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Pentacrinites from the Lower Jurassic of the Dorset Coast of Southern England

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The Lower Jurassic rocks exposed in the sea cliffs around Lyme Regis, on the Dorset coast of southern England, are justly renowned for the wealth of fossils they have yielded to collectors over nearly two centuries. Although it is the vertebrates for which the site is best known, including some of the earliest discoveries of ichthyosaurs, plesiosaurs and pterosaurs, it is the invertebrates that account for the great majority of fossils. Impressive and beautiful though some of the ammonites and other fossils are, none of these invertebrates, or indeed any of the vertebrates, can match the beauty of what is perhaps the best-known fossil species found here, the crinoid *Pentacrinites fossilis*. The preservation of some specimens is extraordinary. Not only do they occur as large tangled groups with virtually every ossicle intact, but commonly they are coated with a thin film of pyrite, giving the impression that the whole fossil has been cast in bronze or gold. Some specimens have been justly claimed to be among the most beautiful fossils ever found (Fig. 189).

How have they come to be preserved in this way? The answer is an equally remarkable story that has been a source of discussion for more than 150 years.

ANCIENT DORSET

Nearly all specimens of *Pentacrinites fossilis* from the Dorset coast have been recovered from a 2-m interval within the *obtusum* Zone of the Lower Jurassic (Sinemurian) Black Ven Marls (approximately 190 million years old). Early accounts considered the crinoids to be confined to a single impersistent band, the 'Pentacrinite Bed', but it is now known that the thin crinoid lenses may occur at any level within this 2-m thickness and occasionally outside it. This part of the Black Ven Marls is dominated by dark, well-laminated, oil-rich mudstones quite atypical of the environments in which crinoids are usually found. Indeed, the crinoids are the only large, apparently benthic organisms in these mudstones. The remainder of the fauna is dominated by pelagic or nektonic organisms, particularly ammonites. The presence of *Pentacrinites fossilis* here would appear, therefore, to be an enigma, because crinoids cannot survive where oxygen levels are low, yet both the lithology and the remainder of the fauna indicate that the environment was anoxic.

CRINOID LENSES AND FOSSIL WOOD

As early as 1836 William Buckland noted that groups of *Pentacrinites fossilis* were commonly associated with the thin lenses of coalified driftwood that are common in this part of the succession. More important, he noted that these pieces of fossil driftwood invariably lay above the crinoid lenses rather than beneath them. From this he concluded that they had lived attached to pieces of

Hans Hess, William I. Ausich, Carlton E. Brett, and Michael J. Simms, eds., *Fossil Crinoids*.

Fig. 189. Intact crown of *Pentacrinites fossilis* on lower surface of 'Pentacrinites Bed', *obtusum* Subzone (Sinemurian), Charmouth. (The Natural History Museum, London; courtesy A. B. Smith.) ×1.

driftwood floating at the surface of the sea and that they had died when the driftwood and its crinoid cargo sank to the sea floor. This idea was not universally accepted, although its cause was championed elsewhere in relation to the similar occurrences of the giant crinoid *Seirocrinus* in the German Posidonienschiefer (see Chapter 23), and it remained a contentious issue, with *Pentacrinites fossilis* usually depicted in reconstructions as a benthic crinoid.

The relationship between *P. fossilis* and the associated driftwood is not, in itself, sufficient to convince everyone that these crinoids were pseudoplanktonic, living suspended beneath floating objects. Furthermore, the first *in situ* observations of living isocrinids in the early 1970s convinced some that the longer-stemmed pentacrinitids would easily have been capable of raising their crowns above the anoxic conditions close to the sea floor (Rasmussen 1977). However, with the development of the discipline of taphonomy, it was realized that if *P. fossilis* really had been pseudoplanktonic, then the way in which its remains became incorporated into the fossil record should be quite different from that of other fossil crinoids whose benthic mode of life was not in question. To establish whether the pentacrinitids really were different from other crinoids required detailed detective work into the morphology and preservation of these two groups of crinoids (Simms 1986).

DISARTICULATED BENTHIC CRINOIDS

Although fragmentary crinoids are not uncommon in the Lower Jurassic of the Dorset coast, intact specimens are decidedly rare. Other than *Pentacrinites fossilis* itself, the most common of these is a small isocrinid, *Balanocrinus gracilis*, which occurs in the *stokesi* Subzone of the Lower Pliensbachian in the area around Golden Cap, several kilometres to the east of Lyme Regis. This crinoid is not normally associated with driftwood, and because of its occurrence with a rich benthic fauna including bivalves, brachiopods and ophiuroids, there can be little doubt that it was truly benthic in habit. It provides a useful comparison with *P. fossilis*.

