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Comment and reply on “Palaeoenvironmental control on distribution of crinoids in the Bathonian (Middle Jurassic) of England and France” by Aaron W. Hunter and Charlie J. Underwood

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Mariusz A. Salamon, Przemysław Gorzelak, and Michał Zatoń (2010) have presented an interesting discussion of our paper. We would like to thank these authors for bringing the extensive work on crinoid systematics and palaeoecology from Eastern Europe (Pisera and Dzik 1979; Głuchowski 1987; Salamon et al. 2006, 2008; Salamon and Zatoń 2006, 2007; Salamon 2008a, b, c, 2009; Zatoń et al. 2008) to our attention. Some of this important data was inadvertently omitted from, or post-dated the acceptance of, Hunter and Underwood (2009).

It should be pointed out that the facies classification used in Hunter and Underwood (2009) were developed to investigate Middle Jurassic (Bathonian) shark ecology (see Underwood, and Ward 2004) and only later independently applied to echinoderm taxa. When crinoid occurrence was plotted onto this facies model, it was evident that the distribution of crinoid species corresponded so well to these particular facies, even though the facies control on other echinoderms, especially asterozoans, is not as clear-cut (Hunter 2006).

The ossicles in our study were bulk sampled from 34 localities. To our knowledge the majority of the studies cited in Salamon et al.'s (2010) discussion (Salamon et al. 2006, 2008; Salamon and Zatoń 2006, 2007; Salamon 2008a, b, c; Zatoń et al. 2008) only come from a far fewer localities. In addition, they do not employ a lithostratigraphic framework comparable to that of Hunter and Underwood (2009: fig. 2), or (with the exception of Salamon 2009) any detailed recording of the sedimentology. Each locality or data point in Hunter and Underwood (2009) is linked to the parent facies by its lithology and to a lesser extent its associated fauna including bivalves which are well known for their ecological zonation (Fürsich 1994). Thus, the majority of data points are not contemporaneous and come from a wide geographical area. We believe that such an approach minimises bias in the palaeoecological trends observed. Our facies classification thus transcends any intra-facies biases caused by the ability of isocrinids to locally migrate (Baumiller and Messing 2007). Furthermore, we clearly state that there will be intra-facies biases caused by: (i) the different ways that isocrinid species disarticulate (Messing and Llewellyn 1992), (ii) local transportation, and (iii) time averaging. None of these factors however affects the overall general pattern of our data. This does not mean that our facies data are free from tapho-

nomic bias and we freely admit that our published paper lacks the analytical taphonomic methods mentioned by Salamon et al. (2010). However, “taphofacies” details were removed from earlier versions of the manuscript on the advice of the reviewers but, as noted by Hunter and Underwood (2009: 81), they have been published by Hunter and Zonnerveld (2008) and are reproduced herein (Table 1). All of the factors (abrasion, bioerosion, and level of disarticulation) mentioned by Salamon et al. (2010) are taken into consideration.

Pluricolumnals were indeed rare in our samples and ossicles were sometimes abraded. However the level of disarticulation and abrasion was carefully examined within our residues to differentiate autochthonous, para-autochthonous and allochthonous assemblages (according to Hunter and Zonnerveld 2008), with the occurrence of associated remains of molluscs and vertebrates of known palaeoenvironmental distribution also being used to this end. The preservation within each of our 9 facies was remarkably consistent with little or no evidence of faunal mixing due to reworking or significant transportation (other than in the single sample containing largely allochthonous material).

