LECTURE

Memorable moments in the history of crinoids: highlights of their evolution and adaptation

Summary of lecture presented to a joint meeting of the Society with the Yorkshire Geological Society on Saturday, 9th November 2002 by Dr Mike Simms of the Ulster Museum, Belfast

Compared with other, more mobile, echinoderms, such as sea urchins and star-fish, the plant-like crinoids, or sea lilies, would seem to have rather limited potential for conquering the world's oceans. But in late Palaeozoic times they were by far the most diverse and abundant echinoderm group and even today >600 living species are known. Typical crinoids comprise a highly jointed stem or column, used for attachment and elevation above the sea floor; a somewhat rigid cup, housing the vital organs, usually of 2 or 3 interlocking circlets of plates; and highly jointed, and usually branched, arms which form the feeding structures of the animal. This multi-element skeleton and its morphological division into stem, cup and arms, and the filter-feeding lifestyle which it supports, are features largely inherited from the earliest crinoids and their ancestors >500 Ma ago. Each of the ossicles of which the crinoid skeleton is made are a single crystal of calcite, an inherently brittle and highly inflexible material which imposes 'architectural' constraints on crinoid morphology. However, each calcite ossicle has a stereom structure, a ramifying network of cavities filled with soft tissue, which imparts much greater resistance to fracture than does solid calcite. In turn, each ossicle is connected to adjacent ossicles by soft tissues which impart flexibility to the skeleton. It is only within the limits imposed by these inherited and architectural constraints that crinoids can adapt to their environment and, through evolution, improve the way they feed and reproduce.

During the evolution of crinoids each of these three divisions, stem, cup and arms, has shown such evolutionary changes, often through ingenious adaptations and economic use of the basic building materials.

The main function of the cup is to house and protect the vital organs of digestion, nervous control, and the water vascular system characteristic of all echinoderms. In the earliest crinoids it comprised 4 circlets of plates, each offset and interlocking with adjacent circlets. However, reducing the cup to three, or even just two, offset and interlocking circlets does not significantly compromise its rigidity and this has happened independently in several crinoid groups. Its shape varies from saucer, to bowl, cone or globe-shaped, but its upper surface is covered with a plated flexible membrane or more rigid structure onto which both the mouth and the anus open. The obvious problem here of potential contamination of food is overcome in many crinoids by the development of an anal cone or tube, an analogy perhaps being drawn here with the tall chimneys found at many chemical and industrial works.

The arms support the tiny tube feet, which capture food particles and pass them down to the mouth. Increasing the effective arm length, usually by branching of various types, therefore increases the food-gathering capacity of the arms. Often the arms divide equally but one type of branching, called endotomy, in which smaller side branches arise at regular intervals from one side of a main arm branch, has been likened to the pattern of roads on a banana plantation. The analogy here is that this represents the most efficient configuration for a large filtration fan using a minimum of materials (Cowen, 1981), yet it is a pattern seen in very few crinoids. The arms may have additional uses in respiration and locomotion. Most post-Palaeozoic crinoids have some muscular articulations in the arms, in contrast to the entirely ligamentary arm articulations of

