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Palaeoenvironmental control on distribution of crinoids in the Bathonian (Middle Jurassic) of England and France

AARON W. HUNTER and CHARLIE J. UNDERWOOD



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Bulk sampling of a number of different marine and marginal marine lithofacies in the British Bathonian has allowed us to assess the palaeoenvironmental distribution of crinoids for the first time. Although remains are largely fragmentary, many species have been identified by comparison with articulated specimens from elsewhere, whilst the large and unbiased sample sizes allowed assessment of relative proportions of different taxa. Results indicate that distribution of crinoids well corresponds to particular facies. Ossicles of *Chariocrinus* and *Balanocrinus* dominate in deeper-water and lower-energy facies, with the former extending further into shallower-water facies than the latter. *Isocrinus* dominates in shallower water carbonate facies, accompanied by rarer comatulids, and was also present in the more marine parts of lagoons. *Pentacrinites* remains are abundant in very high-energy oolite shoal lithofacies. The presence of milleriacrinids within one, partly allochthonous lithofacies suggests the presence of an otherwise unknown hard substrate from which they have been transported. These results are compared to crinoid assemblages from other Mesozoic localities, and it is evident that the same morphological adaptations are present within crinoids from similar lithofacies throughout the Jurassic and Early Cretaceous.

Key words: Echinodermata, Crinoidea, lithofacies, palaeoecology, Jurassic, Bathonian, England, France.

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Introduction

The environmental palaeoecology of Mesozoic echinoderms, and specifically crinoids, has received comparatively little study, probably due to the lack of complete specimens in many rock formations. The palaeoecology and taphonomy of Palaeozoic echinoderms on the other hand, has received much more attention, with many notable investigations on niche differentiation, tiering, and autecology (e.g., Titus 1979; Ausich 1980; Brett and Eckert 1982; Franzen 1983; Brett 1984, 1985; Brett and Brookfield 1984; Ausich and Lane 1985; Kammer 1985; Taylor and Brett 1996; Holterhoff 1997; Kammer and Lake 2001). Fossil echinoderm diversity is comparable to that of vertebrates in the number of taxonomic units defined (Benton and Simms 1996), although this may be due to many workers concentrating on well-preserved specimens (Donovan 1996). Despite this, the echinoderm fossil record abounds with fragmentary remains in the form of isolated ossicles, but these are commonly dismissed as unidentifiable, weakening any conclusions made on diversity and ecology.

The goal of this study is to collect un-biased data detailing the occurrence of Middle Jurassic crinoid genera using bulk sampling techniques in an attempt to reconstruct the original palaeoecology setting and distribution of these organisms. This is achieved by explaining the nature of the lithofacies and describing their sedimentological and biological composition in terms of both crinoids and associated fauna. The hope is that a robust pattern of distribution can be recognised

and it is not significantly influenced by transport or the post-mortem disarticulation specific to the group of crinoids.

To avoid ecological biases associated with studies on material from obrution deposits (e.g., Hess 1975, 1999; Simms 1989b, 1999), it is necessary to consider fragmentary remains. For this study, unbiased samples of disarticulated crinoid remains (ossicles) were extracted from Bathonian (Middle Jurassic) sediments of central and southern England and northern France using bulk sampling techniques. These samples were collected from a wide range of marine and marginal marine lithofacies, including open marine, carbonate shelf and lagoonal settings. Museum material was not suitable for palaeoecological study, but exceptionally well preserved, rare specimens from museum collections (e.g., Natural History Museum, London, UK and Naturhistorisches Museum, Basel, Switzerland) were used as aids for the identification of the disarticulated ossicles. Although articulate crinoids (which include all post-Paleozoic taxa) are classed as type two echinoderms, a group that includes regular echinoids and most Palaeozoic crinoids (see Brett et al. 1997), they are less likely to survive long distance transport intact, as echinoids may (Kidwell and Baumiller 1991), and the stem morphology may differ fundamentally from that of Palaeozoic forms. Isocrinids, for example, possess autotomy articulations allowing the stem to disarticulate in a non-random way and survive in the substrate Meyer et al. (1989). Baumiller (2003: 243) stated that crinoids can serve as “sensitive indicators of post-mortem depositional processes be-

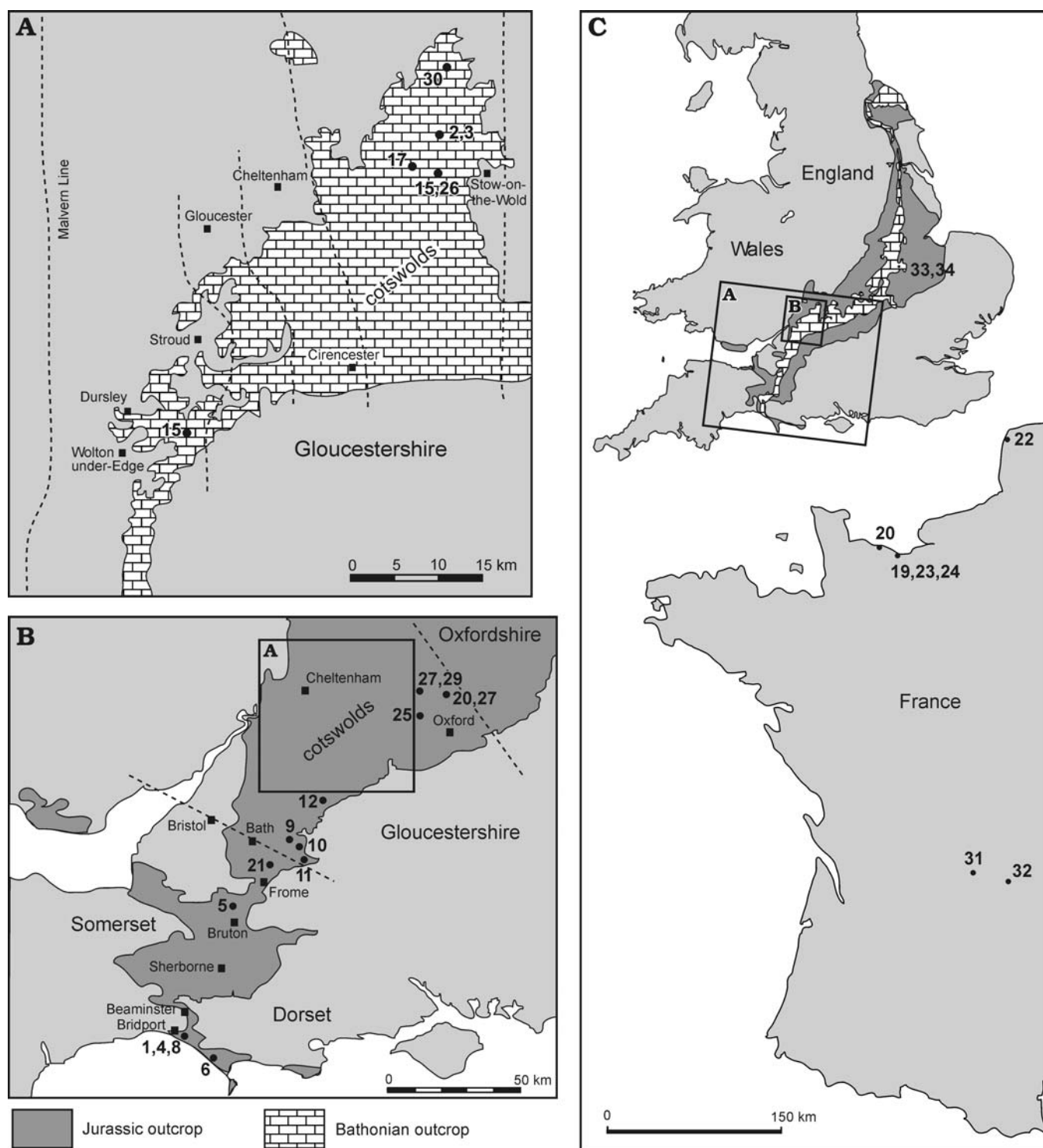


Fig. 1. Field localities in England and France (see Appendix 1) showing Jurassic and Bathonian outcrops. 1, *Rhynchonelloidella wattonensis* Beds 14 (= Wattonensis Beds 14), Watton Cliff; 2, Bed Z, Blockley Station Quarry; 3, *Pecten* Bed, Blockley Station Quarry; 4, Wattonensis Beds 3–11, Watton Cliff; 5, *Rugitella* Beds, East Cranmore; 6, Boueti Bed, Herbury Point; 7, Lower Cornbrash, Kirtlington; 8, Forest Marble, Watton Cliff; 9, Bradford Clay, Browns Folly; 10, Bradford Clay, Forest Marble, Old Canal Quarry; 11, Bradford Clay, Springfield; 12, Forest Marble, Sunhill Bradford Bed; 13, Sharps Hill Formation, Northleach; 14, Hampen Marly Formation, Hampen Cutting; 15, Sharps Hill Formation (Eyford member), Hampen Cutting; 16, Eyford Member, Huntsmans Quarry; 17, Sharps Hill Formation, Hornsleaslow Quarry; 18, Stonesfield Slate, Stonesfield; 19, Argiles de Lion, Sword Beach; 20, Caillasses de la Basse-Ecarde, Juno Beach; 21, Bath Rags, Ford Road Cutting; 22, Calcaire des Pichotts, Belle Houlefort; 23, Calcaire de Langrune, Sword Beach; 24, Caillasses de la Basse-Ecarde, Sword Beach; 25, Taynton Limestone, Huntsmans Quarry; 26, Sevenhampton Rhynchonellid Bed, Taynton Limestone, Hampen Cutting; 27, Rutland Formation, Woodeaton Quarry; 28, Forest Marble Formation, Kirtlington Old Cement Works; 29, White Limestone, Ardley Member, Kirtlington; 30, Sharps Hill Formation, Oakham Quarry; 31, Causses du Quercy Limestones, Dordogne Valley; 32, Doue Oncolite, Doue Valley; 33, Blisworth Limestone, Ketton Castle Cement Quarry; 34, Rutland Formation, Ketton Castle Cement Quarry.

Table 1. Table of definitions for the numbered Middle Jurassic (Bathonian) facies types 1–9 showing the unifying characteristics, including principal sediments and fossils, and the established interpretations.

