

AN UNEXPECTED CRINOID – CEPHALOPOD ASSOCIATION FROM THE BLUE LIAS FORMATION (LOWER SINEMURIAN, LOWER JURASSIC) NEAR WATCHET, SOMERSET, ENGLAND

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Paul, C.R.C. 2018. An unexpected crinoid – cephalopod association from the Blue Lias Formation (Lower Sinemurian, Lower Jurassic) near Watchet, Somerset, England. *Geoscience in South-West England*, **14**, 167–175.

Palmer's bed E(V) in Hellwell Bay, near Watchet, Somerset contains many nautiloids (*Cenoceras*) but few ammonites. It is exposed in two parts 160 and 130 m long east and west of the groyne, with 24 and 21 nautiloids recorded, respectively. Twelve nautiloids lie on their left side, 14 on their right and a further eight are vertical or nearly so. Others are too eroded to tell. Fifteen nautiloids host epifaunal oysters, with a further 14 having oysters and/or byssally-attached bivalves (pectinids, ?pterids) preserved nearby. Fourteen nautiloids and the largest ammonite from the east exposure plus 18 nautiloids from the west have crinoid debris (*Isocrinus psilonoti*) associated with them. The crinoid debris rarely extends >1 m from the centre of the cephalopod shells. At least 17 more similar patches of crinoid debris occur, without associated cephalopods. Between patches, with or without cephalopods, crinoid debris is very rare. Crinoids were apparently associated with large cephalopod shells. Living isocrinids are unable to attach directly to substrates, but entangle the cirri on their stems with other benthic objects to help anchor themselves. A similar relationship apparently occurred between the fossil cephalopods and isocrinids, which were not attached to floating cephalopod shells.

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Keywords: Crinoids, *Isocrinus*, nautiloids, *Cenoceras*, Blue Lias Formation, Sinemurian

INTRODUCTION

Although rare, associations between crinoids and cephalopods have been reported previously in the literature. For example, Simms (1989a, pl. 2, fig. 3) illustrated three small examples of *Pentacrinites doreckae* Simms, 1989a, attached to a large ammonite. Pentacrinid crinoids are frequently found attached to fossil wood and they have been repeatedly interpreted as having led a pseudoplanktonic mode of life (see the review by Simms, 1986), although others (e.g., Rasmussen, 1977; Kauffman, 1981) have disputed this interpretation. Nevertheless, it does raise the possibility that pentacrinids may have been able to attain a pseudoplanktonic mode of life by attaching to floating cephalopod shells as well as to floating wood. Isocrinid crinoids, on the other hand, have always been interpreted as obligate benthos (Rasmussen, 1978; Simms, 1986). The association reported here is unexpected for two reasons; it largely involves the nautiloid *Cenoceras*, despite the fact that ammonites are generally more common and diverse in the British Lower Jurassic, and it exclusively involves benthic isocrinid crinoids. Almost all the material discussed occurs in a single limestone bed (Palmer's, 1972, series E, bed V; hereafter 'bed V' for brevity) exposed in Helwell Bay, east of Watchet, Somerset, which Whittaker and Green (1983, p. 61) suggested corresponds to their bed 228. Palmer (1972, p. 23) specifically mentioned that his bed V contained the nautiloid *Cenoceras*, so the exact bed is known in Palmer's (1972) numbering scheme. However, Palmer was uncertain how the beds in his series E exposed in Helwell Bay correlated with the general succession he recognized, hence there is some uncertainty as to precisely which of Whittaker and Green's (1983) beds is involved. The latter authors suggested that Palmer's beds E(I) to E(XV) correlated with their beds 224 to 238 (Whittaker and Green,

1983, Table 7, p. 61), which makes Palmer's bed V equivalent to Whittaker and Green's bed 228. In their description of the section Whittaker and Green (1983, p. 66) recorded the presence of *Cenoceras* sp. in the shale immediately above bed 228. Whittaker and Green attributed this level to the Semicostatum Zone, in the Lower Sinemurian stage, but it has since been established that it lies within the upper part of the Bucklandi Subzone (Page, 1992, p. 138; Simms *et al.*, 2004, fig. 2.18, p. 86).

The purposes of this paper are to document the crinoid- cephalopod association, to interpret its original significance to the animals involved and any possible relevance to the sedimentation processes during the deposition of the Blue Lias Formation in Somerset.

METHODS

The exposures of Palmer's bed V occur either side of three groyne in Helwell Bay, together with a very small exposure between the middle and western groyne (Figure 1). The eastern exposure is about 160 m from east to west and the western exposure about 130 m. The bed is about 30 cm thick. Crinoid debris occurs in patches usually less than 2 m across and separated by crinoid free limestone. The entire exposure was searched for patches of crinoid debris, which were photographed and a 10-figure grid reference (giving a nominal accuracy of 1 m) recorded for each occurrence using a hand held GPS device. The presence or absence of any cephalopods associated with the crinoid debris was recorded, together with a record of the diameter of the cephalopod and its orientation (lying on the left or right side or orientated vertically) wherever