The rarity of intact crinoids reflects the speed with which the meagre soft tissues decay and the ossicles disarticulate following death. In most instances this disarticulation can be prevented only by rapid burial of the live crinoids by sediment thick enough to prevent scavengers and burrowers from reaching them subsequently. The specimens of *B. gracilis* from Golden Cap are preserved in lenses of fine sandstone or siltstone within a predominantly mudstone succession. The crinoids commonly appear to float within the sediment, individuals and parts of individuals being separated from others by a layer of sediment. Preservation is equally good whether the specimens are developed from the upper surface or the lower, although the stem and arms are commonly fractured at autotomy planes. Such preservation is just as one would expect in benthic crinoids that were enveloped by a sudden influx of sediment. In some instances this traumatic event appears to have triggered the autotomy of parts of the arms and stem.

The preservation of *P. fossilis* contrasts starkly with this. The crinoids occur as thin lenses composed almost entirely of crinoid ossicles cemented together with a syntaxial calcite overgrowth. Virtually no sediment occurs within these crinoid lenses, and there is no change in lithology above and below them. Furthermore, although the lower surface is commonly exquisitely preserved with every ossicle intact, the upper surface invariably shows some dissociation of the ossicles, with clear evidence of size-sorting by currents. It is clear from this that *P. fossilis* was not preserved by rapid burial in sediment and that, in fact, the animals' remains lay exposed on the sea floor for some time and were buried only slowly. It would appear that the softness of the sea floor muds, holding the ossicles in their original positions, and the absence of disruptive benthic organisms in this anoxic environment ensured the remarkable preservation of these crinoids.

PENTACRINITES FOSSILIS: A PSEUDOPLANKTONIC CRINOID

It might be argued that, rather than sinking from the surface to a more or less permanently anoxic sea floor, *Pentacrinites fossilis* inhabited the area during brief oxygenated spells and was then killed as anoxia returned. However, evidence from the associated pieces of driftwood establish quite unequivocally that *P. fossilis* must have been pseudoplanktonic. The position of the driftwood, above the crinoids, has already been mentioned and tends to support William Buckland's (1836) original suggestion that the crinoids were attached to floating driftwood. When the driftwood finally sank, waterlogged and overloaded by its cargo of crinoids and other organisms, the crinoids would reach the bottom first and the driftwood would come to rest on top. Benthic crinoids are known to use sunken pieces of driftwood as an anchorage (see Chapter 28), and it is conceivable that current activity rolled a piece of driftwood over so that it came to lie on top of the crinoids. However, a remarkable discovery in 1985 showed that *P. fossilis* must have colonized pieces of wood while floating at the surface and that this species was unable to survive in the anoxic conditions on the sea floor. The specimen in question is a fragment of highly compressed, coalified driftwood. The fragment is only 12 cm wide and 18 cm long, but it was clearly part of a much larger log at least 20 cm in diameter. Mature specimens of *P. fossilis* are preserved as a thin layer on the underside of the driftwood and extend a short way beyond its margin. The upper surface seemed devoid of any crinoid remains until examined closely. Along the one remaining original edge of the log, a band approximately 2 cm wide was covered with innumerable tiny white dots less than 1 mm across. Under the microscope, each was revealed to be the tiny attachment disc for the stem of a larval crinoid. A single, slightly larger attachment disc was present at one end of the driftwood fragment. The larval attachment discs were confined almost entirely to this marginal band, with only one small group further towards the centre. Their distribution coincides almost perfectly with a scenario in which *P. fossilis* colonized floating logs. The optimum position for the crinoids would have been on the underside of the log, a position that would have been occupied first (Fig. 190). As the log sank lower in the water, higher parts of it would have become accessible to and colonized by new larvae. However, the sinking of the log under its increasing burden would have been a sudden event and, as it entered the anoxic zone at the sea floor, would have resulted in the death of all the inhabitants of the log, from the earliest colonizers on the underside to the latest recruits along the upper edge. The virtual absence of attachment discs from the upper part of the log shows that, although it was now fully submerged as it lay on the sea floor and available for further colonization, none of the original inhabitants of the log survived to grow larger and no new recruits were able to occupy the vacant space.

