LECTURE

Upright individuals and death by decapitation: unusual preservation of some Lower Palaeozoic crinoids

Summary of lecture presented to a joint meeting of the Society with the Yorkshire Geological Society on Saturday, 9th November 2002 by Dr. Stephen Donovan, of Nationaal Natuurhistorisch Museum, Leiden, The Netherlands

One of the simplest deductions that can be made concerning fossil crinoids is that the stem was upright and the crown was elevated above the seafloor. The image of the upright crinoids feeding with their outstretched arms is familiar from textbooks. However, the first observations of extant stalked crinoids, which live at a water depth of 100+ m, were only made using research submersibles in the 1970s (Macurda and Meyer, 1974) and earlier reconstructions got the orientation wrong. Originally thought to be rheophobes, living in low-energy environments with the crown spread to catch a gentle rain of detritus, they are now known to be rheophiles and orientate the crown perpendicular to the current to act as a fine 'fishing net.' If such a basic interpretation was incorrect, perhaps other deductions about fossil crinoids are in need of review.

Almost invariably, complete fossil crinoids are preserved parallel to bedding, that is, in a presumed death orientation, but were they necessarily upright in life? Some stalked crinoids may indeed have had recumbent columns, but the majority are interpreted as being elevators. How do we confidently recognise that this elevation occurred? Only rarely we find fossil crinoid columns preserved in an elevated position. Unusually, crinoid columns are preserved perpendicular to sub-perpendicular to bedding (=life orientation) in the Upper Silurian Moydart Formation, Arisaig Group, of Nova Scotia (Donovan and Pickerill, 1995). Such preservation has only rarely been reported previously. These columns invariably lack the crown and any obvious mode of attachment. Loss of the crown presumably occurred after the distal column was buried; the stalk may even have continued to live after loss of the crown (see below). Absence of any obvious root structure may be due to cut effect or could be indicative that at least some Palaeozoic crinoids lacked an identifiable attachment. Burial was rapid, but not enough to topple the crinoids, and occurred as a series of sediment influxes.

A further recent observation on extant crinoids is that loss of the crown does not necessarily lead to death of the column. Studies of extant stalked crinoids have shown that their stems are capable of surviving after detachment of the crown following self-mutilation, called autotomy (Oji and Amemiya, 1998), or predation (Donovan and Pawson, 1998), presumably feeding subsequently by the absorption of nutrients through the ectoderm (West, 1978). Isolated fragments of isocrinid column may survive for over a year under laboratory conditions and bourgueticrinid columns apparently endure following predatory decapitation, sealing over the wound with stereom and in some examples growing apical, root-like structures (Fig. 1a).

Such abilities may now be invoked to explain the common preservation of certain Palaeozoic crinoids without the crown, due to either predation or autotomy. Locally common crinoid pluricolumnals (that is, fragments of column) from the Upper Ordovician (Cincinnatian) of Kentucky, Ohio and Indiana that have rounded ends reminiscent of the overgrowths seen in modern bourgueticrinids following predation (Fig. 1b, c) (Donovan and Schmidt, 2001). These pluricolumnals are derived from the gracile disparid crinoid *Cincinnaticrinus* Warn & Strimple. Such specimens have hitherto been interpreted as globular distal attachments or distal terminations of mature individuals that have become detached from their holdfasts. However, it is more probable, by analogy with similar overgrowths in extant, decapitated bourgueticrinids (Fig. 1a), that some or all of these specimens represent overgrowths of the column following predation. If this new interpretation is correct, then implications include post-decapitation survival of crinoid stalks is now recognised for most of the history of this group and lethal predation on crinoid crowns occurred at least as far back as the late Ordovician.

The crinoids originated in the early Ordovician. The specimens illustrated herein (Fig. 1b, c) suggest that predation was an early phenomenon in the group's history. It seems probable that such predation was relatively uncommon, otherwise it should have been widely documented already. This is supported by studies of modern *Democrinus* spp., in which, from a sample of about 250 individuals, only 1.6% showed this pattern of predation (Donovan and Pawson, 1998), although many more specimens were regenerating one or more arms. The most probable predators in the Cincinnatian were vagile cephalopods, which are common fossils in the Upper Ordovician of the American Midwest, rather than the rarer fishes.

