Palaeoecology and taphonomy of a fossil sea floor, in the Carboniferous Limestone of northern England

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Abstract: Death assemblages preserved on bedding planes - fossil 'sea floors' - are important palaeontological sampling points. A fossil sea floor from Salthill Quarry (Mississippian), Clitheroe, Lancashire, preserves a mixture of crinoid debris with rarer tabulate corals and has yielded a rich diversity of palaeoecological information. Identifiable crinoids include *Gilbertsocrinus* sp. and a platycrinitid, associated with columnals/pluricolumnals, brachials/arms and a basal circlet, crinoid-infesting tabulate corals such as *Cladochonus* sp. and *Emmonsia parasitica* (Phillips), and the spoor of a pit-forming organism. Long pluricolumnals showing sub-parallel orientations suggest a current azimuth; one coral is silicified with the mineral beekite.

Biotic interactions between ancient organisms include the obvious, the subtle and the problematic (Boucot 1990). Obvious associations include the direct evidence provided by cephalopod hooks (=prey) preserved in the stomachs of predatory ichthyosaurs (Pollard, 1968), and intergrowths of Pliocene corals, bryozoans and barnacles (Harper, 2012). Subtle might include changes in morphology to mammalian herbivore teeth in response to changing vegetation (Winkler, 2011). The problematic include distinct boring or embedment structures preserved in what were skeletons of live (Donovan & Jagt, 2002) or dead organisms (Donovan, 2014), but whose producer remains unknown. All three forms of interactions between ancient organisms may be locally common in the fossil record, but are only recognisable if we look for them; otherwise, they will fail to yield new data or pose new questions. Our penchant for collecting solitary specimens or bulk samples, both worthy methodologies, may mean that we fail to find the true 'snapshot' of time that is represented by the bedding plane.

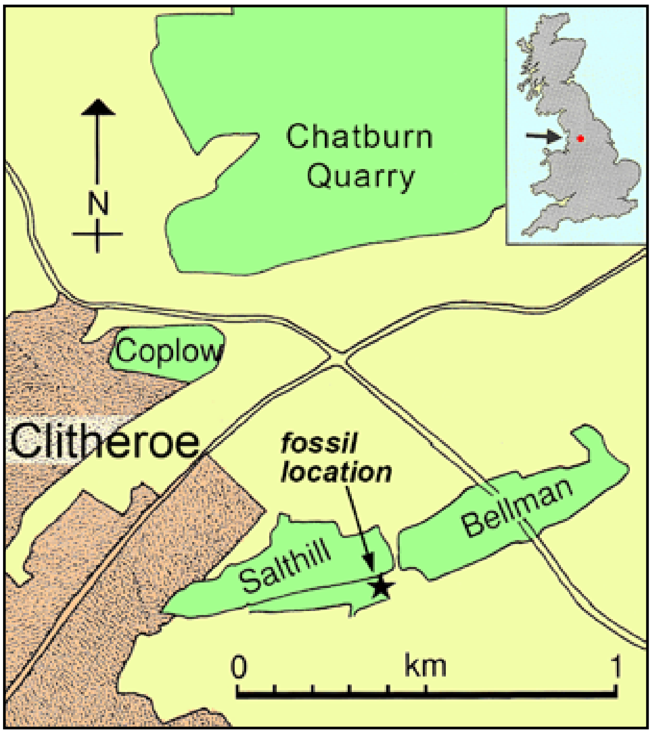

Figure 1. *The disused Salthill Quarry and the Bellman, Chatburn and Coplow quarries, northeast of Clitheroe.*

Studies of fossil bedding planes and the palaeontological associations preserved thereon are not currently in vogue in palaeontology, where the database is currently more important than the unique specimen; it may be that bedding planes are currently more important as sources of information to sedimentologists and ichnologists. Perhaps palaeontologists should once again return to the bedding plane assemblage as a unique source of information.

To give one example of the importance of the bedding plane view, Martin & Rindsberg (2011) examined a stratigraphic section in the Late Pleistocene Silver Bluff Formation of St. Catherines Island, Georgia, USA, in exquisite detail. This unit is only about 1.5 m thick, but they teased out a mass of stratigraphic, sedimentological and ichnological detail. Previous interpretations have favoured a "… marine still-stand facies and … marine firm-grounds or terraces formed during a Silver Bluff sea level high" (p120). In contrast, Martin and Rindsberg recognized a foredune facies overlain by backdune, storm-washover fan and backdune meadow facies.