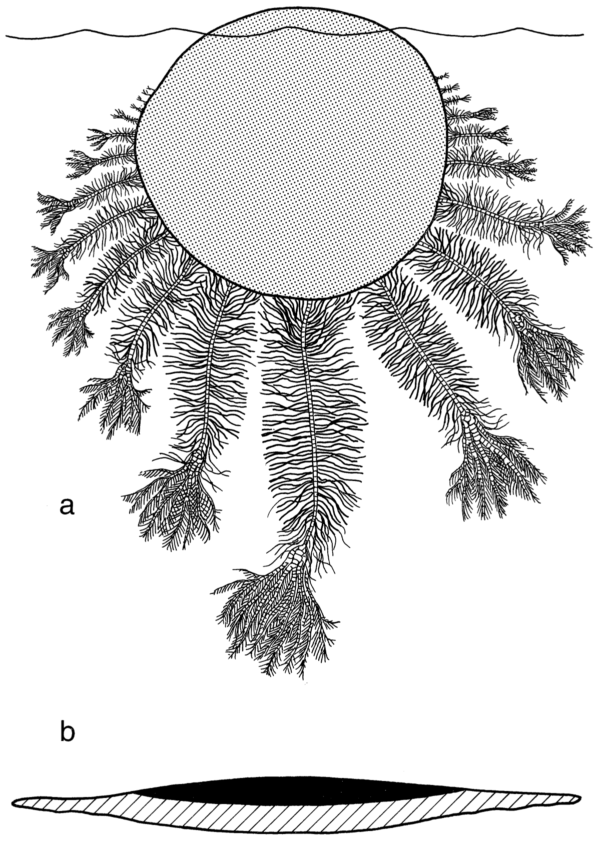

Fig. 190. (a) Reconstruction of distribution of short-stemmed *Pentacrinites fossilis* on floating driftwood reflecting colonization by successive generations of larvae on progressively higher parts of the log. (b) Cross-sectional appearance of coalified driftwood (black) after burial and compression; the larger crinoids are seen as a layer (hatched) extending from beneath the coalified driftwood. (After Simms 1986.) ×0.2.

Other aspects of the driftwood–crinoid relationship support the pseudoplanktonic model. The largest examples of *Pentacrinites* are confined to large pieces of driftwood, as might be expected, but in the case of benthic crinoids even large individuals may be found associated with quite small pieces of driftwood. Another feature of *P. fossilis*, and of its sister genus, *Seirocrinus*, is what has been termed the 'all or nothing rule' (Wignall & Simms 1990). Where these crinoids do occur on a piece of driftwood, they occur in great abundance and with a range of sizes, whereas other pieces are entirely devoid of crinoids. This suggests that a major barrier, in the form of vast stretches of open ocean, prevented all but a handful of crinoid larvae from ever reaching new, uncolonized pieces of driftwood. Instead, most larvae seem merely to have joined their parents on an increasingly overloaded ark. Such constant recruitment to the same piece of driftwood was clearly unsustainable, merely hastening the demise of the colony. In effect, each family group was committing a slow, inadvertent suicide. In contrast, benthic crinoids are not so dependent upon such specific substrates, but show a much more even distribution. Where they do occur associated with driftwood, it is commonly only in small numbers because many other niches are also available to them.

The stem length of *Pentacrinites fossilis* varies widely (Fig. 191). Short-stemmed individuals have closely spaced, long cirri. Such specimens resemble those of the invariably short-stemmed *Pentacrinites dichotomus* from the Toarcian of southern Germany (see Chapter 23). On the other hand, stems may reach 1 m in length; such stems commonly have highly cirriferous proximal regions and distal regions with very small, widely spaced cirri. However, one example of a distal-most stem with