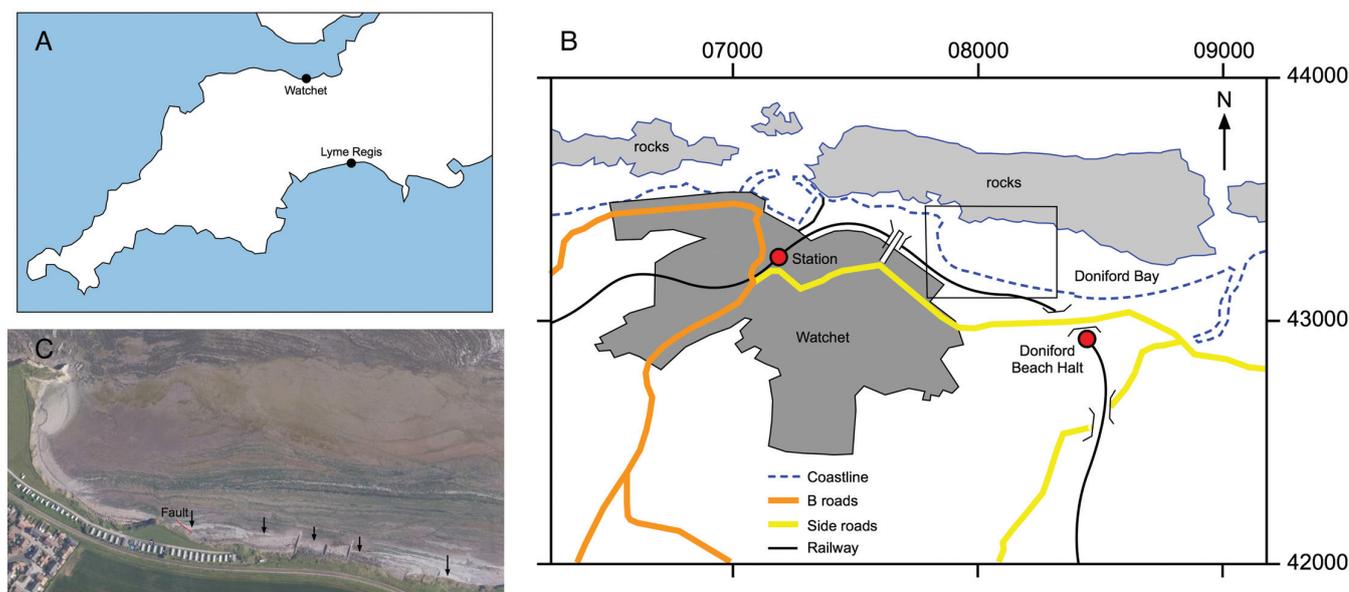


Figure 1. (a) Position of Watchet and Lyme Regis in SW England; (b) Location of exposure in Doniford Bay, Watchet (outline rectangle); (c) Google Earth image of exposure of bed V in Helwell Bay (arrows). Numbers in (b) refer to Ordnance Survey Grid References.

this was possible. To facilitate later discussion cephalopods were assigned numbers in the field, whereas crinoid patches without an associated cephalopod were assigned letters of the alphabet.

If crinoids were present two radii were measured from the centre of the cephalopod shell to the furthest extent of the crinoid debris as a means of estimating the area over which the crinoid debris was spread. In the absence of cephalopod shells two diameters of the patch of crinoid debris were recorded for the same purpose, usually N–S and E–W. Any cephalopod shells not associated with crinoid debris were also recorded, photographed and their size and orientation recorded as well. Ammonite shells were distinguished from nautiloid shells. Only one, the largest, was associated with crinoid debris. The same records were made for it as for the nautiloids. Presence of epifauna (usually oysters) attached to the cephalopod shells was recorded as well as any cemented or byssally attached bivalves close to the cephalopod shells.

For the crinoid debris an estimation of the degree of disarticulation was recorded and any special features, such as more or less complete cirri, photographed. The presence of pluricolumnals from the stem was recorded together with the number of ossicles involved or the total length, if the number of ossicles was uncertain. In addition, diameters of isolated ossicles preserved parallel to bedding were recorded to ascertain if more than one crinoid animal had contributed to the debris patch. Diameters that differed by > 1 mm were taken to indicate more than one crinoid was present due to the difficulty of measuring star-shaped ossicles accurately in the field. Modification of the crinoid debris patches by burrows was also noted.

RESULTS

In all 46 nautiloids were identified in the three exposures, 24 in the eastern exposure, 21 in the western and one between the middle and western groyne. All the nautiloids belong to the genus *Cenoceras* (Fig. 2a), probably *C. intermedium* (Sowerby, 1816), although the whorl cross-sections do not match that illustrated in Evans *et al.* (2014, fig. 4, p. 13). The lateral sides of the whorl are almost parallel, whereas Evans *et al.*'s illustration shows the whorl cross-section tapering distinctly towards the venter. Nevertheless, the flattened venter is obvious in specimens orientated with the coiling axis more or less horizontal (e.g., Fig. 2b). The nautiloids reach a maximum diameter of about 30 cm and many seem to have been mature.

Twelve of 16 measurable nautiloids where one could be certain the measurement was the true diameter were 25–30 cm in diameter; two more where the measurement was a minimum also exceeded 25 cm diameter. Twelve nautiloids lay on their left side, 14 on their right, eight were vertical and one oblique to bedding. As the venter is flat in this species, the vertical specimens were still in a fairly stable orientation. The remaining nautiloids were too incomplete to decide on their orientation. Fifteen nautiloids had attached epifauna and a further four possibly did. In addition, 14 nautiloids had cemented or byssally-attached bivalves (pectinids or possibly pteriids) preserved nearby.

Preservation of the nautiloids varies considerably. Specimen 14 (Fig. 2c) is apparently complete and uncrushed, whereas specimen 15 (Fig. 2b) has a crushed phragmocone, but an undamaged body chamber. In specimen 16 (Figure 2d) only the body chamber is preserved and in specimen 43 (Fig. 2e) only a very thin and incomplete outline of the shell is preserved. All four examples are preserved vertically in the sediment. Similarly, specimen 39 (Fig. 2f) has some of the outer shell of the body chamber still preserved and apparently crushed flat as well as septa in the phragmocone, whereas specimen 25 (Fig. 3a) has no septa preserved and an incomplete body chamber. Other specimens are damaged (e.g., specimen 22, Fig. 3b) or substantially incomplete (e.g., specimen 39, Fig. 3c).

