Ruminations on the 'Salthill bug'

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Abstract: Trace fossils are an important part of the sedimentary record, providing data of relevance to palaeontology, sedimentology and stratigraphy. What they cannot do is give definitive evidence of the producing species unless the two occur in close association. But the nature of the producer can be inferred and its habits deduced. Borings in fossil crinoids from the Mississippian of Clitheroe, Lancashire, UK, were the spoor of an unknown producer, the 'Salthill bug'. It was most likely a worm *sensu lato* with a free-swimming larval stage. The shallow pits, assigned to the trace fossil *Oichnus paraboloides* Bromley, were domiciles of a gregarious, filter-feeding organism which preferentially selected an elevated site on a fossil crinoid, most commonly on the stem. The 'Salthill bug' was probably a snug fit in its pit.

A trace fossil provides information. It is a different suite of information from a body fossil, yet no less relevant to studies of sedimentology, palaeontology and stratigraphy. There is, perhaps, a tendency to 'look down' on trace fossils by some palaeontologists because the producing organism cannot be named to species except in rare circumstances. Yet the contribution to palaeoecology that is made by a trace fossil outweighs any perceived inconvenience to not being able to add one more species to the faunal list. If a producing organism can be named, perhaps by being preserved in an ancient or Recent trace (such as Pickerill & Forbes 1978; Conway Morris *et al*. 1982), then this should be regarded as a bonus; the true palaeobiological value of any trace must be its contribution to our perception of the form and habits of the unknown producer, and its environment (such as Yochelson & Fedonkin 1993; Pickerill & Blissett 2000).

Borings are an important and distinctive part of the record provided by trace fossils. Significantly, shelly boring organisms may be preserved *in situ* and thus provide the identity of the producer (such as Donovan 2013), assuming that they are not nestlers which later invaded the empty borehole. But many borings are produced either by larger, predatory organisms such as carnivorous snails (Bromley 1981; Pickerill & Donovan 1998), which devour their prey and move on, or unmineralized 'worms' *sensu lato* in constructing a domicile. The latter leave behind a borehole into which they fitted. Thus, we have some simple indications of the size and shape of the producer without quite knowing just what it was and what it looked like.

Donovan and Tenny (2022) recently speculated on the nature and ecology of a Mississippian organism that produced pits assignable to the ichnospecies *Oichnus paraboloides* Bromley, 1981, invasive in the endoskeleton of fossil crinoids. My own interest in this association goes back over 30 years (Donovan 1991, 2015; Donovan & Tenny 2015, 2022; Donovan *et al*. 2005; Folmer & Donovan 2021) and I have long been resigned to not knowing the precise identity of the producer. (Or, less probable, could it be producers, as a great diversity of organisms might generate *O. paraboloides*; Bromley 2004?) In the present paper, I am once again in pursuit of the habits of the producing organism, speculating on its nature on the basis of a new specimen collected recently.

Locality and horizon

(Abridged from Donovan & Tenny 2022). Salthill Quarry, Clitheroe, Lancashire, UK, is a geological Site of Special Scientific Interest (Fig. 1). This disused quarry is now shared between several industrial units and a geological trail. The crinoid- and blastoid-rich beds are best exposed at locality 4 of Kabrna (2011; NGR SD 755 425), a scraped, sloping area well-known to collectors, albeit rather overgrown (Donovan *et al*. 2014). It exposes the Salthill Cap Beds (of Miller & Grayson 1972), Hodder Mudstone Formation, and Worston Shale Group, resting unconformably on the Clitheroe Limestone Formation (Riley 1990): Dinantian (Mississippian, Lower Carboniferous), lower Chadian in age (Ausich & Kammer, 2006).

The specimens discussed herein are deposited in the collections of the Natural History Museum, London (prefix NHM). Crinoid terminology follows Moore *et al.* (1968, 1978); trace fossil terminology follows Häntzschel (1975).

Description

A crinoid pluricolumnal, NHM EE 17716 (Fig. 2), which is both swollen and pitted. Height about 18.5 mm, composed of 12 columnals; diameter varying between about 6.5 and 12.0 mm. Articular facet circular; lumen central, small, pentastellate; radial symplectial articulation; other details not apparent. Pluricolumnal heteromorphic, columnals of varying height, but precise pattern of columnal insertion indeterminate due to disruption by the swollen column. Latera planar and unsculptured.