The ability for the column to survive following decapitation may have been a contributory factor in the development of large scale deposits formed primarily of crinoid debris called regional encrinites, which were accumulated in the Ordovician to Jurassic, that is, during the interval when stalked crinoids were a common component of the shallower water benthos. Regional encrinites are generally recognized to represent unusual deposits which show patterns of sedimentation different from other bioclastic accumulations (Ausich, 1997). It is not known how long such 'headless' crinoids may have survived, although modern isocrinid column fragments can live for over a year, at least, following autotomy (Oji and Amemiya, 1998). If predation on

crinoid-rich sea floors was higher than has hitherto been recognized, then disarticulated skeletal elements may have been added to the sediment budget during defaecation by predators, while the 'headless' crinoids persisted amongst unaffected individuals, acting as baffles to current flow and aiding accumulation.

Literature

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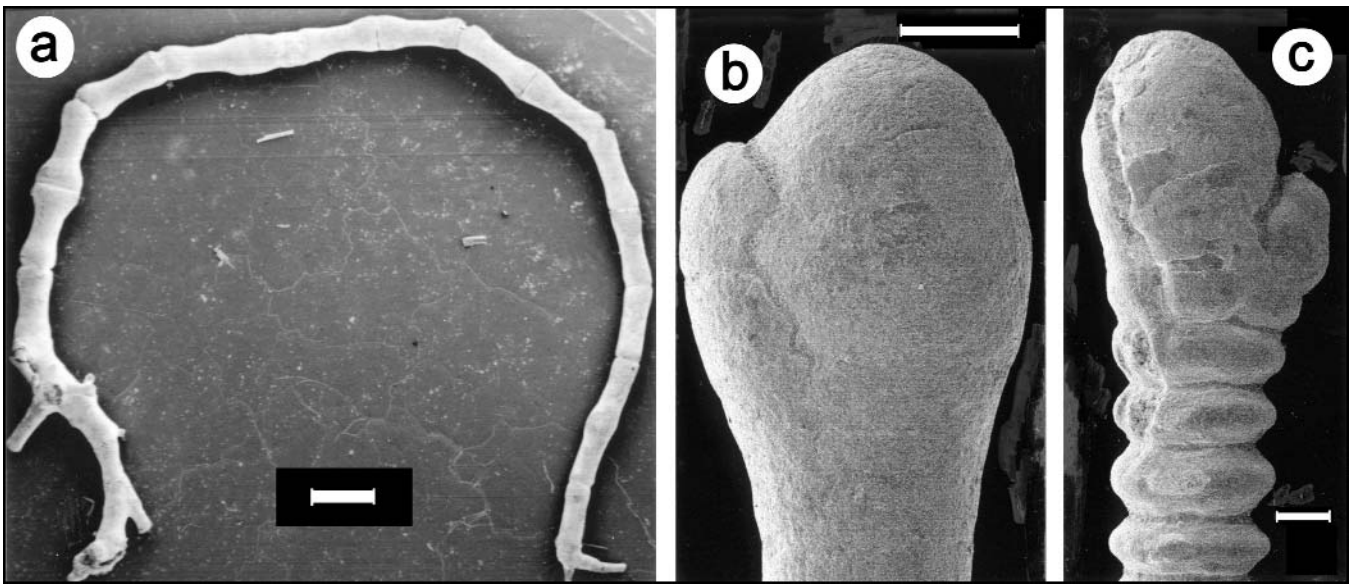

Figure 1. 'Headless' crinoids, ancient and modern.
a. Decapitated Recent bourgueticrinid, *Democrinus chuni* (Döderlein), south Atlantic Ocean (after Donovan and Pawson, 1998, fig. 1A). Complete specimen with attachment (left) and apical overgrowth (right); the curvature is due to storage in a glass jar. (USNM E11616).
b and **c**. Upper Ordovician crinoids interpreted as decapitated, *Cincinnaticrinus* spp. from Kentucky and Ohio, U.S.A. (after Donovan and Schmidt, 2001, fig. 3D, B, respectively). (b: BMNH EE 6641. c: BMNH EE 6642).
Specimens: National Museum of Natural History, Smithsonian Institution, Washington (USNM) and Natural History Museum, London (BMNH). Scanning electron micrographs of specimens coated with 60% gold-palladium. Scale bars are 1 mm long.