Facies types	neritic mudstones (lithofacies 1)	brachiopod-rich limestone (lithofacies 2)	shelly carbonate shelf (lithofacies 3)	channelised bioclastic limestone and shelf shelly oolite (lithofacies 4, 5)	argillaceous shelf and embayment (lithofacies 6)	oolitic shoal (lithofacies 7)	marine lagoon (lithofacies 8)	restricted lagoon (lithofacies 9)
Principal sediments	mudstones	nodular limestones, shelly silty marls	bioclastic limestones	oolitic shelly clean washed limestone and oolitic limestones	shelly mudstones, silty-oolitic limestone	oolitic limestones	shelly mudstones to muddy limestones and oolitic rich limestones	mudstones siltstones
Principal fossils	bivalves, belemnites	bivalves, brachiopods, bryozoans, belemnites	bivalves, gastropods, brachiopods, bryozoans	bivalves, brachiopods, bryozoans	bivalves, brachiopods, gastropods corals	bivalves, brachiopods	bivalves, brachiopods	bivalves, brachiopods
Palaeoecological interpretation	offshore, low energy shelf	offshore, low energy shelf	offshore, low energy very shallow shelf	shallow carbonate dominated low energy shelf	low energy inner muddy shelf and outer lagoon	oolitic high energy shoal system	carbonate/muddy low energy marine lagoon complex, shallow subtidal	restricted low energy lagoon complex

cause differential disarticulation can be correlated with exposure time and degree of transportation”. In support of this, Baumiller (2003) proposed a semi-quantitative scale for the disarticulation state of stalked crinoids, which is used along with the taphofacies used in Hunter and Zonneveld (2008) to assess the fidelity of the assemblages herein. Other studies that support the use of disarticulated material for paleoecological analysis include Lane and Webster (1980), Holterhoff (1997) Meyer et al. (2002), and Botquelen et al. (2006).

As in any palaeoecological analysis, this study involved examination of Recent animals in order to understand their autecology. The restriction of stalked crinoids to deep-water settings presents many obstacles to their study (see Baumiller et al. 1991), so comatulids have received far more attention (e.g., Meyer and Macurda 1977, 1980; Macurda and Meyer 1983; Meyer et al. 1984; Messing 1985; Meyer and Meyer 1986). Still, several studies on stalked crinoids (Macurda and Meyer 1974, 1976a, b; Messing et al. 1988; Llewellyn and Messing 1993; Messing 1993; Baumiller and Messing 2007) have provided a solid framework for this study.

Institutional abbreviation.—BM(NH), Natural History Museum London, UK.

Other abbreviation.—EOD, environment of deposition.

Previous work

The localities sampled in the present study include some deposits that were among the earliest to have been scientifically studied by modern geologists (e.g., Smith 1817). Although large and diverse museum collections, including numerous crinoid ossicles, have been established as a result, most of the crinoid material has been ignored and typically catalogued as “Crinoidea indet”.

Although disarticulated remains have been used extensively in studies of Palaeozoic deposits, they are less often investigated in the post-Palaeozoic. Exceptions include the Triassic of Europe, North America and New Zealand (see Hagdorn 1983; Schubert et al. 1992; Hagdorn and Baumiller 1996;

Eagle 2003), the British Lower Jurassic (Simms 1989b), and the uppermost Cretaceous of Northern Europe (Rasmussen 1961; Jagt 1999). However, these studies are largely taxonomic and stratigraphic, and British Middle Jurassic crinoid faunas have not yet been subject to paleoecological and taphonomic treatments. Hess (1972, 1973, 1975) monographed both fragmentary and exceptionally preserved Jurassic echinoderms (including crinoids) from northern Switzerland and adjacent countries (reviewed in Hess 1999), and more recently (Hess 2006) examined Lower Jurassic (Upper Pliensbachian) encrinites from Arzo, southern Switzerland, for which he provided useful palaeoecological interpretations. Mayer (1990) documented the preservation and ecology of Middle Jurassic crinoids from France and attempted to set out a lithofacies scheme similar to that used in this study. However, his dataset used only isolated information from obrution-lagerstätten. These, and the obrution deposits from the British Middle Jurassic (Simms 1999), Poland (Radwańska 2005), and Russia (Klikushin 1982) remain the nearest comparable analogues to the material discussed here. None of these apart from Hunter and Zonneveld (2008) has incorporated the lithofacies analysis presented in this paper.

Methodology

A total of 45 samples were collected from 34 localities across southern, central and eastern England, and northern and south-western France (see Fig. 1, Appendix 1). Samples were collected along the Bathonian outcrop in central and southern England, mainly from poorly lithified beds. A “sample” is a large quantity of mudrock or unlithified limestones collected from a single stratigraphic horizon or bed within a logged section. Each was collected from a single formation or member at a defined point or numbered locality (Figs. 1, 2, Appendix 1). Samples typically weighed 20–40 kg, with smaller 10 kg samples taken from localities where collecting was restricted by conservation issues or limited exposure of thin horizons. Many of these samples were the same as those used by Underwood and Ward

				France				
		Zone	Subzone	Boulonnais France	Calvados (14) Normandy France	Dordogne Valley France		
Bathonian	Upper	<i>Clydoniceras</i> (<i>Clydoniceras</i>) <i>discus</i>	<i>C. (C.) discus</i>	Calcaire des Pichotts (Loc. 22)	Argiles de Lion (Loc. 19)	?Causses du Quercy Limestones (Loc. 31)		
			<i>C. (C.) hollandi</i>		Calcaire de Langrune (Loc. 23)			
		<i>Oppelia</i> (<i>Oxycerites</i>) <i>aspidoides</i>			Caillasses de la Basse- -Ecarde (Loc. 20, 24)			
		<i>Procerites</i> <i>hodsoni</i>		Calcaire de Ranville				
	Middle	<i>Morrisiceras</i> (<i>Morrisiceras</i>) <i>morrisi</i>		Calcaire de Blainville	Calliasse de Blainville		?Causses du Quercy Limestones (Loc. 31)	
			<i>Tulites</i> (<i>Tulites</i>) <i>subcontractus</i>					Calcaire de Blainville
		<i>Procerites</i> <i>progracilis</i>			Caillasse de Fontaine-Henry			
		<i>Asphinctites</i> <i>tenuiplicatus</i>			Calcaire de Creully			
	Lower	<i>Zigzagiceras</i> (<i>Zigzagiceras</i>) <i>zigzag</i>	<i>Oppelia (Oxycerites)</i> <i>yeovilensis</i>		Calcaire de Caen		Marnes de Port	
			<i>M. (Morphoceras)</i> <i>macrescens</i>					
			<i>P. (Parkinsonia)</i> <i>convergens</i>					

Fig. 2. Lithostratigraphic correlation of the sampled formations, members and beds for the Bathonian. Source of data: Cope et al. (1980), Rose and Pareyn (2003). →

(2004), with sieve residues from the same samples commonly used for both studies. Due to their complex sedimentological framework, these samples have been grouped into several of distinct lithofacies (see Table 1).

Ossicles were extracted from mudrocks [primarily unlithified clays or marls rather than indurated claystones or marlstones; see Pickerill et al. (1998) for precise definition] or unlithified limestones, using the bulk sampling and sieving techniques of Ward (1981), with most sediment samples 20–40 kg dry weight. We sometimes refer to the rocks in this study as “sediments” in a palaeoenvironmental context to define their pre-diagenetic sedimentary origin. Some echinoderm remains were removed from oolitic and bioclastic limestones by etching in 10% acetic acid; echinoderm material is typically more resistant to acid dissolution than associated ooids and carbonate cement. Material was typically sieved at

355 mm, with all specimens picked from samples down to 4 mm and smaller subsamples being picked to 1 mm.

Crinoid specimens typically consisted of disarticulated remains, with isolated columnals and common pluricolumnals in the coarser sieve fractions, and cirrals dominating the finer fractions. Because total sample weight varied between sampled beds, the relative numbers of each stalked crinoids genus were typically represented as a ratio of total individual columnals in each sample, and therefore of the facies as a whole. Ratios of brachials and cirrals were used in those acid-etched samples and those of facies 6 (see Appendix 1 for details) from which it was not possible to extract well preserved columnals. Pluricolumnals did not occur in high enough numbers to represent the relative proportions of elements. Instead, they were used to quantify the degree of disarticulation and the proportions of the different elements. Although the role of bio-

England

Fleet Lagoon (Weymouth Anticline) Dorset, UK	West Bay (Bridport) Dorset, UK	South Mendips Somerset, UK	Bath Area, UK	Cotswolds Gloucestershire, UK	Oxford area Oxfordshire, UK	Ketton Rutland- Northamptonshire Lincolnshire, UK		
Lower Cornbrash	Lower Cornbrash 14 m	Lower Cornbrash 2.1 m	Lower Cornbrash 1.5 m	Lower Cornbrash 2.1 m	Lower Cornbrash >3 m (Loc. 7)	Lower Cornbrash 1.5 m		
Upper Forest Marble 76 m	Forest Marble 26 m	Forest Marble 30 m (Loc. 8)	Forest Marble 23 m	Forest Marble 30 m (Loc. 12) Boueti Bed	Forest Marble 7 m (Loc. 28)	Blisworth Clay 3–5 m		
Digona Bed 15 m			Hinton Sands					
Upper Forest Marble 18 m		Loc. 9, 10, 11						
Boueti Bed 0.30 m (Loc. 6)		Boueti Bed	Great Oolite (Loc. 21)					
Upper Fullers Earth Clay 12 m	Upper Fuller's Earth Clay 38 m	Upper Fuller's Earth Clay 43 m	Upper Fuller's Earth Clay 28 m	Upper Fuller's Earth Clay 43 m	Bladon Member 2–5 m	Blisworth Limestone 1.7–2.9 m		
Elongata Beds 0.6 m	Elongata Beds 0.6 m		Fuller's Earth		Ardley Member 2–5 m (Loc. 29)			
Wattonensis Beds 30 m	Wattonensis Beds 7.5 m (Loc. 1, 4)	Rugitela Beds (Loc. 5)	Rugitela Beds	Shipton Member 10 m	Shipton Member 4 m	Blisworth Limestone 1 m (Loc. 33)		
Lower Fuller's Earth Clay 270 m	Lower Fuller's Earth Clay 46 m	Ornithella Beds	Ornithella Beds				White Limestone	White Limestone
		Milborne Beds	Milborne Beds					
				LFE Clay 5 m	LFE Clay 5 m			
		Knorri Clays 0.75 m	Knorri Clays 0.75 m					
						Fullonicus Limest. 1.15 m		
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				Zigzag Bed 0.15 m	Clypeus Grit 6 m		Hook Norton Member 4 m	
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				Anabacia Limestone 3.4 m	Anabacia Limestone 3.3 m			
Zigzag Bed 0.15 m								

corrosion is largely unknown in modern crinoids (Ameziene 1991), physical abrasion is clearly observed in all the fossil residues in this study. The levels of abrasion and degree of disarticulation were thus used to discuss the fidelity of lithofacies. These are both based on the taphofacies classification presented in Hunter and Zonneveld (2008).