Three small, circular, shallow pits in latus assigned to *Oichnus paraboloides* Bromley. All pits of similar diameter, about 2.0-2.5 mm, but none is deep enough to penetrate axial canal. Two pits are adjacent; all three are centred to eccentric on sutures between columnals. All pits are on the same side of the pluricolumnal.

Discussion

Donovan and Tenny (2022) made several incisive comments on the form and function of the organism that generated these pits in both dead and live crinoids, the 'Salthill bug'. The crinoid NHM EE 17716 was

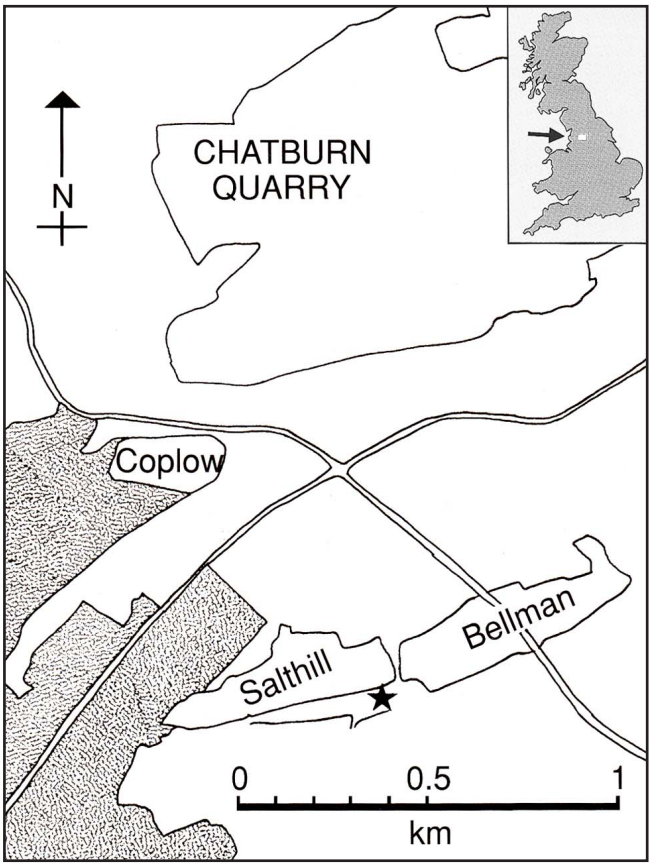

Figure 1. *Map of the north-east Clitheroe area, showing the relative geographical positions of Coplow and Salthill (both disused), and the working Bellman and Chatburn quarries (after Donovan 1992, fig. 1). The star indicates the position of the surface of the locality discussed herein, the scraped surface at Salthill Quarry. The inset map indicates the position of the main map (arrowed) in mainland Britain.*

obviously alive when infested as indicated by its swollen growth reaction to the pits (Fig. 2). I have used the principal points made by Donovan and Tenny (2022) to determine sub-headings below, and to guide me in adding information and ideas to their original determinations.

Nature of the producer

Bromley (2004, p 466) reviewed the producers of small round holes in shells as known at the present day, but '… confident identification of the borer is not common'. He also considered that '*Oichnus* appears to be unimportant from the Carboniferous to Triassic' (Bromley 2004, p 467). This ignored, for example, the evidence from Salthill Quarry and elsewhere in the Mississippian of the British Isles (such as *O. simplex* in Trearne Quarry, Ayrshire; Donovan & Hoare 2019).

But *O. paraboloides* is a simple trace fossil — in this example, just parabolic pits in a stereom calcite substrate — and we must assume that not all groups of Palaeozoic pit-formers have survived to the present day. Donovan and Tenny's (2022) small, unmineralized invertebrate must still be the correct interpretation. If the pits were produced by small arthropods or

Figure 2. *Crinoid pluricolumnal from Salthill Quarry, Clitheroe, NHM EE 17716, lateral view showing circular pits,* Oichnus paraboloides *Bromley, associated with swelling. Scale bar in mm. Specimen uncoated.*

minute shelled molluscs, there would be at least some likelihood of skeletal elements being preserved in the pits, which they are not. So, as unsatisfactory as such a broad-brush identification must be, it is most likely that the boring organism was some sort of 'worm' *sensu lato* with a free-swimming larval stage (also see 'Gregarious habit', below). The free-swimming larva would be able to swim to an elevated position on a live crinoid; a benthic larva would have to scale the stem like a platyceratid snail (Schoor *et al*. 2020).