Considering the stratigraphic position of the limestone bed in question, it can reasonably be assumed that all of the crinoid debris derived from the isocrinid, *Isocrinus psilonoti* (Quenstedt, 1858), since this is the only large isocrinid documented at this level in the Sinemurian (Simms, 1989a). Modern isocrinid crinoids have an extensive stem, up to 1 m long (Fig. 4a, b). The stem grows by the addition of nodal columnals immediately below the cup (see Macurda and Roux, 1981, pl. 7, figs 2, 3) and subsequently by the addition of internodal columnals between successive nodals (see, Donovan, 1984; Simms, 1989b). Nodals are distinguished by the presence of cirri, finger-like lateral branches that end in a terminal hook (see Macurda and Roux, 1981, pl. 6, figs 3, 4; Donovan, 1984, pl. 76, fig. 1) and can be used to anchor the crinoid to the substrate. Articulations between columnals show the characteristic petal-like pattern of raised crenellae that interlock with the adjacent columnal (Simms, 1989a, fig. 8a, p. 8; Macurda and Roux, 1981, pl. 16, fig. 6), except that the articulation between nodals and the internodals immediately below (infranodals) is usually planar (compare Macurda and Meyer, 1975, pl. 1, figs 1 and 2) and forms a surface at which

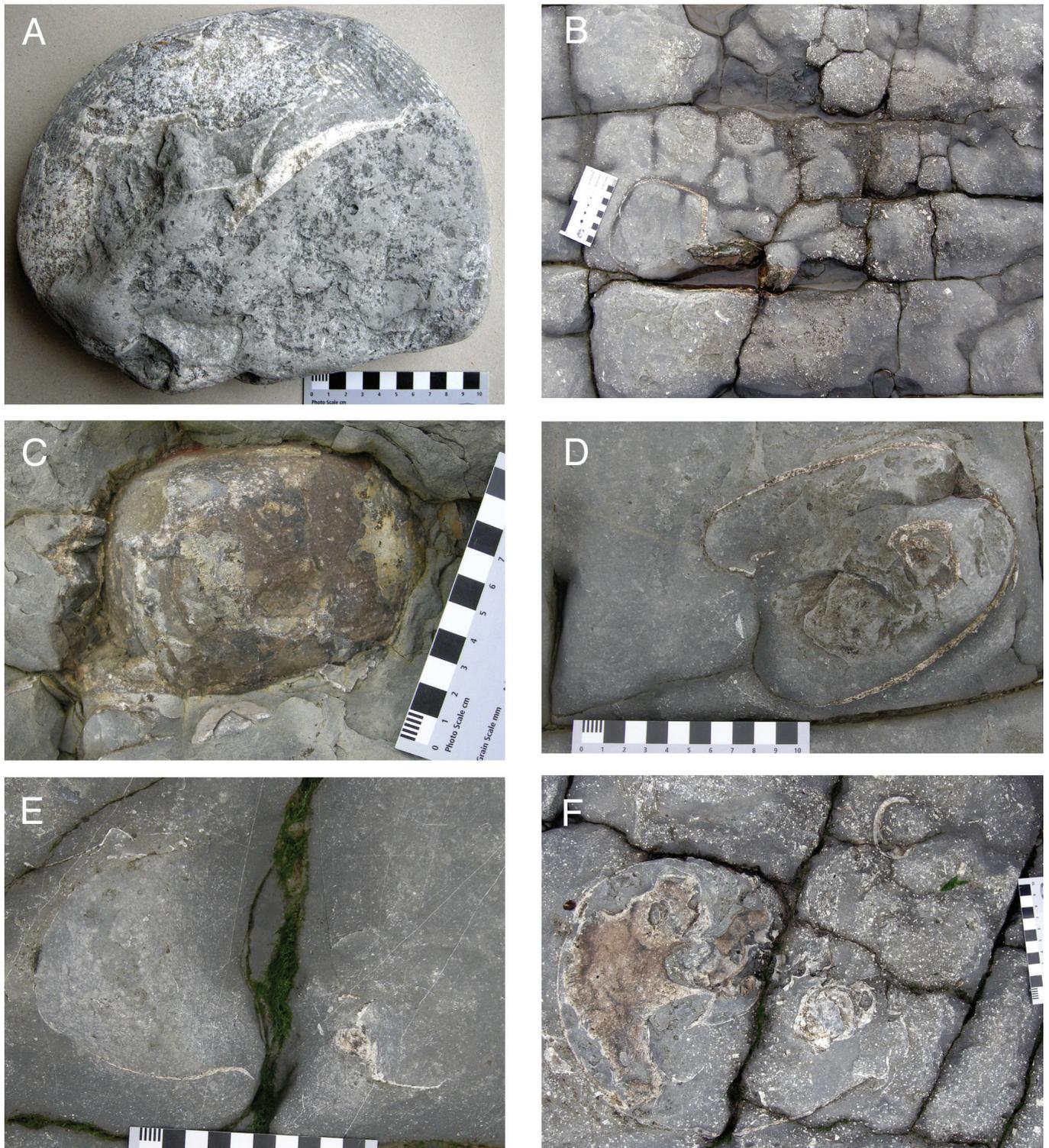


Figure 2. The nautiloid *Cenoceras*. (a) LYMPH 2018/12. Found loose on Monmouth Beach, west of Lyme Regis, Dorset. Note the spiral ornament and the relatively thick shell. B-F In situ, Bed V, Doniford Bay, near Watchet, Somerset; (b) Vertically orientated nautiloid showing flat venter and crushed phragmocone, surrounded by crinoid debris; (c) An uncrushed, vertical *Cenoceras* apparently without any associated crinoid debris; (d) A *Cenoceras* specimen that preserves only the body chamber; (e) A poorly preserved *Cenoceras* with only traces of the shell remaining; (f) A *Cenoceras* specimen with flattened body chamber and some septa preserved in the phragmocone, surrounded by crinoid debris.