Although the application of formal systematic palaeontology on such remains is deemed inappropriate at this stage, Table 2 gives taxonomic affinities of all identifiable examined material and figured specimens, including published diagnostic characters (e.g., Hess 1975; Rasmussen 1978). Because these are not always sufficient for identifying disarticulated ossicles, the senior author has re-examined the complete intact specimens and identified additional characters that are diagnostic but not exclusive to the genus. Comatulids could only be distinguished by their centrodorsals; other ossicles, such as brachials with syzygial articulations, lack specifically diag-

nostic characters. Thus, the proportions of crinoids within comatulid-bearing samples did not directly relate to the proportions of living crinoids. As only relative proportions of crinoids were used to characterise crinoid-facies relationships, this was not a problem.

Geological setting

The stratigraphy of the British Bathonian, though complex, has been studied extensively (e.g., Callomon and Cope 1995). We regarded this sequence as the most suitable stratigraphic level on which to concentrate the study, as to the British and French Bathonian have the greatest diversity of sedimentary environments/facies in the Middle Jurassic, although there is sequence deletion in the Bathonian that has prevented a stratigraphic investigation. Although all of the studied for-

mations are included within the Great Oolite Group, oolitic limestones are only found in the central part of the British study area, especially around the Cotswold Hills (Callomon and Cope 1995) where they represent barrier shoal facies. South of the oolite belt, the facies typically suggest open marine environments, whilst to the north there was an extensive lagoonal complex with varying salinities (Arkell 1956; Hallam 1978, 1992). This belt of oolitic rocks prograded to the south throughout much of the Bathonian. The barrier system finally broke up in the Upper Bathonian allowing what was probably a more mud-dominated ramp to develop, with channels filled with bioclastic material (Sellwood and McKerrow 1974). These sections are also home to some oolite deposits (e.g., Bradford Clay). Apart from the breakdown of the shoal system during the Bathonian, no major events or significant changes in the fauna appeared during this interval. The changes seen among the different lithofacies/depositional environments appear to have been purely ecological and taphonomic effects. The main limitation of the British Bathonian is the lack of more “neritic formations” typical of many other levels within the British Jurassic (e.g., British Liassic).

Each sampled horizon represents a time-averaged unit. Assuming a constant depositional rate throughout each horizon period, each bulk sample should represent all the echinoderms that lived and died in the time interval during which that lithology was deposited, however short lived. The lithofacies were defined as a combination of several sample horizons that characterise a single lithofacies belt. We used the unifying characteristics of each lithofacies (Fig. 2) to define the environment of deposition (EOD). The aim was to establish the relationship of the echinoderms to these EODs and lithofacies belts.

Ossicles within some units have been transported, e.g., the Forest Marble at Kirtlington (Oxfordshire), described by Andrew Milner (personal communication January 2004) as an everglade-like lagoon environment that was submerged and exposed regularly due to its coastal setting, thus leading to the reworking of fragments. However, it is possible to differentiate allochthonous from autochthonous elements by examining the products of the residues and degree of abrasion. In the case of Kirtlington, the invertebrate fossils of the Mammal Bed were reworked (Evans and Milner 1994), but the articulated pluricolumnals and unabraded columnals in this study indicate that the more articulated echinoderms in the lower parts of the Forest Marble Formation were not transported. Furthermore, fossils may be affected by long-term transport from one area to the other through down-slope movement or minor gravitational processes (Daniel Blake, personal communication October 2003). This may be true for individual lithologies (Kroh and Nebelsick 2003), but when grouped into lithofacies or EODs (with more than one sample point represented), transport of an echinoderm element between the lithofacies (outside EOD boundaries) will leave signatures in the neighbouring lithofacies/EOD that is abraded and reworked. Thus, at least two allied lithologies or samples, which are largely para-autochthonous, are used to define the lithofacies/EOD

types in this study. All studied lithologies are well represented in the Bathonian with the exception of the neritic mudstone lithofacies; the rarity of this latter type requires Lower and Middle Jurassic analogues to be used in its interpretation (detailed information about the individual localities included in each facies is given in Appendix 1).

Lithofacies

Lithofacies 1: neritic mudstone (localities 1–3).—One sample from Watton Cliff: Upper Bathonian, *Procerites hodsoni* Zone, *Procerites quercinus* Subzone, from the Dorset-Jurassic Coast World Heritage Site. Only one sample was examined due to the poorly fossiliferous nature of this facies. However, samples from similar lithofacies from the Lower Jurassic were examined for comparison (see localities 2, 3 in Appendix 1). This lithofacies exists within a large section of poorly fossiliferous mudstones that dominates much of the Bathonian of southwest England. These mudstones are considered as offshore to deeper shelf (Callomon and Cope 1995). The sampled section at Watton Cliff is a shell bed within a unit of black, partly laminated mudstones. The stratigraphical relationships between this and other associated units are complicated by faulting (see Underwood and Ward 2004). Echinoderms are relatively uncommon and the fauna is dominated by oysters, with subordinate belemnites and thin-shelled bivalves. Ammonites are rare, and brachiopods and bryozoans virtually absent.

Lithofacies 2: brachiopod-rich limestone (localities 4, 5).—Five samples from two localities in the lower part of the Upper Bathonian (*Procerites hodsoni* Zone), typically in close stratigraphical association with lithofacies 1 above. Samples consist of bioturbated and variously shelly, silty marlstones and claystones alternating with nodular micrites. Echinoderms were minor elements of the diverse fauna, which contained abundant brachiopods, bryozoans, oysters, and belemnites. Ammonites were very rare. Although also representing a neritic palaeoenvironment, this facies differs from the neritic mudstone lithofacies in reflecting seafloor conditions suitable for a rich and more diverse benthos.

Lithofacies 3: shelly carbonate shelf (localities 6, 7).—Two samples from two Upper Bathonian localities in southern England defined by two horizons: the *Goniorhynchia boueti* Bed (= Boueti Bed), Herbury Point, Dorset, and the Lower Cornbrash, Kirtlington Old Cement Works, Oxfordshire. This lithofacies consists primarily of shelly bioclastic oomicrite and pelmicrite (packstones and wackstones). Both units sampled represent laterally extensive beds with rich and diverse marine faunas, including brachiopods, bivalves, bryozoans and echinoids. Echinoderm material is uncommon.

Lithofacies 4: channelised bioclastic limestone (localities 8–12).—One densely fossiliferous sample from the Upper Bathonian *Clydoniceras discus* Zone in the Forest Marble Formation, exposed at Watton cliff and overlying the Boueti Bed. Bivalves and crinoids in this lithofacies are considered typical of hardgrounds (Palmer and Fürsich, 1974; Hunter

2004). An additional three localities representing the Bradford Clay, an obrution deposit that is known to preserve hardgrounds within the Forest Marble, were studied from museum collections.

Lithofacies 5: shelf shelly oolite (localities 20–24).—Four samples from two localities from the lower part of the Upper Bathonian, *Procerites hodsoni* Zone (see Appendix 1). Separated from the better-sorted oolites of the main shoal systems (Wyatt and Cave 2002), this facies consists of clean, strongly cross-stratified but relatively poorly-sorted oolite alternating with bioclastic lenses and channel fills, sometimes in a muddy matrix. Samples were collected from sites in England and France, both probably represented oolite-dominated systems from a time after the breakup of the true barrier shoal system (Wyatt and Cave 2002). Shelly faunas are diverse and many shells are well preserved. Shelly assemblages are dominated by bivalves or brachiopods, with gastropods, bryozoans, corals, and echinoderms all being locally common.

Lithofacies 6: argillaceous embayment and outer lagoon (including Tilestones lithofacies) (localities 13–19).—Nine samples from seven localities, all from the Lower to Middle Bathonian, *Asphinctites tenuiplicatus* and *Procerites progradilis* zones. One sample was recorded only from a museum collection (see locality 13 in Appendix 1). This lithofacies is equivalent to the muddy embayment and shelly-oolitic lagoon facies and tilestone facies of Underwood and Ward (2004) and consists of relatively variable, shallow-water shelly mudstones. We also include the lithologically distinct Stonesfield Slate, which consists of laminated and very low angle cross-stratified silty and micro-oolitic limestone (Boneham and Wyatt 1993) and is interpreted as representing lower shoreface (Underwood and Ward 2004). Found in association with oolite shoal and more restricted lagoonal lithofacies, these rocks commonly contain dispersed ooids, indicating deposition in close proximity to higher energy environments. Samples in the higher-energy palaeoenvironment (but not in the low diversity Stonesfield Slate) typically contain rich and often diverse fauna of bivalves, commonly with abundant brachiopods, nerineid gastropods, and corals. Echinoderm remains are fairly common, but of low diversity.

Lithofacies 7: oolitic shoal (localities 25–26).—Two samples from a single Middle Bathonian, *Procerites progradilis* Zone locality in the Taynton Limestone Formation. Despite the abundance of oolitic sediments within the Great Oolite Group, the majority are poorly fossiliferous and not suitable for bulk sampling. Sampling concentrated on the most shelly lenses, typically at the base of shallow channels. The samples consisted of well-sorted and internally homogeneous oomicrites and oosparites, with rare bioclasts. Samples were treated with acid to remove small fragments. This lithofacies was formed by the mobile oolitic shoal system that existed throughout much of the Bathonian. Wyatt (1996) recognised four units culminating in the shoal being broken up.

Lithofacies 8: marine lagoon (localities 27–32).—Six horizons at three localities in Oxfordshire from the Upper Batho-

nian, upper part of the *Clydoniceras discus* Zone. Sections varied from shelly mudstones through muddy limestones and micrites to oolitic or clastic-rich limestones, all deposited in lagoonal or restricted marine conditions. Oysters dominate the relatively low diversity faunas; echinoderms are quite common, but of low diversity. Palmer (1979) interpreted samples from the White Limestone Formation as representing a shallow water subtidal environment of the Oxfordshire Shallows. Included within this lithofacies are two samples of the lagoonal facies of the Forest Marble Formation. These differ largely in the presence of scattered ooids in the sample, but similarities to the other aspects of the facies suggest that the ooids may be allochthonous.