Orientation and function of the pits

The latera of this pluricolumnal are only visible through *c*. 200 degrees, but all the pits that are visible are clustered in a tight group vertically, suggesting that there was some advantage to this situation. The most likely explanation is that this was the up current side of the stem (compare with Donovan 1991). This assumes that the 'Salthill bug' was a filter feeder, facing into the water current to harvest plankton.

It is highly unlikely that the 'Salthill bug' was parasitic (Donovan 2015). Although preserved, in part, infilled by diagenetic calcite, the pits are seen to be shallow and certainly do not perforate the axial canal; that is, the 'Salthill bug' was not harvesting nutrients or tissues from the crinoid. The only unmineralized tissues in the calcite of the pluricolumnal would have been mutable collagenous tissues (Emson & Wilkie 1980), at best likely to be a very poor source of food. Such an elevated position away from the seafloor would also suggest that a predatory habit was unlikely.

Gregarious habit

Many extant, sessile invertebrates are gregarious, in part being attracted to a suitable substrate by the pioneer infesters releasing species-specific organic molecules into the environment to appeal to conspecific larvae (Clare 2011). Such a habit is at least suggested by the close clustering of pits (compare with Donovan *et al*. 2006; Donovan 2015). Post-settlement relocation may have been impossible, as in barnacles (but see speculations in Donovan & Lewis 2010), and if reproduction required copulation, again like a barnacle, then a gregarious habit was essential.

Substrate

The 'Salthill bug' has only been found infesting echinoderms, most likely only crinoids (the infested pluricolumnals are too robust for blastoids). Other shelly substrates at this site are admittedly rarer, but corals and brachiopods, for example, appear to have been untouched. Whether only certain species were selected for invasion by the 'Salthill bug' is unknown, albeit likely, because the commonest infestations were in stems that remain anonymous, not retaining sufficient evidence to be classified to family, genus or species. However, the cups of two quite different species have been found with borings, namely the disparid *Synbathocrinus conicus* Phillips, 1836, and the monobathrid camerate *Amphoracrinus gilbertsoni* (Phillips, 1836) (Donovan 1991, 2015; Donovan *et al*. 2006; Donovan & Tenny 2022). A future attempt to recognise bored pluricolumnals to morphospecies would be a most worthwhile project.

Did the 'Salthill bug' only invade live substrates or would it produce pits in dead crinoids? One study (Donovan & Tenny 2015) identified both from one specimen: one group of pits had engendered definite growth reactions, whereas others had not, even in the same specimen. This study is still considered valid. From the above arguments, infestation of an elevated, live host would be preferable, yet scenarios can be formulated where there was no option, but to make pits in a dead crinoid.

Size of the producer

Was the producer the same size as or smaller or bigger than the *O. paraboloides* pits? Other borings are commonly inhabited by borers that fit their borehole snuggly (such as several examples in Kelly & Bromley 1984). A pit that is larger than the producer is counterintuitive, needing more energy to make it than a cut to size pit. A producer that is larger than the pit might be possible if it had a protective shell that could close over or into the pit like the operculum of a gastropod. Nonetheless, a producer the same size as the pit seems the most likely explanation.

References

Ausich, W. I., Kammer, T. W. 2006. Stratigraphical and geographical distribution of Mississippian (Lower Carboniferous) Crinoidea from England and Wales. *Proceedings of the Yorkshire Geological Society*, **56**, 91–109.

Bromley, R. G. 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica*, **16**, 55–64.

Bromley, R. G. 2004. A stratigraphy of marine bioerosion. In: The application of ichnology to palaeoenvironmental and stratigraphic analysis / edited by D. McIlroy. *Geological Society Special Publication*, **228**, 455–479.

Clare, A. S. 2011. Toward a characterization of chemical cues to barnacle gregariousness. *In*: *Chemical Communication in Crustaceans* / edited by T. Breithaupt & M. Thiel. New York: Springer, 431–450.

Conway Morris, S., Pickerill, R. K. & Harland, T. L. 1982. A possible annelid from the Trenton Limestone (Ordovician) of Quebec, with a review of fossil oligochaetes and other annulate worms. *Canadian Journal of Earth Sciences*, **19**, 2150–2157.

Donovan, S. K. 1991. Site selectivity of a Lower Carboniferous boring organism infesting a crinoid. *Geological Journal*, **26**, 1–5.

Donovan, S. K. 1992. A field guide to the fossil echinoderms of Coplow, Bellman and Salthill Quarries, Clitheroe, Lancashire. *North West Geologist*, **2**, 33–54.