the stem preferentially breaks when stressed (Macurda and Roux, 1981, pl. 16, fig. 1). Hence, isocrinid stems usually terminate in a break with cirri extending from the terminal nodal ossicle. *Diplocrinus* (*Annacrinus*) *wyvillethomsoni* uses the terminal cirri to anchor itself to stones on rocky substrates (Conan *et al.*, 1980, fig. 6, p. 253). When detached, modern

isocrinid crinoids have been observed using their arms to crawl to more suitable places for long-term attachment (Baumiller and Messing, 2007). Surprisingly, detached parts of the stem are able to survive for over a year after separation from the rest of the stem (Oji and Amemiya, 1998).

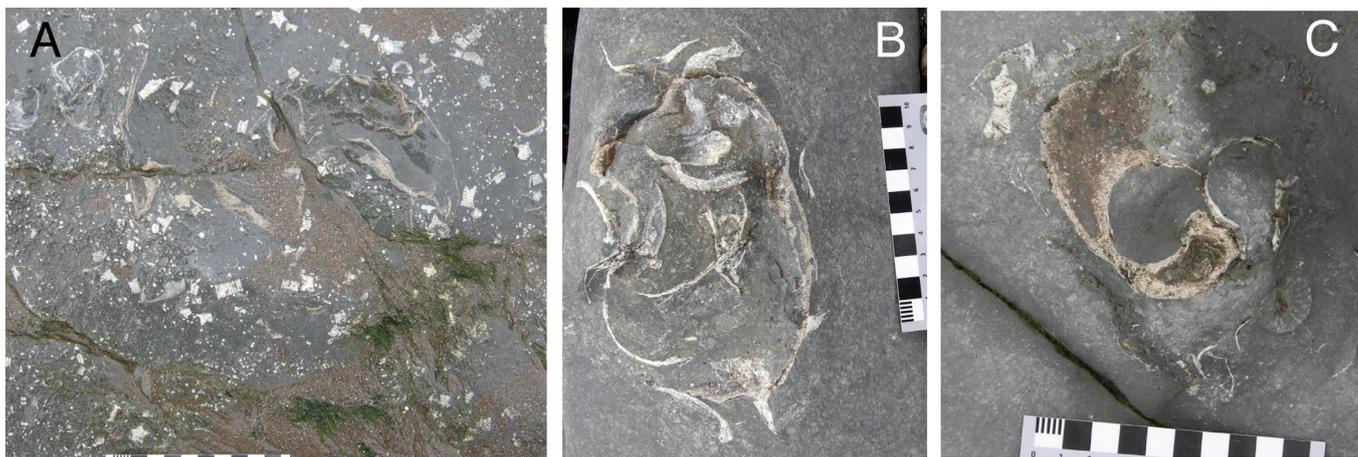


Figure 3. The nautiloid *Cenoceras*. In situ, Bed V, Doniford Bay, near Watchet, Somerset. (a) Poorly preserved *Cenoceras* with only the faintest outline of the shell and no septa preserved; (b) A significantly damaged *Cenoceras*; (c) A *Cenoceras* of which only a small portion remains.