Lithofacies 9: restricted lagoon (localities 33–34).—Eight samples from two localities: seven from the *Asphinctites tenuiplicatus* to *Procerites progradilis* zones of the Lower to Middle Bathonian Rutland Formation at Ketton, Rutland, and one from the overlying Blisworth Clay. Shell beds were sampled from within the basal, most marine, parts of the shallowing-upwards cycles of mudstones and siltstones. These cycles typically terminate in rootlet beds at Ketton. The low diversity but abundant bivalve faunas from both sites suggest that salinity was somewhat reduced. Marine elements are recorded at Ketton, including echinoderm specimens from several cycles, and rare lingulid and rhynchonellid brachiopods from the lowest cycle.

Diversity and distribution of the crinoids within particular facies

The detailed occurrence of each crinoid genus is detailed in the section below with taxonomy and sample sizes given in Table 2. While the ratios of the different elements within the facies are given in Fig. 3 (note worthy only elements that are strictly analogous can be used, for instance, isocrinid columnals). Cross-facies distributions are shown in Fig. 4.

Lithofacies 1: neritic mudstone.—Large numbers of columnals were collected and were all attributed to two taxa in a ratio of two columnals of *Chariocrinus* cf. *wuertembergicus* to every five of *Balanocrinus* cf. *subteres* (Fig. 3). All columnals are small, chiefly 2–3 mm in diameter with high columnals. *Chariocrinus* cf. *wuertembergicus* and *B. cf. subteres* pluricolumnals typically consist of 3–4 and 4–6 columnals, respectively, although one well-preserved pluricolumnal of *B. cf. subteres* has ten columnals. This crinoid assemblage is distinct from that of the brachiopod-rich limestone, and justifies separating bed 14 (Wattonensis Beds) from the other levels sampled at Watton Cliff. Data from the Lower Jurassic (Lower Pliensbachian) of Blockley Quarry mirrors the diversity seen in this assemblage, with *Balanocrinus* sp. 1 and *Isocrinus* dominating [*Chariocrinus* did not appear until the Toarcian (Simms 1989b)].

Lithofacies 2: brachiopod-rich limestone lithofacies.—Crinoids were found in all Watton Cliff samples containing

Table 2. Systematic table for the crinoids, showing key generic and specific diagnostic characters, nomenclature used, available material and source of a definitive description (from articulated forms). Abbreviations: br., brachials; cd., centrodorsal; col., columnals; cren. crenulation; internod.; internodals; nod.; nodals; nodi., noditaxis.

Class	Order/Suborder	Superfamily/Family	Genus	Species	Material/ Figure	Occurrence	Diagnostic characters	References
Crinoidea Miller, 1821 Articulata Zittel, 1879	Millericrinidia Millericrinina ¹ Sieverts-Doreck, 1952	Millericrinidae Jaekel, 1918	<i>Millericrinus</i> d'Orbigny, 1841	<i>Millericrinus</i> cf. <i>exilis</i> (de Loriol, 1882)	50 col. (Fig. 7C)	locality 8	col. have fewer cren. than <i>Apiocrinites</i> cren. flatten towards the lumen, with a large, unornamented area	de Loriol 1882
		Apiocrinitidae d'Orbigny, 1840	<i>Apiocrinites</i> Miller, 1821	<i>Apiocrinites</i> sp.	30–35 col. + proximal col. (Fig. 7A, B)	locality 8	uniserial col. have no interarea en- larged, proximal col. are concave	Rasmussen 1978
	Isocrinida Sieverts-Doreck, 1952	Isocrinidae Gislén in Hess, 1972	<i>Chariocrinus</i> Hess, 1972	<i>Chariocrinus</i> aff. <i>wuertembergicus</i> Oppel, 1856	2 nodi., 60 col., 10 br. (Fig. 5E–G)	locality 4 (beds 3, 9)	col. pentalobate to pentagonal, sharp interradial internodal diameter 3.5 mm, 7–18 col. per nodi.	Hess 1975
				<i>Chariocrinus</i> sp. 1	3 nodi., 20 col., 20 br. (Fig. 5C, D ₁ , D ₂ , H, I)	localities 4 (beds 3, 9), 5, 17	nodi. with 5–11 internodals; primi-br. with weak symmophy	Hess 1975 ³
			<i>Balanocrinus</i> Agassiz in Desor, 1845	<i>Balanocrinus</i> cf. <i>subteres</i> (Münster in Goldfuss, 1831)	3 nodi., 22 col. (Fig. 5B)	locality 4 (bed 14)	slightly convex with almost straight interraddii, col. circular or pentalobate; the nod. larger than internod.	Simms 1989b Hess 1972
				<i>Balanocrinus</i> sp. 1	6 nodi. sections, 21 disarticulated (Fig. 5A)	localities 2, 4 (beds 3, 9)	col. pentagonal to circular, uniform radiating cren; nod. have 1–5 cirrus sockets; nodi. 6–10	Simms 1989b ³
		<i>Isocrinus</i> von Meyer in Agassiz, 1836	<i>Isocrinus</i> <i>nicoleti</i> (Desor, 1845)	<i>Isocrinus nicoleti</i> (Desor, 1845)	7 nodi., 115 col. (Fig. 6A–F, M ₁ , M ₂)	localities 7, 8, 21, 23, 28, 30, 31	nod. sub-pentagonal to pentalobate; col. with elliptical petals, marginal and adradial cren. diminish in size towards the interraddial; 8 internod. per nodi. (6, 8, 10)	Hess 1972
				<i>Isocrinus</i> sp. 1	6 nodi., 207 col., 60 br., 414 cirri (Fig. 6N, O)	localities 14, 17 (beds 43, 50)	primi-br. have strong symmophy; col. are pentalobate to pentastellate; nodi. 5–11	Rasmussen 1978 ³
				<i>Isocrinus</i> sp. 2	10 col., 414 cirri (Fig. 6I, J)	locality 25	col. with elliptical petals, cirri, rounded in section	Hess 1975 ³
				<i>Isocrinus</i> sp. 3	37 col. (Fig. 6G, H)	locality 29	small synarthrial col., col. lack simplexes that are not cryptosymplectial, flattened, and featureless ²	Simms 1989a ³
	Comatulida Clark, 1908	Pentacrinidae Gray, 1842	<i>Pentacrinites</i> Blumenbach, 1804	<i>Pentacrinites</i> cf. <i>dargniesi</i> (Hess, 1972)	307 cirri (Fig. 5J, K)	locality 25	cirri, long, narrow, elliptical to rhombic in section, with clear dor- sal and ventral ridges	Simms 1989b Hess 1972
		Solanocrinitacea Solanocrinitidae Jaekel, 1918	<i>Solanocrinites</i> Goldfuss, 1829	<i>Solanocrinites</i> <i>ooliticus</i> (Gislén, 1925)	5 cd. ossicles (Fig. 7D, E, G)	locality 8	cd.; conical, dorsal surface has ir- regular shallow pits with stellate deepening in the flattened centre; ventral surface with stout ridges ra- diate from lumen	Gislén 1925
		Comatulid indet.			>300 br. (Fig. 7D, F)	locality 8	br. syzygial articulations with radiating ridges	Goldfuss 1829

¹ does not include *Ailsacrinus* (Taylor, 1983); ² possibly indicate juvenile columnals; ³ contains diagnosis of genus; new species awaits formal systematics.

large quantities of shelly material but were absent from the shell-poor levels of beds 5 and 7 (Wattonensis Beds). *Chariocrinus* cf. *wuertembergicus* and *Balanocrinus* cf. *subteres* were recorded from all crinoid-bearing levels, with *C.* cf. *wuertembergicus* dominating the most productive sample (Watton Cliff, bed 3) with a ratio of 7 to 2 columnals (Fig. 3) with high columnals. Crinoid occurrences in this bed and smaller accumulations in the calcareous, clay-rich beds 9 and 11 (Wattonensis Beds) were accompanied by common rhynchonellids. The single sample from the second site of the *Rugitella* Beds, East Cranmore, contain a few ossicles of *Chariocrinus* sp.

Lithofacies 3: shelly carbonate shelf.—The two samples of this facies yielded remains of different taxa of crinoids. *Chariocrinus* sp. 1 was recorded from the Boueti Bed, whereas the Lower Cornbrash yielded columnals of *Isocrinus* sp. The dissimilarities between these two samples and the small quantity of columnals found casts doubt on whether both of these deposits are related to neighbouring facies.

Lithofacies 4: channelised bioclastic limestone.—Crinoid remains were abundant and diverse and included up to five genera. Almost all specimens were abraded to some degree, suggesting that the assemblage likely contains a mixture of parautochthonous and allochthonous elements. Ossicles of

Isocrinus nicoleti are abundant, but poorly preserved. Millericrinid columnals are particularly common, and include *Millericrinus* cf. *exilis* and *Apiocrinites* sp. Comatulids are represented by centrodorsal ossicles and syzygial brachials. *Solanocrinites ooliticus* was identified from centrodorsals, although specific identification of other elements is not seldom possible. The small proportion of specifically identifiable comatulids probably results in their under-representation amongst the identifiable fossils, and their frequencies cannot be readily compared to those of stalked taxa.

Lithofacies 5: shelf shelly oolite.—Crinoid material was generally abundant, dominated by *Isocrinus nicoleti*, and included uncommon, well-preserved, semi-articulated specimens. Comatulids were present at the French sites, but absent from English samples. On the other hand millericrinids were rare in the Normandy localities. Despite the small sample sizes collected from the Bath Rags at Ford Road Cutting, a large number of well-preserved columnals were extracted, including pluri-columnals with 6–8 columnals of *Isocrinus nicoleti*. Localities from the Normandy coast were particularly rich in crinoid material with the exception of the Argiles de Lion (Sword Beach). Crinoid columnals of *I. nicoleti* were also present in the lags at the base of each cross bed within the thick sequence of the Calcaire de Langrune (Sword Beach). This shoal-like lithology covers the poorly lithified sandy substrates of the Caillasses de la Basse-Ecarde (Sword Beach) that preserve semi-articulated specimens of *I. nicoleti*.