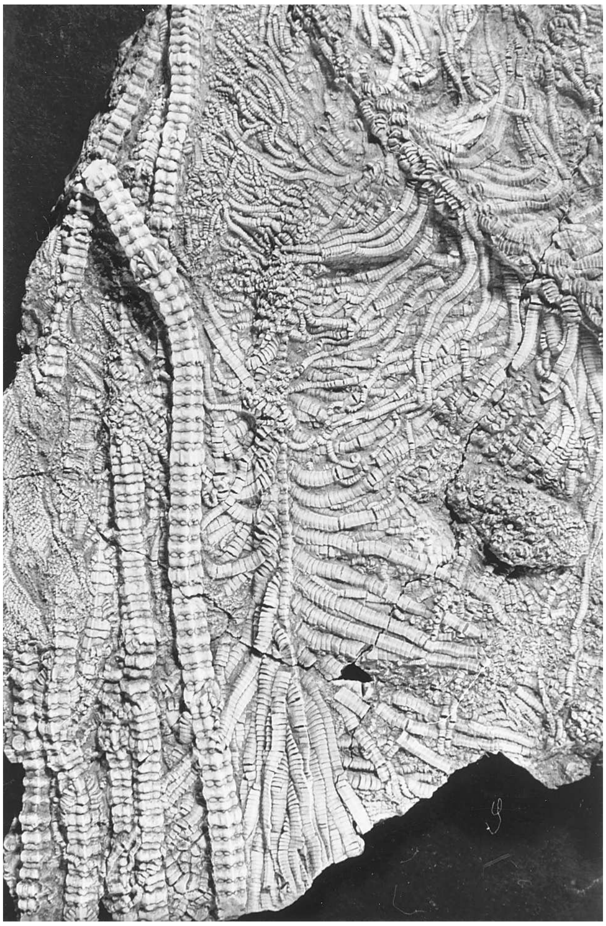

Fig. 191. Variation along the stem of *Pentacrinites fossilis* with cirriferous proximal stems in the right part of the figure and a bundle of stems from a more distal region with short, widely spaced cirri in the left part. Sinemurian, *obtusum* Subzone, Charmouth. (The Natural History Museum, London; also figured by Simms 1986.) ×1.

closely spaced nodals bearing long cirri is also known (Simms 1989). These differences may be related to the mode of attachment or to the size and shape of the supporting log.

Living attached to floating driftwood must have presented many hazards to these crinoids. Although the larval crinoids were attached by a cemented disc, this was abandoned when the crinoids were only 2–3 cm high and the cirri were used for attachment throughout the remainder of their life. Considering how crucial this was to their very existence, there does not seem to have been a standard strategy for ensuring firm attachment by the cirri. The development of cirri in *P. fossilis* shows interesting variation, with two distinct populations present even within single colonies. Some individuals have stems no more than 20 cm long along which the cirri are densely crowded and very long. In contrast, others have stems perhaps as much as 1 m in length along which the cirri are, except in the proximal region of the stem, widely spaced and very short. Commonly, these longer stems occur tangled together into large bundles, and occasionally at their distal end there is a second region of long, closely spaced cirri like those in the proximal region of the stem. Presumably these long cirri were used to grasp irregularities in the surface of the driftwood or, particularly in the case of the short-stemmed individuals, to attach to other individuals. Later species of *Pentacrinites*, such as the Toarcian *Pentacrinites dichotomus* and the Middle Jurassic *Pentacrinites dargniesi*, are only short-stemmed. A number of specimens of *P. dichotomus* are not associated with driftwood, suggesting that they may have exploited a different floating substrate, such as vesicular seaweed. As described in Chapter 25, *P. dargniesi* must have formed mats that drifted along the bottom. All in all, pentacrinitid colonies give the impression that their overall strategy for attachment was along the lines of: grab hold of anything and hope you don't fall off! This appears not always to have been entirely successful. Isolated specimens or groups of *Pentacrinites* are not uncommonly found in these anoxic mudstones and represent individuals that did become detached and sank to the sea floor.

Even for those that did not suffer this fate, there was no certainty that the driftwood would stay afloat for long under its increasing burden of crinoids. Yet *Pentacrinites* and *Seirocrinus* are among the largest crinoids known. How, and why, did they reach such huge sizes? First, the enormous obstacle that larvae faced in locating new pieces of driftwood in the vastness of the oceans may account for the large size of the adults, which need to produce a very large number of offspring. To ensure that they reached adulthood before the driftwood sank, they had an unusually fast growth rate, as indicated by growth lines on brachials (Simms 1986). This may have been achieved through a highly efficient, endotomous pattern of arm branching akin to the pattern of roads on an ideal banana plantation (Cowen 1981). The length of time that driftwood stays afloat may also greatly exceed the 1.5 years once thought to be the limit. Observations at Spirit Lake, near Mount St Helens, indicate that driftwood may remain afloat for more than 15 years, ample time for these crinoids to reach the spectacular size of some individuals.

The stratigraphic and geographic distribution of *P.*

fossilis is somewhat enigmatic. Although it is known to span several ammonite zones through the Sinemurian, it is common only in a 2-m interval that can be traced some distance. Rather than there having been a massive increase in the population of this crinoid, it seems more likely that the driftwood upon which these crinoids were dependent was caught in an oceanic gyre, rather akin to the Sargasso Sea, that became established during the deposition of this 2-m thickness of mudstones. The driftwood, and its cargo of crinoids, circled slowly in this gyre until sinking to the sea floor. Outside of such gyres this concentrating effect did not operate and hence *P. fossilis* is much more widely scattered.

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