In considering the ichnology of the storm-washover fans, the authors went in two different directions to find support for their observations and interpretations. Reviewing the literature, it appeared that the ichnology of ancient storm-washover fans has been examined only rarely. Previous research suggested storm-washover fans to be little bioturbated and to have a low diversity of trace-makers. They are typically identified from their stratigraphic position and sedimentary structures, yet Martin & Rindsberg showed that trace fossils provided strong, even distinctive supporting data. Their second direction was direct observation of modern storm-washover fans on St. Catherines Island. These provided information supporting their interpretations, but also showed what is lost in examining a vertical stratigraphic section. Succinctly put, these are the large traces that are more apparent in bedding plane view, principally produced by terrestrial tetrapods, mainly large birds and medium-sized mammals. The evidence may be there, but it cannot be seen without an exposed bedding plane.

This description is of a very different example, chosen from a rock unit, the Carboniferous Limestone (Mississippian), that is widespread in the British

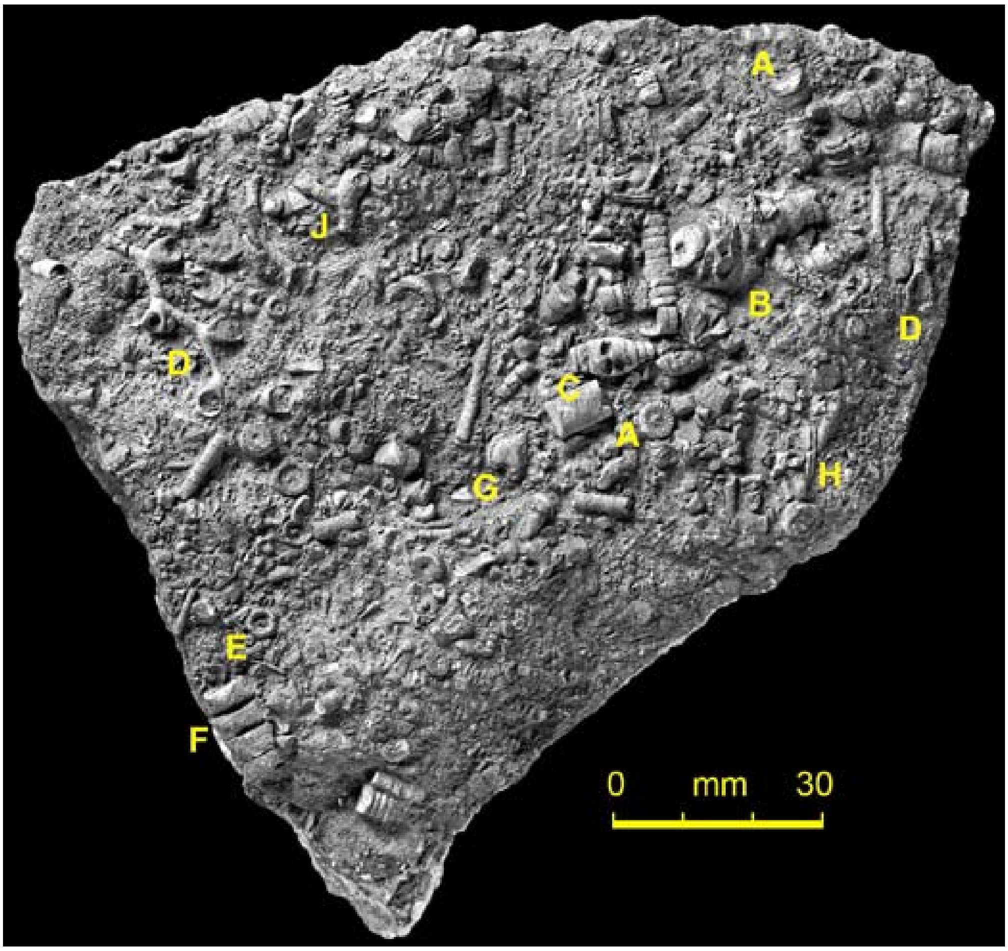

Figure 2*. Specimen BMNH EE5717 is a slab of crinoidal biosparitic limestone from Salthill Quarry, Clitheroe, Lancashire.*

A: Two columnals of probable Gilbertsocrinus *Phillips.*

B: Pluricolumnal encrusted by tabulate coral colony, Emmonsia parasitica *(Phillips).*

C: Pluricolumnal with multiple borings and showing growth reaction.

D: Two specimens of Cladochonus *M'Coy.*

E: Probable basal circlet of a crinoid cup.

