pointing downward are long, the rest of them short and rather irregularly developed. Bases from a few to 15 mm, axial insertions 1.2 mm in diameter.' (Małecki 1982: 70). Unfortunately, there is no explanation as to what 'flat surfaces' represent in this case, but it is otherwise typical that, yet again, echinoids form the substrate of these examples.

Thus, in the majority of cases recorded in the literature, the substrates of bourgueticrinid holdfasts are medium- to large-sized echinoid tests of the holasteroid genus *Echinocorys* Leske, 1778. So

**TABLE 1.** Current repository and details of provenance of specimens studied (see Figs. 1–3).

| | | |
|---|---|---|
| NHMM 2010 166 | CPL SA quarry; Haccourt, province of Liège, northeast Belgium | Gulpen Formation, Lixhe 1 Member; late Maastrichtian |
| NHMM 2010 167 | ENCI-Heidelberg Cement Group quarry; Maastricht, province of Limburg, the Netherlands | Gulpen Formation, Vijlen Member; late Maastrichtian |
| NHMM 2010 168 | disused quarry between Houtain-Saint-Siméon and Roclenge-sur-Geer, province of Liège, northeast Belgium | Gulpen Formation, Lixhe 1 Member; late Maastrichtian |
| NHMM 2010 169 | CBR-Lixhe quarry; Lixhe, province of Liège, northeast Belgium | Gulpen Formation, Lixhe 3 Member(?); late Maastrichtian |
| NHMM MD 5005 | ENCI-Heidelberg Cement Group quarry; Maastricht, province of Limburg, the Netherlands | Maastricht Formation, basal Gronsveld Member; late Maastrichtian |
| NHMM PK 1488 | CPL SA quarry; Haccourt, province of Liège, northeast Belgium | Gulpen Formation, upper third of Lixhe 1 Member; late Maastrichtian |
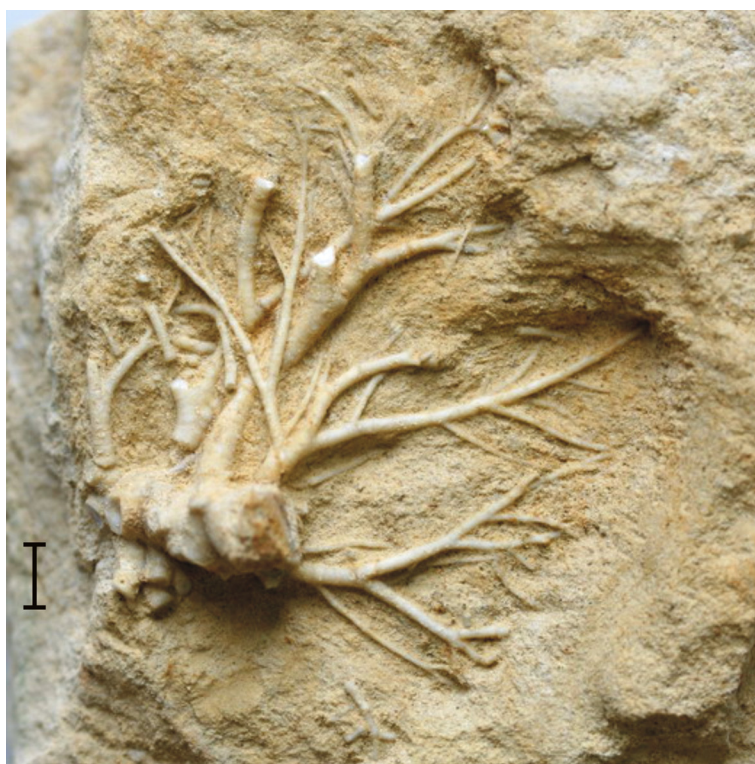
**FIGURE 3.** Radicular attachment of *Dunnicrinus aequalis* (d'Orbigny, 1840) (NHMM MD 5005). Scale bar represent 5 mm.

far, only Małecki (1982) appears to have referred to small specimens; unfortunately, none of these were illustrated. The material that he did figure (his Pl. 23, Figs 5, 6) was comprised of stout forms comparable to those illustrated by Wittler (2001); in one example (Małecki 1982: Pl. 23, Fig. 6), two terminal plates can be seen in close proximity. Wittler (2001) was certainly right in claiming that *O. spinosa* represented crinoid holdfasts rather than octocoral bases. However, we do not subscribe to his suggestion that a new generic name would be needed to draw attention to this fact. Rather, we much prefer the neutral term 'bourgueticrinid holdfast' over the 'parataxon' *O. spinosa*. Indeed, as noted above, a more precise reference to *Bourgueticrinus* can be made if associated thecal or columnal material proves to be of such type.