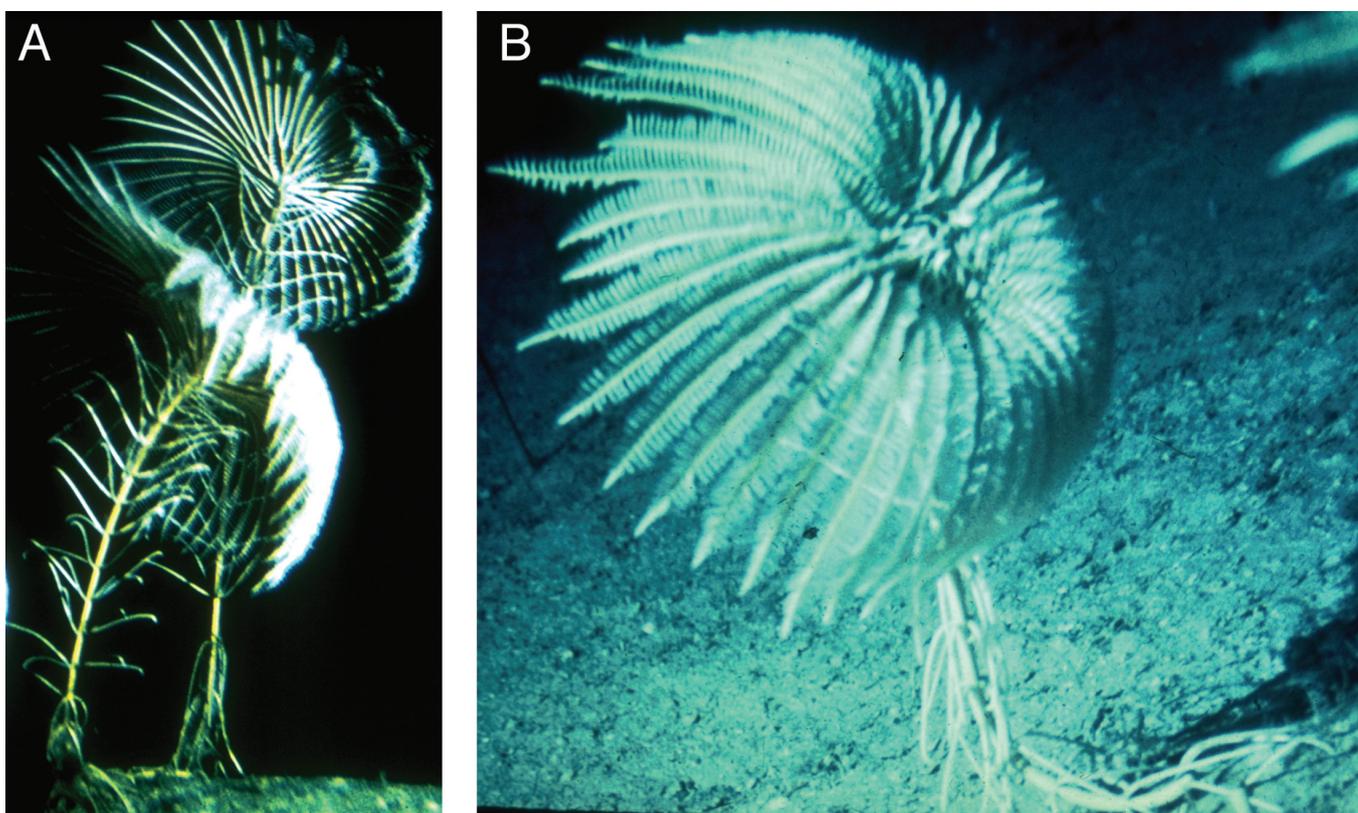


Figure 4. The modern isocrinid crinoid *Cenocrinus asterius* off the N coast of Jamaica. (a) Two examples to show the extensive stem, with radiating cirri, which are used to prop up the vertical portion of the stem (right example); (b) Another example to show that the stem curves round and lies parallel to the substrate. It is not rooted into the sediment. Images provided by D. B. Macurda Jr.

Isocrinids lack the ability to secrete a terminal disc and so cannot anchor themselves directly to solid substrates (Simms, 1986). Photographs taken from submersibles show that the stem is also not buried within soft substrate like the roots of a plant. Usually the lower half or so of the stem curves round parallel to the substrate (Fig. 4b herein; Macurda and Meyer, 1974, fig. 1f; Baumiller *et al.*, 2008, fig. 2a). Cirri are used to enhance attachment to the substrate by gripping any suitable object. Fujita *et al.* (1987, fig. 3, p. 342) show *Metacrinus rotundus* with its stem wedged around the edge of a large boulder. In addition, at the point of flexure cirri are used to support the erect part of the stem (Fig. 4a herein; Macurda and Meyer, 1974, fig. 1e). In this way the stem is able to elevate the cup well above the substrate. Isocrinid crinoids form filtration fans with their arms and feed from horizontal currents (Macurda and Meyer, 1976).

Isocrinus psilonoti has star-shaped columnals with smooth latera and between 14 and 24 ossicles per noditaxis (Simms, 1989a, fig. 11, p. 37). The maximum number of articulated columnals recorded in Bed V was 16 columnals, with pluricolumnals reaching 23 mm in length. In *I. psilonoti*, the column does not taper away from the cup (Simms, 1989a, pl. 7, figs 5, 6), and both nodals and internodals from the same individual are the same diameter.

The crinoids are substantially disarticulated although the preservation varies a little. In particular, those patches within burrows involve smaller ossicles than outside the burrows (Fig. 5). In addition, pluricolumnals are rarer and involve a smaller number of ossicles within the burrows (maximum 6). Altogether, the crinoid material is more completely dissociated within burrows. At least 16 patches of crinoid debris involved pluricolumnals. In addition, at least 15 patches involved crinoid



Figure 5. A large crinoid patch redistributed within *Thalassinoides* burrows. Note that in general, the crinoid debris is finer-grained within the burrows than in the central area above the measure, which is 5 cm wide. From an unidentified limestone bed in Helwell Bay, Somerset.

stem ossicles that differed in diameter by more than 1 mm (Fig. 6).

Thirty two of 46 nautiloids were associated with crinoid debris, as was the single largest ammonite in bed V (27 cm in diameter; Fig. 7). One other ammonite (58 cm in diameter) in a different bed and another fragment of nautilus shell in the next weak limestone bed above bed V (i.e., bed VII) also had associated crinoid debris. Within bed V at least another seventeen patches of crinoid debris occurred with apparently no cephalopod shell associated with them (Table 1). The mean distance between patches of crinoid debris, with or without associated cephalopods, was 9.5 m (Fig. 8). The longest radius of a patch of crinoid debris measured round a cephalopod shell was 1.65 m and it was the only radius to exceed 1 m. The mean of all the radii was 0.55 m. Crinoid patches without associated cephalopod shells covered an area of 0.60 m² on average (Table 2). Thus, it seems the crinoid patches are isolated by an average of about 8.5 m of sediment lacking any crinoid debris. Irrespective of the cephalopod shells, the crinoid debris is not scattered randomly or uniformly through bed V, but clearly in discrete patches and a majority of those patches had cephalopod shells near their centres.

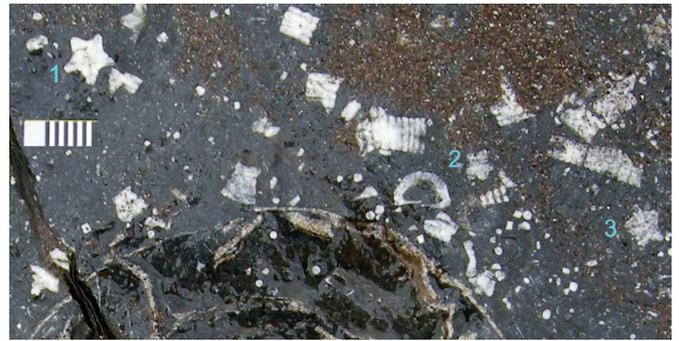


Figure 6. Crinoid columnals of different diameters in the same patch of debris in bed V, Doniford Bay, near Watchet, Somerset. **1** is 11.8 mm, **2** is 7.0 mm and **3** is 9.3 mm across at their widest. Scale bar in mm.