F: Pluricolumnal of a platycrinitid crinoid.

G: Brachial ossicle.

H: Fragment of arm.

J: Indeterminate coral, with beekite silicification.

Isles, although there are myriad other possibilities, both older and younger (Donovan *et al*., 2014). In all such studies, diverse lines of evidence are utilised to demonstrate where the fossil specimens represent a life (Littlewood & Donovan, 1988) or death assemblage (Donovan, 2012), as defined by Ager (1963) and others. A death assemblage can be considered to represent a continuum between two end-members, mixtures of fossils that never lived in the same environment during life, such as benthic fossils mixed with nektonic and planktonic taxa, and those that potentially lived together, but were transported and may have been disarticulated/broken before final burial. David Lewis (Natural History Museum, London) refers to such fossil-rich death assemblages on bedding planes as 'fossil seafloors' and recognises their importance in acting as sampling points for the ancient biota at the time and place of deposition.

This account squeezes out palaeoecological information regarding one group, the crinoids, from a 'fossil seafloor' specimen collected many years ago. The specimen has already been figured and some points discussed (Donovan, 1991b), but these and other data are considered in more detail herein. The specimen is important because of the number and variety of crinoids and corals preserved in a limited area, and the information it provides on diverse aspects of the environment and biotic interactions. As in any palaeoecological study, much information is lost and irretrievable; however, what is known in this example is unusually rich. Terminology of the crinoid endoskeleton follows Moore *et al*. (1978) and Ubaghs (1978). The specimen is deposited in the Department of Earth Sciences, Natural History Museum, London.

Locality and horizon

The specimen was collected from float at Salthill Quarry, Clitheroe, Lancashire, England (Fig. 1), from float at or near point 3 of Grayson (1981); locality 4SH+5SH of Ausich & Kammer (2006) and locality 4 of Kabrna (2011) [SD755425]. It is derived from the Salthill Cap Beds (Miller & Grayson, 1972) in the Dinantian (Mississippian, Lower Carboniferous), Tournaisian, lower Chadian (George *et al*., 1976; Donovan & Sevastopulo, 1985; Ausich & Kammer, 2006).

Descriptions of the fossils

The specimen, BMNH EE5717, is a slab of crinoidal biosparitic limestone about 146 mm long, 122 mm wide and 38 mm thick. The illustrated surface (Fig. 2) is rich in bioclastic debris, particularly crinoids, mainly columnals and some long pluricolumnals with rarer brachials, but also including some tabulate corals. There is a great diversity of ossicle morphologies. Long pluricolumnals and at least one arm fragment show a sub-parallel orientation corresponding to the length of the page in Figure 2; other pluricolumnals are approximately perpendicular to these. Of the many ossicles, the following are of particular note.

A: Two circular columnals, each with a small, circular, central lumen surrounded by a narrow, raised perilumen; a broad, circular, depressed areola; and a marginal crenularium with some crenulae extending further towards the lumen than others.

B: A robust pluricolumnal of circular section, 24 mm long, heteromorphic with at least three orders of columnals, the two higher orders with convex latera, the third with planar latera. Articulation is symplectial, that is, by interlocking radial ridges and grooves. The pluricolumnal is encrusted by a tabulate coral; there is no obvious growth reaction of the stereom calcite of the crinoid.

C: A pluricolumnal 12 mm in length that bears multiple cup-shaped pits each assigned to the trace fossil *Oichnus paraboloides* Bromley, 1981. The pits are rounded, but more oval than circular; two shallow pits appear to merge as a figure-of-eight. There has been a strong stereom calcite growth reaction by the crinoid; at its narrowest the column is 2.5 mm in diameter, but it is swollen to a maximum diameter of 6.0 mm. The column is probably heteromorphic, but swelling has deformed the shape of most columnals.

D: Two specimens of stalked tabulate corals are labelled (D): a preserved length of about 30 mm on the left, but broken from any attachment; and a disarticulated cup of this taxon is on the right.

E: A small circlet of five, equal, regularly-disposed plates.

F: This pluricolumnal, unlike others on the slab, consists of elliptical columnals. It is four columnals in length, each of which is about the same size. Latera are slightly convex and unsculptured.

G: A large brachial (=arm plate), poorly preserved.

H: The oral surface of a long, slender, unbranched crinoid arm.

J: This poorly preserved, branched coral has a mineralised surface of concentric, ring-like structures.