Lithofacies 6: argillaceous embayment and outer lagoon.—Crinoid assemblages from all samples are dominated by columnals of *Isocrinus* sp. 1; a sample from the Fullers Earth Formation at Hornsleaslow also contained brachials. Ossicles from Hornsleaslow have a ratio of three *Chariocrinus* sp. 1 columnals to every two *Isocrinus* sp. 1. columnals (Fig. 3) with low columnal height. Both samples from the Hampen Marly Formation (beds 43 and 50) contained small quantities

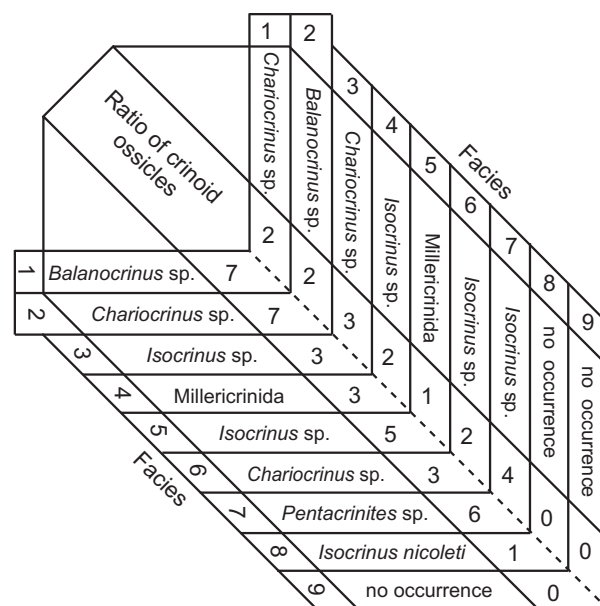


Fig. 3. Approximate ratio of crinoid ossicles in relation to each other (generated while picking samples). The lithofacies are numbered 1–9. The ratios are constructed from columnals in lithofacies 1–5 and 8, brachials and columnals in lithofacies 5, and cirri in lithofacies 7.

of cirral ossicles of *Pentacrinites* cf. *dargniesi*. A sample collected at Juno Beach (Caillasses de la Basse-Ecarde) from inter-reef facies also yielded isocrinids resembling *Isocrinus* sp. 1. The exceptional occurrence of *Ailsacrinus* also occurs within the Sharps Hill Formation (Taylor 1983; Simms 1999).

Lithofacies 7: oolitic shoal.—The high-energy palaeoenvironment represent by the oolite shoal systems [mobile barrier shoal system (Wyatt and Cave 2002)] made preservation in the barrier shoal system different from the other palaeoenvironments. Few crinoid columnals are preserved, but cirral ossicles are common. Within one of the Taynton Limestone

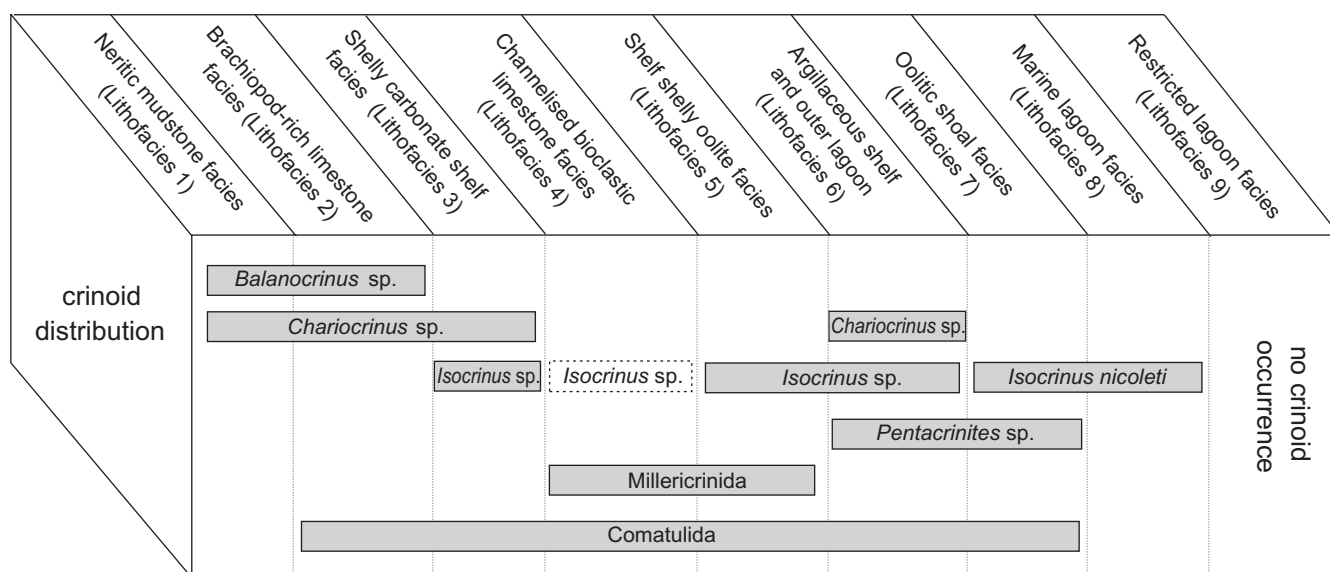


Fig. 4. Distribution of the different crinoid groups across the numbered facies 1–9. The bars represent the presence of diagnostic ossicles.

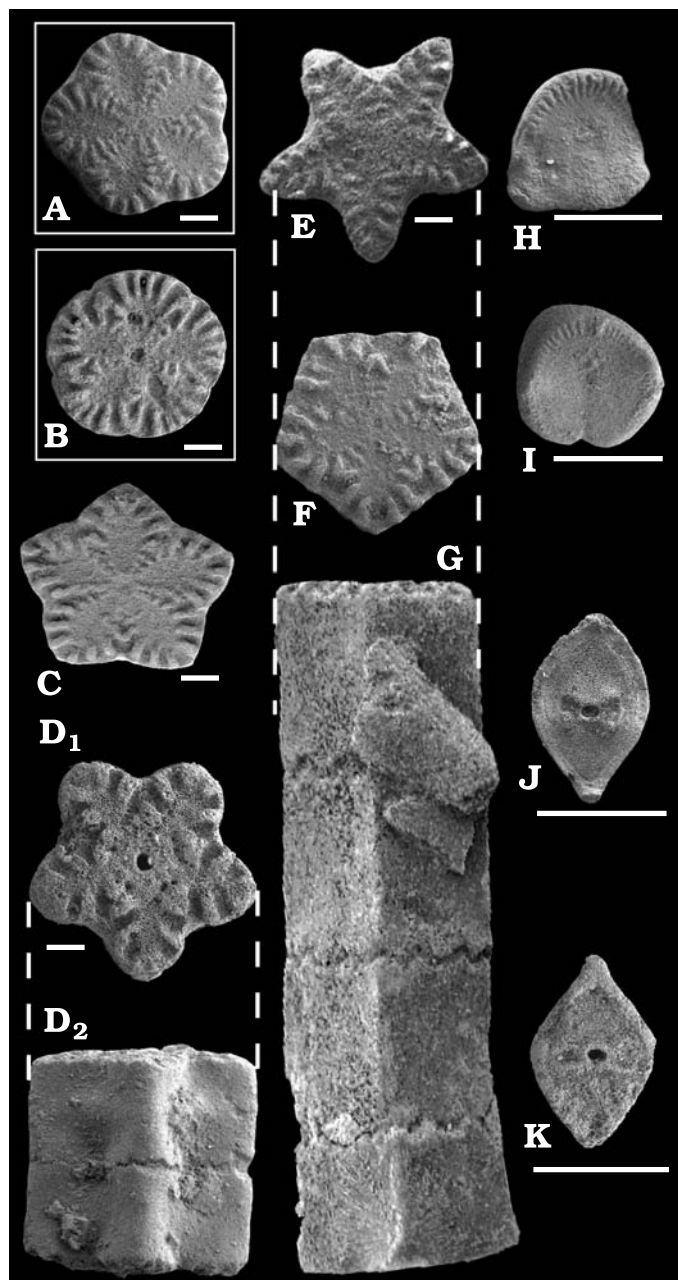


Fig. 5. Bathonian (Middle Jurassic) crinoid elements from England. **A.** Symplectial articularium of *Chariocrinus* sp. 1, BMNH EE 5770, bed 14. **B.** Symplectial articularium of *Balanocrinus* cf. *subterres* (Münster in Goldfuss, 1831), BMNH EE 5771, bed 9, Watton Cliff. **C.** Symplectial articularium of *Chariocrinus* sp. 1 BMNH EE 5772, East Cranmore. **D.** *Chariocrinus* sp. 1, BM(NH) EE 5773, Hornsleaslow. **D₁**, symplectial articularium; **D₂**, noditaxis. **E.** Symplectial articularium of *Chariocrinus* aff. *wuertembergicus* (Oppel, 1856), BM(NH) EE 5774, bed 3, Watton Cliff. **F.** Symplectial articularium of *Chariocrinus* aff. *wuertembergicus* (Oppel, 1856), BM(NH) EE 13500, bed 3 Watton Cliff. **G.** Noditaxis of *Chariocrinus* aff. *wuertembergicus*, BM(NH) EE 5775, bed 3, Watton Cliff. **H, I.** Cryptosyzygial articularium of brachial *Chariocrinus* sp. 1, Hornsleaslow, BM(NH) EE 5776 (**H**) and BM(NH) EE 13501 (**I**). **J, K.** Articularia of cirral ossicles of *Pentacrinites* cf. *dargniesi* (Hess 1972), Taynton Limestone, BM(NH) EE 13502 (**J**) and BM(NH) EE 5777 (**K**). Scale bars 3 mm.

samples from Huntsmans Quarry, 4 out of 6 of the cirral ossicles (Fig. 3) belonged to *Pentacrinites* cf. *dargniesi* identified

by their distinctive lozenge-shaped cross-section, the remainder being of *Isocrinus* sp. 2. Unidentifiable comatulid centro-dorsals are also present. Laterally equivalent beds sampled in the Boulonnais lacked accumulations of cirri.