Figure 7. The largest ammonite in Bed V with crinoid ossicles and a pluricolumnal in the body chamber, Doniford Bay, near Watchet, Somerset. Note the epifaunal oysters on the outside of the ammonite (centre).



Figure 8. Scatter plot of crinoid patches and cephalopods superimposed over a Google Earth image of the exposures of Bed V (arrowed), Doniford Bay, near Watchet, Somerset. Colour key. Red dots = nautiloids only, blue = crinoid patches only, mauve nautiloids plus crinoids, green = the single large ammonite in bed V with associated crinoid debris. 2 = two nautiloid shells within 1 m of each other. Peripheral numbers refer to Ordnance Survey Grid References. **F** marks a fault truncating western end of exposure of bed V. Width of field of view approximately 450 m. Note the fossil occurrences extend beyond the east end of the exposure of bed V. See text for discussion of this point.

Specimen number	Nautiloid	Crinoid
1	Y	
2	Y	
3	Y	
4	Y	
5	Y	Y
6	Y	Y
7	Y	Y
8	Y	Y
9	Y	
10 (Ammonite)		Y
11	Y	
12	Y	Y
13	Y	Y
14	Y	
15	Y	Y
16	Y	
17	Y	Y
18	Y	Y
19	Y	
20	Y	Y
21	Y	Y
22	Y	Y
23	Y	
24	Y	Y
25	Y	Y
26	Y	Y
27	Y	Y
28	Y	
29	Y	Y
30	Y	Y
31	Y	Y
32	Y	Y
33	Y	Y
34	Y	Y
35	Y	Y
36	Y	Y
37	Y	
38	Y	Y
39	Y	Y
40	Y	Y
41	Y	Y
42	Y	
43	Y	
44	Y	
45	Y	Y
46	Y	Y
47	Y	
A		Y
B		Y
C		Y
D		Y
E		Y
F		Y
G		Y
H		Y
I		Y
J		Y
K		Y
L		Y
C1		Y
C4		Y
C5		Y
C7		Y
C12		Y
Totals	46	49

Table 1. Numbers of cephalopods and crinoid patches in bed V at Helwell Bay near Watchet, Somerset, England.

Patch No	Easting	Northing	E-W (cm)	N-S (cm)	Radius	Area (m ²)
C1	08390	43051	130	90	55.00	0.950
A	08382	43048	80	65	36.25	0.413
B	08378	43048	40	45	21.25	0.142
C4	08377	43057	90	90	45.00	0.636
C5	08371	43056	35	80	28.75	0.260
E	08343	43073	80	85	41.25	0.535
C7	08183	43116	20	8	7.00	0.015
F	08114	43131	200	120	80.00	2.011
H	08083	43140	70	140	52.5	0.866
J	08049	43149	60	50	27.50	0.238
K	08036	43144	90	75	41.25	0.535
C12	08024	43139	90	85	43.75	0.601
Mean			82.08	77.75	39.96	0.600
SD			47.55	34.31	18.49	0.525
Coef V (%)			57.93	44.13	46.27	87.42

Table 2. Calculated area of crinoid patches not associated with cephalopods

INTERPRETATION

Cephalopod preservation

It seems unlikely that all the cephalopods were deposited at the same time after a mass kill or after breeding as their state of preservation differs considerably. For example, specimen 14 (Fig. 2c) is well preserved, apparently complete and lacks associated crinoid debris. It lies vertically in the sediment with the highest part just below the top surface of bed V. The exposed part reaches 9 cm whorl thickness. Vertically, the specimen must be even wider (estimated at least 15 cm high) yet it shows no evidence of having been exposed on the sea floor. A complete *Cenoceras* 25 cm in diameter is 18 cm high when the aperture plane is horizontal. Specimen 14 appears to have been buried completely when the carbonate sediment was deposited. If complete, which seems likely as it is apparently undamaged, it must rest on a surface near or below the middle of bed V, which is of fairly uniform thickness at about 30 cm thick. Specimen 39 (Fig. 2f) lies on its left side, has preserved septa and a crushed part of the body chamber wall on its upper surface. It seems to rest on a much higher level within bed V and the exposed part appears to have been crushed. In contrast, other examples, e.g., specimens 25 (Fig. 3a) or 35 (Fig. 9a) were clearly damaged before final burial and show missing

or damaged septa. Equally, specimen 8 not only lacks septa but has an epifaunal oyster cemented to the inside of the body chamber (Fig. 9b) and so lay exposed on the sea floor for long enough for the epifauna to grow to 64 mm across. The solitary, large ammonite with associated crinoid debris (Fig. 7, specimen 10) has epifaunal oysters up to 42 mm across on the outside of its last whorl. Yet other examples show only fragments of the original cephalopod shell (e.g., specimen 24, Fig. 9c). Finally, specimen 22 (Fig. 3b) is both incomplete and associated with epifauna. Nautiloid specimens buried within bed V are more complete and better preserved than those near the top surface. It seems likely that they were more or less completely buried within the limestone bed soon after death, whereas those nautiloids that were only partially buried in bed V had the upper part eroded away, damaged or had epifaunal overgrowths on them due to prolonged exposure (several years) on the sea floor before final burial.

Crinoid preservation

The fact that the crinoid debris is still patchily distributed strongly suggests that the crinoids originally grew on the sea floor in small clusters, as modern isocrinids are known to do (Macurda and Meyer, 1974; Conan *et al.*, 1980). After death their skeletons disintegrated and fell to the sea floor more or less where the crinoids lived. Currents may have enlarged the debris field and clearly some crinoid material filled burrows, but overall the debris has not been widely distributed from the places where the crinoids lived. The crinoid debris varies in its extent and density, suggesting that the large patches with very dense ossicles grew on the sea floor for longer than those with few ossicles and small areal extent.