Interpretations of the material

The great diversity of crinoid ossicle morphology is indicative of a large diversity of crinoid taxa (Donovan, 1992; Donovan & Lewis, 2011), possibly accumulated over a long period of time; these are supplemented by at least three species of coral (B, D, J). The surface shows some evidence of current action. Many long fossils, mainly pluricolumnals, are orientated either towards the top and bottom of the image or side-to-side. The former group includes the longer specimens, which are interpreted as indicating the azimuth of current flow, being oriented parallel to flow on the sea floor. Some shorter pluricolumnals may have been rolled and, hence, are preserved at 90^0 to the inferred flow.

A: These columnals are most probably from the diplobathrid camerate crinoid *Gilbertsocrinus* Phillips, well known from its thecae in the Clitheroe area (Donovan & Lewis, 2011). The features of the *Gilbertsocrinus* columnal were described in detail by Riddle *et al*. (1988) and Donovan (2006).

B: The encrusting epizoozoan (*sensu* Taylor & Wilson, 2002) coral is *Emmonsia parasitica* (Phillips), which is presumed to infest the column through 360º. Although it is only apparent on the one side of the exposed pluricolumnal, the coral does not spread out over the adjacent bedding surface, suggesting that it continues around the column (*cf*. Smith & Gullick, 1925, pl. 8, fig. 10; Hudson *et al*., 1966, figs 4, 5). That is, the coral almost certainly encrusted the pluricolumnal when it was in an erect position, when the crinoid was alive; less probably, it could have encrusted a dead pluricolumnal on the sea floor which was periodically rolled. This is interpreted as an obligate commensal relationship between the coral and the living crinoid (Donovan 1991b, p251).

C: These prominent pits are not interpreted as predatory or parasitic as they do not penetrate the axial canal; rather, the producing organisms were each building a pit as a domicile. That the crinoid was both alive and reacted against this invasion of its skeleton is indicated by the swollen stereom calcite reaction. Pits in the endoskeleton of Palaeozoic pelmatozoans may be difficult to interpret (Donovan 1991b), but, like other examples in the literature (Brett, 1978; Meyer & Ausich, 1983; Donovan, 1991a), the pit-forming organisms gained two advantages: an elevated position on the crinoid stem, that would have been advantageous in harvesting food from clean water currents, and a protective hard substrate surrounding the borer itself. Further, although there are multiple pits, it is possible that they were formed from a single pit-forming organism varying its position (Donovan & Lewis, 2010).

D: These are specimens of the epizoozoan (*sensu* Taylor & Wilson, 2002) tabulate coral *Cladochonus* sp. These are interpreted as obligate commensals of crinoid stems (Donovan, 1991b) and in "... Devonian examples ... are only found attached to columns on which they are commonly positioned around the entire circumference" (Meyer & Ausich, 1983, p406, referring to McIntosh, 1980). Hudson *et al*., (1966) and Donovan & Lewis (1999) discussed and illustrated *Cladochonus* specimens attached to and intergrown with crinoid columns in life.

E: This is a basal or infrabasal circlet of a small crinoid cup. It is perhaps seen in basal view, the base of the cup being depressed. It is not a pentameric crinoid columnal such as *Barycrinus* Wachsmuth (Donovan & Veltkamp, 1990).

F: This is undoubtedly part of the column of a platycrinitid, monobathrid, camerate crinoid. These are elliptical in section with a synarthrial ('see-saw') articulation corresponding to the long axis of the articular facet (not apparent in this specimen) (*cf.* Donovan & Lewis, 2011, pl. 2, figs B, C). Two genera of platycrinitid are common at Salthill Quarry, *Platycrinites* J. S. Miller (three species) and *Pleurocrinus* Austin & Austin (four species) (Ausich & Kammer 2006), based on morphology of the crowns.

G: Crinoid brachials and arms are less often recognised by palaeontologists, but they are commonly present where there are columnals. This example is unusually large, albeit poorly preserved, and shows the adoral groove adjacent to the letter G.

H: Unlike G, this specimen is gracile and shows the adoral surface of a partial arm, in plan view.

J: This specimen is partially silicified. The surface preservation is called beekite, "... a chalcedonic variety of silica" (Etheridge, 1893, p75), typically formed on invertebrate skeletons with a micro-crystalline structure (Carson, 1991).

In conclusion, it is suggested that the study of fossil 'sea floors' (Donovan *et al*., 2014) has much to offer the systematist, palaeoecologist, taphonomist and ichnologist,though this one example was admittedly chosen with care for the diversity of information that it provides. There is a danger of palaeontologists becoming two dimensional, by studying sections, but not pursuing the bedding plane in the third dimension.

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