Donovan, S. K. 2013. A Recent example of the boring *Gastrochaenolites lapidicus* Kelly and Bromley and its producing organism in north Norfolk, eastern England. *Bulletin of the Mizunami Fossil Museum*, **39**, 69–71.

Donovan, S. K. 2015. A prejudiced review of ancient parasites and their host echinoderms: CSI Fossil Record or just an excuse for speculation? *Advances in Parasitology*, **90**, 291–328.

Donovan, S. K. & Hoare, G. 2019. Site selection of small round holes in crinoid pluricolumnals, Trearne Quarry SSSI (Mississippian, Lower Carboniferous), north Ayrshire, UK. *Scottish Journal of Geology*, **55**, 1–5.

Donovan, S. K., Kabrna, P. & Donovan, P. H. 2014. Salthill Quarry: a resource being revitalized. *Deposits*, **40**, 32–33.

Donovan, S. K. & Lewis, D. N. 2010. Aspects of crinoid palaeontology, Much Wenlock Limestone Formation, Wenlock Edge, Shropshire (Silurian). *Proceedings of the Yorkshire Geological Society*, **58**, 9–14.

Donovan, S. K., Lewis, D. N. & Kabrna, P. 2005. An unusual crinoid-coral association from the Lower Carboniferous of Clitheroe, Lancashire. *Proceedings of the Yorkshire Geological Society*, **55**, 301–304.

Donovan, S. K., Lewis, D. N. & Kabrna, P. 2006. A dense epizoobiontic infestation of a Lower Carboniferous crinoid (*Amphoracrinus gilbertsoni* (Phillips)) by *Oichnus paraboloides* Bromley. *Ichnos*, **13**, 43–45.

Donovan, S. K. & Tenny, A. 2015. A peculiar bored crinoid from Salthill Quarry, Clitheroe, Lancashire (Mississippian; Tournaisian), UK. *Proceedings of the Yorkshire Geological Society*, **60**, 289–292.

Donovan, S. K. & Tenny, A. 2022. A bored cup of the Mississippian crinoid *Synbathocrinus* Phillips. *Proceedings of the Yorkshire Geological Society*, **64**, 1–3.

Emson, R. H. & Wilkie, I. C. 1980. Fission and autotomy in echinoderms. *Oceanography and Marine Biology: An Annual Review*, **18**, 155–250.

Folmer, R. & Donovan, S. K. 2021. Crinoid columns as hard substrates: Salthill Quarry (Mississippian, Lower Carboniferous), Clitheroe, Lancashire, UK. *Proceedings of the Geologists' Association*, **132**, 102–109.

Häntzschel, W. 1975. Trace fossils and problematica (2nd edition, revised and enlarged). In: *Treatise on invertebrate paleontology, part W, miscellanea, supplement 1* / edited by C. Teichert. Boulder & Lawrence: Geological Society of America and University of Kansas, xxi + 269 pp.

Kabrna, P. 2011. Excursion 5. Pendle Hill and Clitheroe. In: *Carboniferous geology: Bowland Fells to Pendle Hill* / edited by P. Kabrna. Craven and Pendle Geological Society, Lancashire, 157–165.
Kelly, S. R. A. & Bromley, R. G. 1984. Ichnological nomenclature of clavate borings. *Palaeontology*, **27**, 793–807.
Miller, J. & Grayson, R. F. 1972. Origin and structures of the Visean "reef" limestones near Clitheroe, Lancashire. *Proceedings of the Yorkshire Geological Society*, **38**, 607–638.
Moore, R. C., Jeffords, R. M. & Miller, T. H. 1968. Morphological features of crinoid columns. *University of Kansas Paleontological Contributions, Echinodermata Article* **8**, 1–30.
Moore, R. C., with additions by Ubaghs, G., Rasmussen, H. W., Breimer, A. & Lane, N. G. 1978. Glossary of crinoid morphological terms. In: *Treatise on invertebrate paleontology, part T, Echinodermata 2, volume 2* / edited by R. C. Moore & C. Teichert. Boulder & Lawrence: Geological Society of America and University of Kansas, pp T229, T231, T233–T242.
Phillips, J. 1836. *Illustration of the geology of Yorkshire, or, a description of the strata and organic remains. Part 2. The Mountain Limestone districts*. London: John Murray.
Pickerill, R. K. & Blissett, D. 2000. A predatory *Rusophycus* burrow from the Cambrian of southern New Brunswick, eastern Canada. *Atlantic Geology*, **35**, for 1999, 179–183.
Pickerill, R. K. & Donovan, S. K. 1998. Ichnology of the Pliocene Bowden shell bed, southeast Jamaica. In: *The Pliocene Bowden shell bed, southeast Jamaica* / edited by S. K. Donovan. *Contributions to Tertiary and Quaternary Geology*, **35**, 161–175.
Pickerill, R. K. & Forbes, W. H. 1978. A trace fossil preserving its producer (*Trentonia shegiriana*) from the Trenton Limestone of the Quebec City area. *Canadian Journal of Earth Sciences*, **15**, 659–664.
Riley, N. J. 1990. Stratigraphy of the Worston Shale Group (Dinantian), Craven Basin, north-west England. *Proceedings of the Yorkshire Geological Society*, **48**, 163–187.
Schoor, D. I. E., Donovan, S. K. & Webster, G. D. 2020. Platycrinitid (Monobathrida) crinoid columnals from the Permian of Timor: form, function, protection and intimate associations. *Proceedings of the Geologists' Association*, **131**, 667–678.
Yochelson, E. L. & Fedonkin, M. A. 1993. Paleobiology of *Climatichnites*, an enigmatic Late Cambrian fossil. *Smithsonian Contributions to Paleobiology*, **74**, iv+74 pp.