At least 15 patches of crinoid debris show ossicles of different diameters (e.g., Fig. 6), indicating that several spatfalls occurred before the crinoids were finally killed. This fact suggests that the crinoids were all killed at about the same time, so that immature crinoids with small columnals died at the same time as mature examples with large columnals. The crinoids were not killed by a sudden influx of sediment or they would be more completely articulated. Equally, they did not all reach maturity and die of old age over a long period of time, or examples with small columnals would not be commonly preserved. Final burial was not immediately, but certainly soon

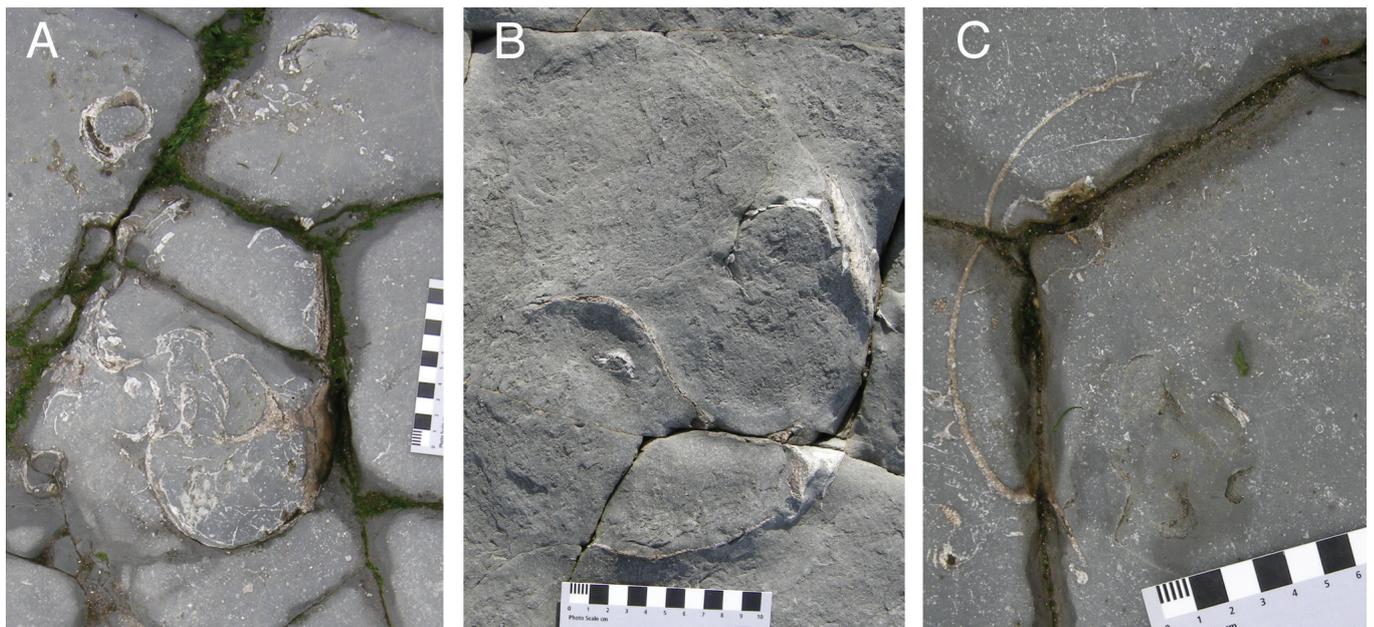


Figure 9. *Cenoceras* from Bed V, Doniford Bay, near Watchet, Somerset, damaged contemporaneously with deposition of the nautiloids. (a) Vertically orientated *Cenoceras* with damaged septa and outer body chamber wall; (b) *Cenoceras* lying on its left side with epifaunal bivalve attached to the inside of the body chamber and missing parts of the shell (bottom left); (c) Partially preserved *Cenoceras* damaged before final deposition.

after the death of the crinoids since some articulated parts of the skeleton (pluricolumnals and cirri) are present in most patches of crinoid debris (Figs 3a, 6). Thus, the skeletons did not disarticulate completely before final burial.

Crinoid debris in *Thalassinoides* burrows appears to be more completely disarticulated than elsewhere, suggesting that the occupants of the burrows may have aided the disarticulation by reworking the crinoid debris (Fig. 5). Equally, it is possible that bottom currents were able to wash only the smaller and most completely disarticulated crinoid material into the burrows. Pluricolumnals are very rare within burrows apparently; the largest seen involves only six columnals (Fig. 5). This, in turn, implies that the largest and most extensive pluricolumnals were not preserved by falling immediately into a protected environment, such as a vacant burrow. Decay of the collagen fibres that bound the pluricolumnals together was incomplete even in examples lying on the open sea floor. This reinforces the idea that sedimentation resumed and completely buried the crinoid debris soon, but not immediately, after death of the crinoids.

Although Oji and Amemiya (1998) have documented isolated lengths of crinoid stem that survived for over a year after becoming detached from the rest of the crinoid, it seems unlikely that this would account for the occurrence of articulated pluricolumnals in the crinoid patches. It is hard to imagine an event that could kill entire crinoids with their crowns elevated above the substrate, but still leave isolated lengths of stem (pluricolumnals) alive on the sea floor. So, I suspect the crinoids were probably killed by a return to poorly oxygenated seawater and that they all died during the same event.