Lithofacies 8: marine lagoon.—*Isocrinus* was the only crinoid genus recovered from this facies. Within most of the samples, the species could be identified as *I. nicoleti*. Samples at Woodeaton Quarry contain poorly preserved columnals of *Isocrinus* sp. 1. At Kirtlington Old Cement Works, well-preserved remains of *I. nicoleti* were collected from the oolitic clay bed (Forest Marble), including pluricolumnals of five to six columnals with low columnal height. At other localities and horizons, such as the grey clays at Kirtlington Old Cement Works, the Sharps Hill Formation at Oakham Quarry, Warwickshire, and the marl partings in the Causses du Quercy Limestones, Dordogne Valley, only isolated and abraded columnals occur (pluricolumnals absent). Consistently small columnals belonging to *Isocrinus* sp. 3 recorded in one sample from the White Limestone Formation (Ardley Member), and also at the Kirtlington Old Cement Works, are thought to represent a population of juveniles, as they show synarthry, a juvenile characteristic (Simms 1989a).

Lithofacies 9: restricted lagoon.—Although small quantities of echinoid and ophiuroid material were recorded from this facies, no crinoids were found with the exception of 1–2, poorly preserved and evidently reworked columnals of *Isocrinus*? sp. in the Blisworth Limestone.

Taphonomy

No complete crinoids were recorded, suggesting that all samples contain material that was transported to some degree. Pluricolumnal preservation and the relative proportions of elements and abrasion may reflect the influence and degree of transportation. In the assemblages from the channelised bioclastic limestone facies (lithofacies 4), the abraded nature of the columnals reflects transportation. This is also true for the oolite shoal facies, where hydrodynamic sorting appears to have preferentially concentrated cirral ossicles. Within the lower-energy, more argillaceous environments, the degree of transport is less clear. The crinoid preservation is remarkably consistent within each of the lithofacies, for example within the higher energy lithofacies there is virtually no pluricolumnals while in the lower energy facies have articulated pluri-columnals. Although Brett et al. (1997) concluded that the primary factor in echinoderm taphonomy is palaeo-environment and sedimentology. We propose there is a second signal influencing the data in this study, namely the way in which crinoids autotomize and disarticulate. The structural and taxonomic similarity of Jurassic and modern isocrinids reflects a strong physiological similarity, which permits the use of modern taxa as models to gauge which of these two factors most influences the dataset.

Isocrinids typically autotomize below nodals (Baumiller et

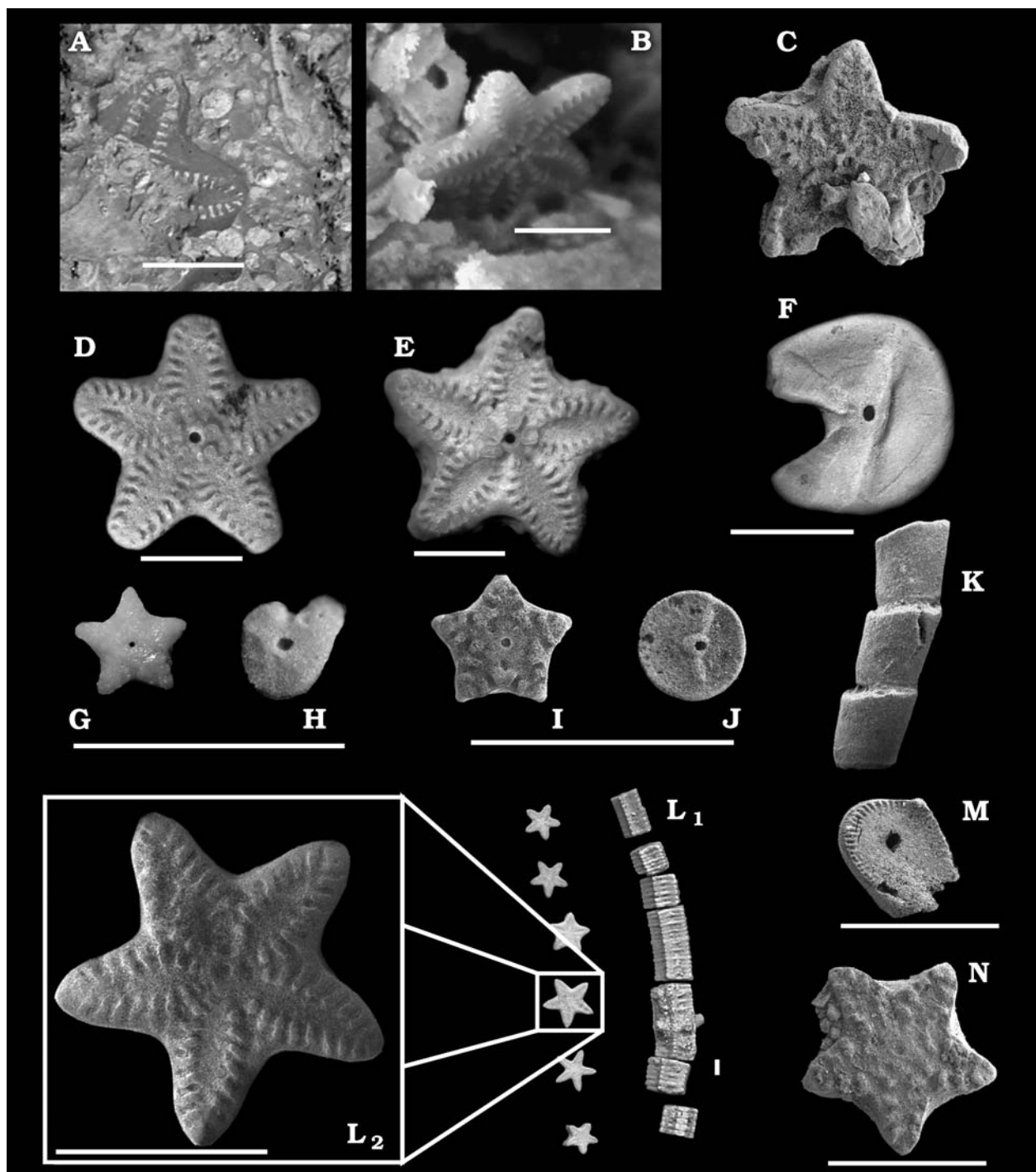


Fig. 6. A–E. Bathonian (Middle Jurassic) crinoid elements from England and France. Symplectial articularium of *Isocrinus nicoleti* (Desor, 1845). A. BM(NH)EE5834, Calcaire de Langrune Sword Beach. B. BM(NH)EE5835, Taynton Limestone, Huntsmans Quarry. C–E. BM(NH)EE36 (C), BM(NH)EE37 (D), BM(NH) EE 13503 (E), Forest Marble, Watton Cliff. F. Brachial muscular synarthry of brachial *Isocrinus nicoleti* (Desor, 1845), BM(NH) EE 5839, Forest Marble Watton Cliff. G. Symplectial articularium of *Isocrinus* sp. 3, BM(NH) EE 5779, White Limestone, Kirtlington. H. Cryptosyzygial articularium of brachial. *Isocrinus* sp. 3, BM(NH) EE 13504, White Limestone, Kirtlington. I. Symplectial articularium of *Isocrinus* sp. 2, BM(NH) EE 13505, Taynton Limestone, Huntsmans Quarry. J. Articularium of cirral ossicles of *Isocrinus* sp. 2 BM(NH) EE 5778, Taynton Limestone, Huntsmans Quarry. K. Pluricirral of *Isocrinus* sp. 2, BM(NH)EE 13506, Taynton Limestone, Huntsmans Quarry. L. *Isocrinus nicoleti* (Desor 1845) BM(NH) EE 5780. Forest Marble, Kirtlington. L₁, noditaxis with articular face of the columnals; L₂, magnified articular face. M. Cryptosyzygial articularium brachial of *Isocrinus* sp. 1 BM(NH) EE 5838 4, bed 50 Hampen Marly Beds, Hampen Cutting. N. Pluricirral and symplectial articularium of *Isocrinus* sp. 1., BM(NH)EE 13507, bed 50, Hampen Marly Beds. Scale bars 5 mm.

al. 1995), actively shedding parts of the stalk in unfavourable conditions. Shibata and Oji (2003) suggested that autotomy

also occurs as a specific, intrinsically programmed event during normal development and is restricted to the arms. Some