LETTER

Comment: is conservation destroying geology?

Tony Waltham (*Mercian Geologist* 2021) is prescient to highlight how conservation, for many, relates to plants and animals, but little to geology. Waltham's before and after images are poignant reminders of what has been lost.

Geology deteriorates at the surface if it is not refreshed; a working quarry presents its geology better than an abandoned, overgrown site. Even when conserved, so-called, it is a responsibility of the conservers to know what their responsibilities entail. I illustrate a failure in care as an adjunct to Waltham (2021). It is the saddest example of disjunction that I know, between the preservers and preserved at a geological Site of Special Scientific Interest (SSSI) — the Mississippian (Lower Carboniferous) crinoid-rich deposits of Salthill Quarry, Clitheroe, Lancashire (Kabrna 2011).

A comparison of the crinoid site in 1985 (not 1986 as incorrectly stated in the original caption to Donovan 2012, fig. 3A, B) and 2010 (Donovan 2011, fig. 1) shows strong contrasts, of an excellent limestone exposure deteriorated to a lawn. The site is managed by the Wildlife Trust of Lancashire, Manchester and North Merseyside, whose website (www.lancswt.org.uk/nature-reserves/salthill-quarry-local-nature-reserve) enthuses about wildflowers and birds, but not that this is a geological SSSI. I summarized this earlier: "… when it was visited by SKD in 2010, the geological features were being overgrown by grasses and other plants; that is, the geological SSSI was being transformed, passively, into a botanical nature reserve" (Donovan *et al*. 2014, p 32).

That things have been improved subsequently was a result, perhaps, not of true enlightenment, but by a reaction by the site's managers to a critical lecture by Paul Kabrna (Donovan *et al*. 2014). In 2013, some of the overgrown beds were exposed, along strike, by a mechanical digger. That is, a small area was excavated and today is only kept free of fresh plant growth by collectors – not your correspondent, I emphasize – continuing to dig this area without permission. But much of the succession is still overgrown and inaccessible.

In conclusion, I agree with Waltham (2021, p 144): "…at too many locations it appears that geo takes a second place to bio…" Salthill Quarry is the most important site for Mississippian crinoids in England, but today it is a lawn with some rock exposed to the side, less than 10% of the area. As such it is much like the White Peak and, I can only presume, other notable areas of British geology.

References

Donovan, S. K. 2011. Salthill Quarry, Clitheroe: a resource degraded. *Deposits*, **25**, 46–47.
Donovan, S. K. 2012. Stanley Westhead and the Lower Carboniferous (Mississippian) crinoids of the Clitheroe area, Lancashire. *Proceedings of the Yorkshire Geological Society*, **59**, 15–20
Donovan, S. K., Kabrna, P. & Donovan, P. H. 2014. Salthill Quarry: a resource being revitalized. *Deposits*, **40**, 32–33.
Kabrna, P. (ed.) 2011. *Carboniferous geology: Bowland Fells to Pendle Hill*. Craven & Pendle Geological Society, Lancashire.
Waltham, T. 2021. Is conservation destroying geology? *Mercian Geologist*, **20** (2), 140–144.

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