Without taphofacies analysis, including a thorough discussion of the associated fauna (Hunter and Underwood 2009: 95–98, appendix 1), any interpretations of crinoid element distribution is suspect. For example, Salamon et al. (2010) note that “very well preserved stalks” of the genus *Pentacrinites* are known from deep water clay (outer shelf) facies of central Poland (Salamon and Zatoń 2007). However, on close examination of their data only one pluricolumnal is mentioned (Salamon and Zatoń 2007: 155), with the single figured example highly abraded (Salamon and Zatoń 2007: fig. 2e) and thus very likely to have been transported. Salamon et al (2010) also point out that *Isocrinus* columnals are abundant in deep water (outer shelf) clay facies (Salamon and Zatoń 2007). Nevertheless the illustrated ossicles either occur in very low numbers (*Isocrinus bajocensis*: = 6 pluricolumnals) or along with the millericrinids are highly abraded and even broken (Salamon and Zatoń 2007: fig. 2a, b, h). These again appear to have and have clearly been transported (probably from a shallower environment to be and mixed with well preserved *Chariocrinus andreae* and *Balano-crinus berchteni* that occur in much higher numbers (>1000 columnals).

Table 1. Table of definition for the numbered taphofacies 1–5 showing the characteristics such as articulation, reworking, abrasion, and transport with examples from the lithofacies, this is further supported by data from associated fauna in Hunter and Underwood (2009) (reproduced from Hunter and Zonneveld (2008: 59, table 2).

Taphofacies	Characteristics	Examples from British-French Bathonian	Associated fauna
Crinoids-taphofacies 1	Obrution Lagerstätten, autochthonous-life assemblage, crinoids preserved fully articulated and in life position	Lithofacies 4 (Bradford Clay, Simms 1999), 5 (<i>Alisacrinus</i> fauna, Taylor 1983)	Well preserved associated fauna of bivalves and brachiopods, can be monogeneric
Crinoids-taphofacies 2	Para-autochthonous, articulated columnals, and pluricolumnals (sometimes cirri) unabraded, reworking, and transport is minimal	Lithofacies 1-2, 5-6, 8 (9)	Brachiopods with articulated valves, and well preserved bivalves
Crinoids-taphofacies 3	Para-autochthonous, no articulated pluricolumnals some minimal abrasion, medium reworking some local transport within the lithofacies	Lithofacies 3	Only some brachiopods with articulated valves, and some bivalves are broken
Crinoids-taphofacies 4	No articulated columnals, cirri mainly preserved. Some abrasion, reworking and sorting is evident, transport within the lithofacies	Lithofacies 7	Brachiopods with disarticulated valves, bivalves are broken
Crinoids-taphofacies 5	Allochthonous some articulated pluricolumnals, extensive abrasion (overgrowth) reworking and sorting is evident, transported from out of the lithofacies	Lithofacies 4 (9)	Brachiopods with disarticulated valves, bivalves are broken, terrestrial fossils

Salamon et al. (2010) question the validity of our statement “*Isocrinus* was mainly restricted to silty and sandy sediments representing shallower-water and higher-energy palaeoenvironments in the Lower Jurassic” (Hunter and Underwood 2009: 91). Our statement is actually related to the data presented in Simms (1989) on the facies preferences of his taxa. However, it should be noted that recent work by Hunter and Clark (2009) demonstrated that the genus *Isocrinus* typifies (although is not entirely restricted to) shallow-water environments such as the Early Jurassic of north-east Scotland. It should also be noted that, even where material described in Hunter and Underwood (2009) is identified only to generic level, the conclusions are likely to only relate to the species concerned. In many cases it would not be expected that the distributions of one species would provide a generalisation for the distribution for all species of the genus; indeed some crinoid genera are well known to have different species showing very different palaeoecology (such as *Pentacrinites*, which contains both benthic and pseudoplanktic species (see Hess 1975, 1999).

Finally, with regard to the millericrinids, we use this term in its widest sense to include both *Millericrinus*, *Apiocrinites*, and *Ailsacrinus* (Millericrinidia). Millericrinids are unlikely to have colonised soft substrates directly but may have attached to bioclasts or lithoclasts in soft bottom environments (Hunter and Underwood 2009: 91). The senior author has presented this hypothesis on a number of occasions (see Hunter 2004) and this is now the subject of further research in progress. In addition, within the samples where allochthonous millericrinids are common, no holdfasts were recovered attached to shells or clasts, and the extremely high energy of the deposit would make it unlikely that any of the clasts present within the unit would have provided a stable substrate for autochthonous crinoids.

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