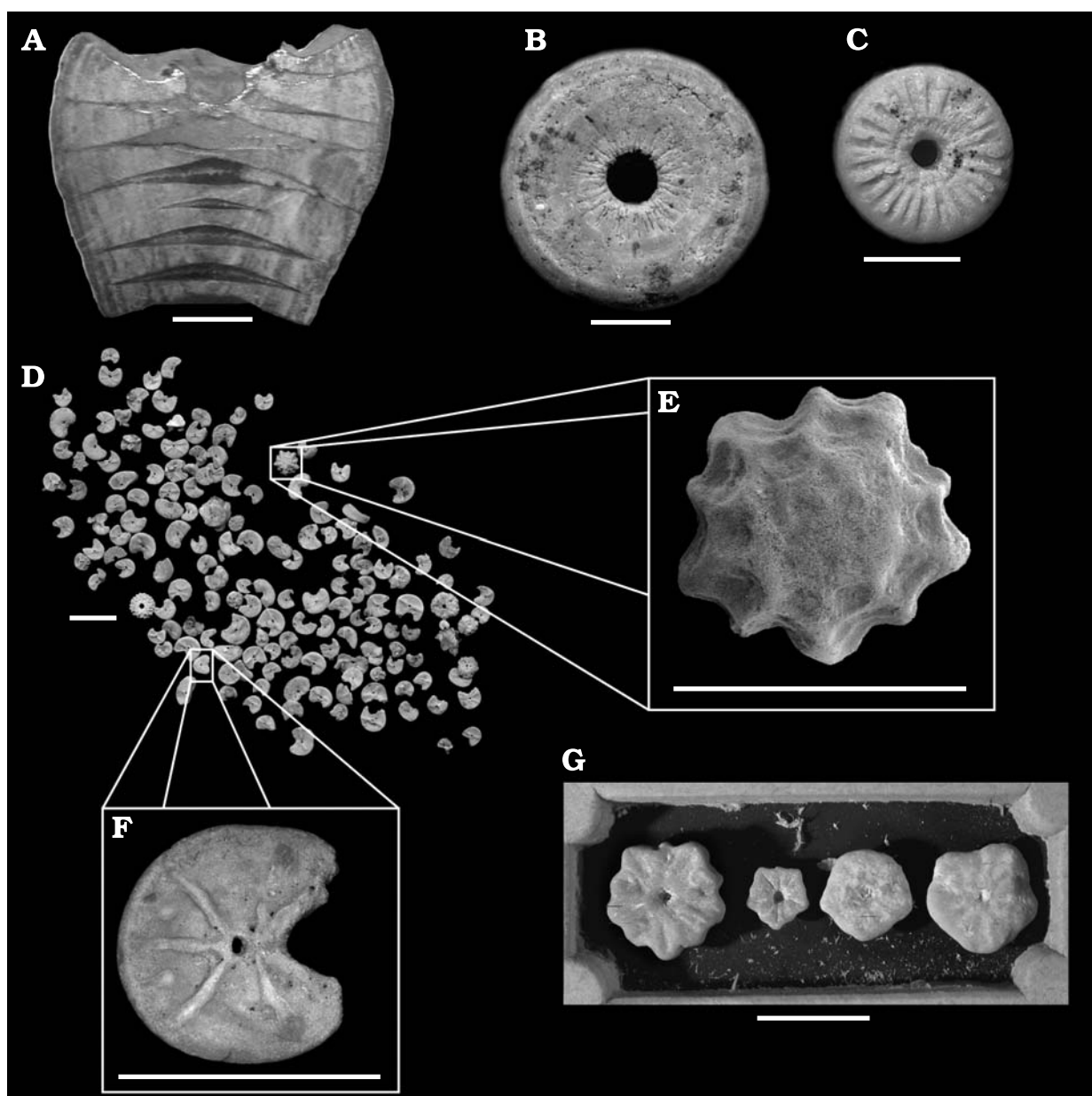


Fig. 7. Bathonian (Middle Jurassic) crinoid elements from England. **A.** Cup *Apiocrinites* sp. **B.** Articular view of *Apiocrinites* sp. 1 BM(NH) EE 5843, Forest Marble Watton Cliff. **C.** Articular view of *Millericrinus* cf. *exilis* (de Loriol, 1882) BM(NH) EE 5844, Forest Marble Watton Cliff. **D.** Brachial ossicles of Comatulid indet. **E.** Centrodorsal ossicle of *Solanocrinites ooliticus* (Gislén 1925) BM(NH) EE 5841, Forest Marble Watton Cliff. **F.** Syzygial articularium of comatulid indet. BM(NH) EE 5840, Forest Marble Watton Cliff. **G.** Centrodorsal ossicles of *Solanocrinites ooliticus* (Gislén 1925) BM(NH) E68067-9, Forest Marble, Gloucestershire. Scale bars: A–D, G, 10 mm; E, F, 5 mm.

crinoids exhibit rapid stalk growth rates despite possessing relatively short stalks (Oji 1989), indicating the high frequency of shedding. Furthermore, living stalked crinoids appear to be capable of voluntary arm autotomy followed by regeneration (Emson and Wilkie 1980; Oji and Okamoto 1994; Oji 2001). Moreover, Amemiya and Oji (1992) suggested that the uppermost part of the stalk, including the basal plates of the aboral cup, has the capacity to regenerate the entire crown. This apparent regeneration of brachial elements could explain the high quantity of brachial ossicles in all the lithofacies. This is also apparent in Recent crinoids for instance in the captive populations kept at the University of Tokyo, Japan brachial el-

ements make up nearly 1/3 of the residue at the base of the aquaria (AWH personal observation 2007). Despite brachial elements of the crown being preserved, the vast majority of ossicles collected in this study belong to columnals and cirri. The number of different elements in each lithofacies could be explained by reference to growth rates measured for the extant crinoid *Metacrinus rotundus*, determined from oxygen isotopic ratios to be 300–600 mm/year (Oji 1989). Although, this could be overestimated by up to 50% as they used isotope ratios as recent data from Messing et al. (2007) estimate *Neocrinus decorus* to have a growth rate of 170 mm/year. This rapid growth of the stalk is explained by the high-energy envi-

ronment the crinoids inhabit, which results in the stem being broken off frequently as a result, *Metacrinus rotundus* tends to possess an ample length of stalk. Roux et al. (1988) David and Roux (2000), applied the growth rates observed in modern crinoids exemplified in the studies by Messing (1985), Roux (1987), and Oji (1989) to calculate how long it takes to accumulate such crinoid limestones, with some success. David and Roux (2000) calculated that the Euville crinoidal limestone (Oxfordian de la Meuse) in France took 24 000 years to accumulate. Due to the nature of preservation in this study, such methods are deemed not applicable.

The possible high productivity of columnals detailed above may explain why, in the present study, crinoid columnals and pluricolumnals commonly occur in much greater abundance than other body parts such as arms and calices. This difference has been attributed to selective preservation (Moore and Jeffords 1968; Baumiller and Ausich 1992; Brett and Taylor 1997), although crinoid stalk fragments might also survive as solitary, decapitated stems. Oji and Amemiya (1998) found that crownless stalks could survive for up to one year, suggesting similar survival in Jurassic taxa. The large numbers of pluricolumnals in most of the sampled marine carbonate and lagoonal mud lithofacies (1–2, 5–6, 8) suggests autochthonous preservation before transport. However, little direct evidence for transport exists, and breakage could also be the result of bioturbation.

Preservation of pluricolumnals varies markedly. The length of noditaxes in this study varies substantially in each facies and between the individual genera (Table 2). This differential preservation could be due to the taphonomic conditions of the EOD, but could also be due to differing specific post-mortem disarticulation of the crinoid groups. For example, within lithofacies 1–2, 5, 6, and 8, long pluricolumnals of *Balanocrinus* and *Isocrinus* tend to be preserved, while those of *Chariocrinus* do not. In modern environments, data by Messing and Llewellyn (1992) (Charles. G. Messing personal communications 2007) demonstrated major differences in the way two crinoids, *Neocrinus decorus* and *Endoxocrinus parrae*, contribute to modern crinoid-rich sediments, specifically that the two species disarticulate at different rates. The abundance of intact, apparently autotomized stalk fragments suggest that *N. decorus* produces sediment at a greater rate than *E. parrae*. Throughout this paper, the ratio of columnals has been used to assess the relative proportions of each crinoid in each lithofacies (Fig. 3). Research by Messing and Llewellyn (1992; Charles. G. Messing personal communications 2007) has demonstrated that it is difficult to assess true populations of crinoids even in modern environments because they disarticulate differently, thus it is not possible to reconstruct the true population of the crinoids in any of the lithofacies.

Most of the crinoid ossicles in the present study were part of the shell debris that formed as taphonomic feedback (that is, all of the biotic elements that were incorporated into the sediment through time) of each lithofacies. Such shell debris are subject to reworking, not only with time averaging, but also in the concentration of elements from a largely heterogeneous

habitat. Such bias was demonstrated by Messing (1993) and Messing and Rankin (1995), regarding variations in the skeletal contribution to sediment by the modern stalked isocrinid *N. decorus*. Their research found that despite active transport of crinoid elements, the majority of ossicles are close to the source area and thus are representative of the living assemblage. Therefore, despite marked variation within this modern environment, the taphonomic feedback can indeed represent the faunal composition of the source area. Using this evidence, we conclude that it is likely that the lower energy lithofacies in the present study (especially those dominated by more muddy deposition) could represent largely in situ preservation of columnals. Although this is not always the case, the presence of cirral ossicles of *Pentacrinites* (and ooids) in some, generally low energy deposits, could indicate periodic transport of material from adjacent oolite shoals.

Although it is likely that the crinoid fragments represent the species composition of the living population, it is unlikely that the columnals represent populations from heterogeneous habitats (patches within an EOD). Research into modern crinoid species shows that they can be very environment and facies specific. Llewellyn and Messing (1993) found ossicles of *E. parrae* in proportionally greater abundance in coarser, highly abraded sediment from a scour pit adjacent to an isolated boulder supporting a dense cluster of over 30 living *E. parrae*, whereas *N. decorus* ossicles dominated extremely well-sorted, rippled sand. Their study illustrates the extremely localised nature of crinoid preservation in modern environments. Their study illustrates the extremely localised nature of crinoid preservation in modern environments. Subsequent mixing of elements within the fossil para-autochthonous assemblages in the present study is likely to mask these effects. The allochthonous faunal component of samples from the marine Forest Marble Formation (lithofacies 4) demonstrates that such specific preservation from different parts of a microhabitat can be deduced from the different types of echinoderm elements. For example, Hunter (2004) demonstrated the apparent transportation of fauna from different parts of a heterogeneous source area. This allows fossils representing organisms from a range of different lithofacies and palaeoenvironments to be reconstructed as a community, including both hard- and soft-substrate-adapted organisms. In short, distinct but coexisting and adjacent palaeoenvironments can be recognised through the separation of obviously transported elements.

Palaeoenvironmental control of crinoid taxa

Crinoid assemblages in the current study within offshore, mud-dominated lithofacies consist of the genera *Balanocrinus* and *Chariocrinus*. Although these occur together in many samples, they nevertheless show different distribution patterns. *Balanocrinus* cf. *subteres* dominates the darker, clay-rich lithofacies, whereas *Chariocrinus* cf. *wuertembergicus* is

the dominant species within more silty and calcareous mudstones containing abundant and diverse benthos. *Chariocrinus* cf. *wuertembergicus* is also present in presumed shallower water settings, such as the *Rugitella* Beds, where *Balanocrinus* and other crinoids are absent. *Chariocrinus* sp. 1 is also present in the Boueti Bed, but not in the Cornbrash. The Boueti Bed shares some lithological characteristics with the brachiopod-rich limestone lithofacies, and shares a fauna dominated by brachiopods and bryozoans. A similar crinoid fauna is, therefore, not unexpected and it may be that the Boueti Bed is palaeoenvironmentally closer to the brachiopod-rich limestone facies than the Cornbrash. A second species of *Chariocrinus* is known only from the presumed shallow, muddy embayment lithofacies of Hornsleaslow, where it is associated with *Isocrinus* (Fig. 4).

Remains of *Isocrinus nicoleti* are largely restricted to shallower-water lithofacies, especially those dominated by carbonate sands. *I. nicoleti* is common within the channelised bioclastic limestone and shelf shelly oolite lithofacies, and is also present in the Cornbrash and the oolite shoal lithofacies. Large numbers of specimens are also present within the fully marine lagoons, reflecting the current conditions necessary for crinoids to feed. The restricted lagoons are interpreted as being too low energy for crinoid feeding. One occurrence of *Isocrinus* contained probable juveniles (Fig. 6). A second species of *Isocrinus* was recorded in one sample at Hornsleaslow, the only co-occurrence with *Chariocrinus*.