The Vijlen and Lixhe members both represent either soupgrounds or softgrounds (see Bromley 1990: 19, for definitions). In such depositional settings, large-sized or tall substrates ('secondary hardgrounds') were much sought after by obligate sessile organisms (see, for example, Schmid 1949; Nestler 1965), so as to find both elevation above the seafloor (and, thus, a more or less prolonged life, with a less likely chance of being smothered by sediment) and to make better use of nutrients. Being suspension feeders, stalked crinoids obviously would favour such substrates, to lift their crown even further above the hostile seafloor and into the particle-laden currents. Although we have only a limited number of specimens available, in all examples illustrated holdfasts are found either close to the tallest point of the echinoid test (the apical disc) or in the centre of that portion of test which was not embedded and shows the highest density of episkeletozoans. From the diameters of the holdfasts, it can be determined that the crinoids attached would have been rather small, with a rather thin stalk.

Such attachment would also have been beneficial for reproduction; eggs and semen could be shed into the water, away from the hostile ooze, so as to increase the chances of fertilization (Lawrence 1987). As computer simulations on Early Jurassic eudesicrinids have shown (Manni *et al.* 1991), crinoid larvae may have had the ability to explore the suitability of a substrate prior to final settlement. In this respect, it is of note that Donovan *et al.* (2007; see also Donovan & Harper 2010) recorded

clustering of conspecific attachment structures of a Silurian crinoid from Gotland (Sweden), which were held to represent successive spat falls. Those authors noted that clustering was either the result of some unknown ecological preference or that such was governed by biochemical cues. In the present examples, the size of the various holdfasts (particularly on NHMM PK 1488) suggests that at least three successive stages of bourgueticrinid settlement are documented, the largest holdfasts partially overlapping a specimen of the 'second spat fall' (Fig. 2D–E). The third phase is illustrated by the cluster of the smallest individuals (Fig. 2E). For these, settlement close to the highest elevation would have been very conducive to further development, were it not for the fact that clustering would almost certainly have had a detrimental effect upon feeding, by interference of neighbours. It appears that tumbling of the echinoid test, by current action or through probing by a predator or scavenger, smothered the juvenile crinoids.

Further, the possible sensory function of such radicular attachments, proposed by Donovan *et al.* (2007), might be inferred in some of these Maastrichtian examples. Although the axial canals of the column and radices of many Palaeozoic crinoids are broad, we do know that the nervous canals of their post-Palaeozoic descendants include nervous tissues (Jefferies 1968: Fig. 5). Juvenile attachments of *Bourgueticrinus* sp. have some radices that suggest a sensory function by their relatively great length. Radice insertion seems to be more or less radial in more complete specimens (Fig. 1F–G), so radices could provide sensory input from all directions. The longest radices on each of the examples occur on opposite sides and extend in almost opposite directions. It could be from these directions—upcurrent and downcurrent—that the most important information regarding feeding currents could be derived.

Similarly, one specimen (Fig. 2C–F) shows a strong asymmetry in radice development, with all major branches directed in almost the same direction. Although most other specimens on this test are disc-like and more radial in their development of radices, they are also much younger and members of later spat falls. But one specimen, best seen in Figure 2F (arrowed), is also extending a robust radice parallel to that of the large specimen. A sensory function, perhaps in an upcurrent direction, is at least possible for such radices. Interestingly, the more mature specimen in Figure 3 preserves branching radices orientated through about 125°, that is, concentrated on one 'side' of the crinoid.

## Acknowledgements

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