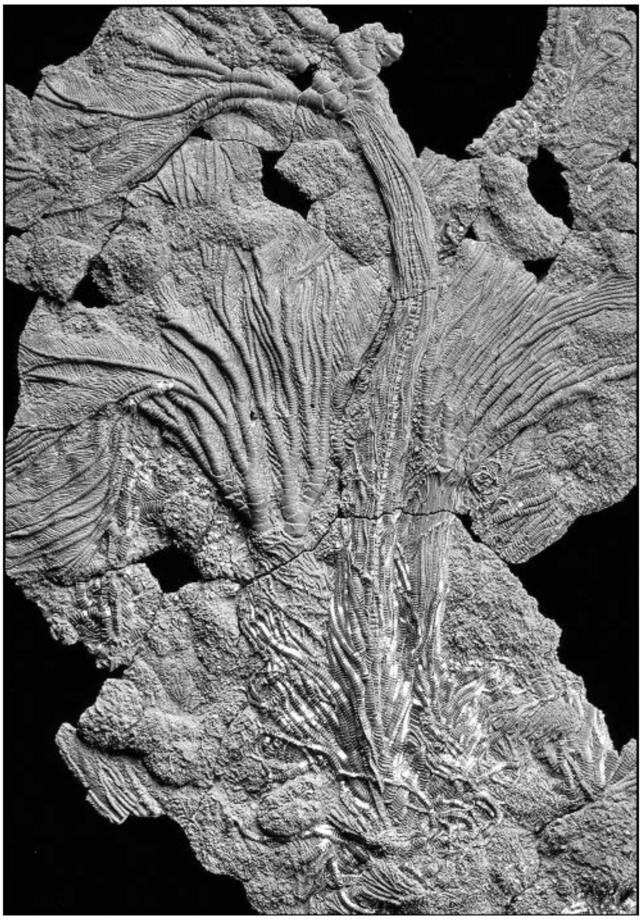

Figure 1. The early Jurassic pseudoplanktic crinoid *Pentacrinites fossilis*, from the Lias of the Dorset coast. This shows the typical morphology of many stalked crinoids - a flexible stem with numerous cirri, a small cup (just visible in the top specimen), and long and highly branched arms. Height of specimen c.250 mm.

Palaeozoic taxa. These muscles provide rapid and active movement to the arms, to the extent that some extant species are know to use the arms for swimming. The smallest of crinoids, termed microcrinoids, have a cup typically no more than 2 mm high and lack arms since energy demands do not require a large food-gathering apparatus.

The crinoid stem serves as an attachment structure and, more importantly, to elevate the feeding structure (the arms) above the sea floor and the benthic boundary layer. Attachment may be by a permanently cemented holdfast or by cirri, flexible appendages arising from the stem and which appear able to grasp sea floor objects or root the animal in softer sediment. In most crinoids the ossicles, or columnals, of the stem are connected by ligaments while crenulations on adjacent ossicles interlock to resist twisting and shearing stresses. During periods of high crinoid diversity, particularly in the Carboniferous, competition between different species of crinoid must have been intense at times. In response to this a distinct tiering appears to have developed, with different species having different stem lengths so that they did not all feed at the same level in the water column (Bottjer and Ausich, 1986). In the dominant extant crinoid group, the comatulids, the stem is absent and cirri arise directly from a centrodorsal plate to which the plates of the cup are attached. They use the cirri to grip on to rocks, corals, or even other crinoids, using these objects as surrogate stems to raise them above the sea floor.

A few crinoids have been interpreted as planktic in habit, floating in the water column. Most of these are tiny microcrinoids from the Mesozoic but one Devonian group, the scyphocrinitids, were quite large and appear to have dangled beneath a large bulbous float formed from highly modified cirri. Three other crinoid groups, the late Devonian melocrinitids, the late Triassic traumatocrinids, and the early Jurassic pentacrinitids, independently adopted a pseudoplanktic lifestyle, attached usually to driftwood or other floating detritus. They include the largest crinoids known, with arm spreads for *Traumatocrinus* and *Seirocrinus* (a pentacrinitid) of >0.5 m and stems of >20 m long in *Seirocrinus*. They also all have endotomously branched arms despite this pattern being generally very rare. It seems that the precarious existence of these crinoids (the driftwood might sink under the increasing weight of its passengers at any moment) exerted intense selection pressure to grow fast, requiring the most efficient filtration fan, and produce huge numbers of offspring so that at least a few might find a suitable floating attachment in the vastness of the open ocean, hence their large size (Simms 1986).

These pseudoplanktic species exemplify crinoid engineering at its best. The same selection pressures produced the same elegant solutions, in the process creating some of the most spectacular and beautiful fossil crinoids ever discovered.

Literature

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