Cephalopod/crinoid association

The 32 nautiloids with associated crinoid debris probably represent a minimum number. For example, specimen 14 (Fig. 2c) is almost completely buried within the sediment and apparently lacks any associated crinoid debris. Nevertheless, it is distinctly possible that crinoid debris exists near the base of the nautiloid hidden within bed V. Equally, several crinoid patches apparently without any associated cephalopod are so deeply excavated near their centres that even an undamaged, relatively thick nautiloid shell could have been completely removed by recent erosion at the top of bed V. It is impossible to be certain that both these examples demonstrate a genuine lack of crinoid/cephalopod association. Nevertheless, the possibility exists and so it is impossible to determine the true proportion of cephalopod/crinoid associations. Only three examples of nautiloid shells were detected in the extensive joint surfaces along the southern edge of the outcrop of bed V. One of the three had associated crinoid debris near its base, but the sample is too small to draw any general conclusions. Again, the single example with crinoid debris near the base of the cephalopod shell demonstrates the possibility that nautiloids deeply buried within bed V may not show any evidence of associated crinoid debris even if it is present.

The crinoids seem to have been associated with the largest cephalopod shells on the sea floor. Wani *et al.* (2005) have shown that modern *Nautilus* shells less than 20 cm in diameter do not float after death. They argued that a similar size limit probably applied to extinct ammonites. Thus one possible cause of the association between the crinoids and cephalopods might be that the crinoids attached to the largest floating cephalopod shells and lived a pseudoplanktonic life style. The crinoids in this case are isocrinids that lack the ability to attach their stems to solid objects (Simms, 1986). Modern isocrinids have stems the distal parts of which lie parallel to the substrate and which turn upwards proximally to elevate the crown above the substrate (Fig. 4b herein; Macurda and Meyer, 1974, fig. 1). Only Jurassic pentacrinids are known to have been able to attach to floating objects, including large cephalopod shells (Simms, 1986). It seems likely that the apparent preferential association of crinoid debris with large cephalopod shells was

simply because the largest shells provided the most secure anchorage for the crinoids.

In summary, it appears that bed V was deposited fairly quickly since cephalopod shells entirely enclosed within it are undamaged and more complete than those only partially buried within it. Nevertheless, large nautiloid shells continued to accumulate on the sea floor and were variously eroded and/or encrusted by epifauna. At the same time crinoid spatfalls occurred over several years and *I. psilonoti* established itself in clusters on the sea floor. The association between the two seems to have involved the crinoids establishing a grip on the cephalopod shells using their cirri directly or by wedging their stems into crevices between the cephalopod shells and the sea floor, as Fujita *et al.* (1987, fig. 4) have shown for the modern isocrinid *Metacrinus rotundus*. Both actions would anchor the crinoids more effectively, especially if the crinoids were gripping the largest shells. Macurda and Meyer (1974) showed that modern isocrinids are rheophilic and take advantage of weak bottom currents to enhance their feeding capacity. It seems likely that *I. psilonoti* did the same. Once one crinoid got a good grip on the substrate it would itself have been a good point of entanglement for juvenile crinoids seeking a firmer anchor. Thus, patches of crinoids of different ages could become established. Finally, something, quite possibly a return to disoxic or even anoxic bottom water conditions, killed all the crinoids more or less simultaneously. The crinoids then disarticulated and their ossicles fell to the sea floor, but were finally buried, along with the cephalopod shells, before all their ossicles completely disassociated.

On 7-8-17 the foreshore was particularly well exposed. Four nautiloids, some with associated crinoids, were seen in the impersistent limestone bed above and one in a similar bed below the main nautiloid bed. These additional nautiloids were sometimes the centres of limestone concretions. Thus, the association of nautiloids and crinoids was not confined to a single bed, but has not been seen elsewhere in the section east of Watchet.

DISCUSSION

Figure 8 shows that about 10 points extend north and east of the exposure of bed V in Helwell Bay, which implies a possible error in plotting. The figure was produced by superimposing a scatter of the 10 figure grid references of all the fossil nautiloids, crinoids and the single large ammonite seen in bed V onto a Google Earth image of Helwell Bay at the same scale. To do this the grid references of five reference points were taken. They were: the westernmost exposure of bed V where it is truncated by the fault, the north ends of the three groynes, and a peculiar, very large cylinder of rock on the shore NE of the easternmost exposure of bed V. The last is thought to be too large to be moved by the tides even under storm conditions and can be seen at the extreme right of Figure 8. Theoretically, 10-figure grid references are accurate to 1 m, but the hand held GPS device used only claims to be accurate to within 5 m. Nevertheless, repeated records of the same spot, for example the single, large ammonite with associated crinoid debris, often lie within 1–2 m of each other even if taken several months apart. The easternmost record of two nautiloids close together is approximately 30 m east of the easternmost exposure of bed V on the Google Earth photo and seems unlikely to be due to a reading error. Equally, the fact that some of the apparently erroneous dots occur to the north of the exposure is unlikely to be due to movement of the fifth reference point, when the other points plot along the narrowest parts of the exposure, which are sometimes only about 1 m wide. For example, the westernmost nautiloid seen in the eastern exposure was very close to the eastern groyne and plots exactly where it appeared to be in the field, as do the two plots in the minute exposure between the groynes. It seems impossible that these points could plot accurately, when the easternmost points plot erroneously. For these reasons, Figure 8 is presented exactly as it appeared on first superimposing the two images.

It is significant that all the apparently erroneous points plot to the north and east of the exposure of bed V. Locally the beds dip north and the Google Earth image implies that the points lie in the beds immediately above bed V. The most likely explanation is that the higher beds have been eroded away since the Google Earth image was taken on December 31st, 2009.

ACKNOWLEDGEMENTS

Professor D. B. Macurda Jr kindly provided the original photographs of Figures 4a and b. Dr M. J. Simms provided additional information concerning the stratigraphy of bed V and a thorough review, which together with the comments of the Editor helped improve the final manuscript significantly.

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