Specimens of *Pentacrinites* were represented almost entirely by cirral material, preventing species-level identification. *Pentacrinites* were common in the oolite shoal lithofacies (Fig. 4), with rare specimens in two samples from an outer lagoon lithofacies (where they are associated with transported ooids). There was no evidence for the genus elsewhere.

Other crinoid taxa such as millericrinids and comatulids were generally rather more restricted in their distribution than the isocrinids. *Millericrinus* sp. and *Apiocrinites* sp. were only recorded in the channelised bioclastic limestone lithofacies (Fig. 4), and appear to be absent from other, lithologically similar lithofacies. Comatulids are at their most abundant within the channelised bioclastic limestone lithofacies, with at least two unidentified taxa present. Comatulids are also present within more oolitic lithofacies but appear to be absent from both offshore and lagoonal muddy lithofacies, although comatulid diversity is difficult to track when compared with those of stalked crinoids (Baumiller et al. 2008).

Crinoid autecology

The differential distribution of the isocrinids and pentacrinitids clearly shows that different species were limited to particular palaeoenvironments (Fig. 4). It is evident from the distribution of Bathonian crinoids that a correlation between columnal height, cirral density, and environmental energy exists. Those taxa with more cirri (and hence shorter internodals) are present in the higher energy facies. This is not un-

expected as cirri are the primary attachment structure of these crinoids (Rasmussen 1977), and higher energy settings are likely to have required more robust attachment. It is evident that localised conditions within palaeoenvironments influenced crinoid distributions. Variations in length of pluricolumnals could influence posture and distribution relative to current flow and topography, as suggested by Messing and Llewellyn (1992). Although David et al. (2006) showed clear relationships between environment, morphology, and taxonomy in the genus *Endoxocrinus*, these data cannot be directly applied to the Jurassic forms, largely due to the incomplete nature of the dataset in this paper. However, David et al. (2007) revealed a link between bathymetry and substrate and the importance of internodals per noditaxis and columnal height to columnal diameter palaeoecological reconstruction.

Fossil crinoid pluricolumnals in the present study area are rare, but the rarity of nodals amongst columnals of *Balanocrinus* cf. *subteres* suggests long internodes (> 30 internodals) and hence relatively few cirri. Pluricolumnals of *Chariocrinus* cf. *wuertembergicus* are also long; specimens from Switzerland typically contain 7–18 columnals per noditaxis. These taxa occur furthest offshore in what were probably the lowest energy palaeoenvironments with more muddy lithofacies. However, the role of columnal length and cirrus density needs to be investigated further using Recent forms in order to test the significance of these Jurassic data. Still, both *Balanocrinus* and *Chariocrinus* were only abundant in shelly sediments; samples poor in shell debris lacked crinoids. Both crinoid taxa may have relied on shells as a substrate for attachment, although alternatively they may simply have preferred palaeoenvironments suitable for shelly benthos.

Columnals of *Isocrinus nicoleti* are present in many of the shallower-water lithofacies and are common in oolitic and bioclastic limestones. *Isocrinus* sp. 1 is also present in some more muddy, lagoonal lithofacies. Both have far fewer columnals per noditaxis than *Balanocrinus* or *Chariocrinus*: 5–8 in *I. nicoleti* and 5–6 in *Isocrinus* sp. 1. Cirral density was further increased relative to that of the other isocrinid genera by having low columnals. Higher cirrus densities presumably allowed better attachment in high-energy conditions.

Pentacrinites cf. *dargniesi* was only recorded from highly mobile, oolite facies. It is highly unlikely they lived in autochthonous oolites but adjacent to them in a channel or at the base of the slope. *Pentacrinites dargniesi*, which was found only rarely and which may be conspecific with *P. cf. dargniesi*, is robust with a short column and high densities of long cirri, perhaps reflecting a similar attachment strategy to *Isocrinus*. Alternatively, Early Jurassic *Pentacrinites* spp. may have been pseudoplanktonic (Simms 1986), although this habit is apparently inconsistent with the distribution of Middle Jurassic species, which are absent from offshore mudstones. Articulated specimens of *P. dargniesi* are commonly found as tangled masses of many individuals, which led Hess (1999) to interpret that it formed mats of individuals, interlinked with their long cirri, which would have drifted along the seafloor close to oolite shoals (although it not clear how they fed).

However, this lifestyle would have left the crinoids prone to destruction within this high-energy environment. It seems more likely that the crinoids attached to the mobile substrate using their cirri, with numerous individuals holding each other in place and possibly even stabilising the sediment surface.

Millericrinids lacked cirri, attached by cementation, and were largely restricted to hard substrates including large shells or pebbles (Hess 1975). Unlike the approximately coeval Bradford Clay, from which *Apicocrinites* is well known (and *Millericrinus* is absent; Palmer and Fürsich 1974), there is no good evidence for a hardground within any of the sections in the present study. It is thus likely that hardgrounds were present elsewhere, and their faunas were transported into neighbouring facies. Perhaps the common mudstone and micrite clasts associated with the millericrinids are the remains of eroded and transported hardground surfaces. The restricted distribution of millericrinids may not represent lithofacies specificity, but may be due to the samples containing allochthonous elements from hardground facies.

The high diversity of taxa from lithofacies 4 could imply that these crinoids, as well as crinoids across all the environments under study (due to different internodal lengths described) could have exhibited a similar manner of trophic tiering. However, the data presented here is not sufficient to complement the extensive work on Palaeozoic crinoids (e.g., Ausich 1980, Bottjer and Ausich 1986).

Comparisons with other crinoid assemblages

Most studies of crinoid palaeoecology have focused on the Palaeozoic, and most taxonomic work on Mesozoic crinoids has omitted such information. In the Middle Jurassic sections not sampled in this study, Bignot (1899) noted *Isocrinus nicoleti* in the sections of Luc-sur-Mer (Normandy) along with *Ailsacrinus prattii* (Carpenter, 1882), while Roux (1978) noted *Apiocrinites elegans* from the “Calcaire de Ranville” also preserved in a hardground setting (Amfreville quarry Normandy) seen in this study. In the Burgundy Basin, both *Apiocrinites* and *Isocrinus* are also associated with oolites (Michel Roux, written communication 2007).

Many of the isocrinid genera mentioned in Simms' (1989b) extensive study of the Lower Jurassic are also present in the Bathonian, with genera exhibiting similar facies specificities in both time periods. Simms (1988) recognised *Balanocrinus* in more clay-dominated sediment and *Chariocrinus* in more silty substrates, a similar situation to that in the Bathonian. In addition, *Isocrinus* was mainly restricted to silty and sandy sediments representing shallower-water and higher-energy palaeoenvironments in the Lower Jurassic. Nevertheless, the occurrences of *Pentacrinites* differ significantly between the Lower Jurassic and Bathonian of both England and Switzerland (Hess 1999). Lower Jurassic occurrences suggest a pseudoplanktic lifestyle (e.g., *Pentacrinites fossilis*), with

specimens typically occurring in laminated offshore mudstones and well-preserved specimens being commonly associated with large pieces of fossil wood. This transformation from a pseudoplanktic to a benthic lifestyle on an unstable substrate appears dramatic, although it is possible that the pseudoplanktic adaptations of earlier species later proved equally suited to a specialised benthic mode of life.

A number of crinoids are known from the Bajocian of Switzerland (Hess 1999), where they typically occur as obrution deposits, with each bedding surface containing only one or two crinoid taxa. Although all of the assemblages lie beneath carbonate sands, differing underlying sediments suggest a number of palaeoenvironments could be represented, with migrating sand waves periodically extending into otherwise lower energy environments (Hess 1999). Specimens of *Chariocrinus* are typical of the deepest, generally muddy lithofacies (Fig. 2) with only rare occurrences in beds of carbonate sand. *Isocrinus nicoleti* dominates assemblages from shallower, more carbonate-rich substrates (Fig. 4) and may be accompanied by *Pentacrinites dargniesi* (Hess 1999). The only comatulid genus found in Swiss Jura is *Paracomatula*, which was not recorded in the present study. It is possible that the palaeoenvironments favoured by *Solanocrinites* were absent in Swiss the Bajocian–Bathonian or that *Paracomatula* was dominant in this region.

Two assemblages of articulated crinoids are well known from the British Bathonian. Numerous specimens of *Apiocrinites parkinsoni* are known from a single locality in the Upper Bathonian Bradford Clay (Simms 1999), where they form part of a well-developed hardground fauna. A second, also monospecific, crinoid assemblage comprises a Lower Bathonian obrution surface covered by *Ailsacrinus* whose vestigial stem is virtually absent and lacks any fixed attachment (Taylor 1983). The sedimentological context of this find is poorly known, and the absence of this species from any of the samples in this paper suggests that it is likely to have been palaeoenvironmentally restricted.

Several Upper Jurassic crinoid assemblages from Switzerland (Hess 1975) and Poland (Pisera and Dzik 1979) include cyrtocrinids not known from the British Bathonian, associated with genera such as *Balanocrinus*, which does occur in the British Bathonian (e.g., *Balanocrinus* cf. *subteres* from the Argovien, Savigna and Effinger Schichten). Some taxa from these faunas (*Millericrinus* sp. from the Terrain à Chailles, and *Apiocrinites roissyanus* (Natica-Schichten and Humeralis-Schichten) show a preference for hard substrates, although it is unclear whether they inhabited hard substrates at these localities. Their presence here suggests a lithofacies bias, as these forms are not known from the more muddy British Oxfordian.

Cretaceous crinoid faunas are much better known than those of the Middle Jurassic (Rasmussen 1961; Jagt 1999; Hunter and Donovan 2005). Mitchell and Langner (1995) discussed crinoids from the Albian with similar distributions of comparable morphotypes to those seen in the Bathonian. Deep-water lithofacies were dominated by isocrinid taxa with long noditaxes, with shallower water lithofacies containing

only taxa with higher cirral densities. Stromatolitic and hard-ground lithofacies, in this case representing very shallow water, lacked isocrinids but contained cementing *Apiocrinites*.

Apart from some notable exceptions (e.g., *Metacrinus rotundus* from Suruga Bay of Japan [Oji 1986]) most modern stalked crinoids are restricted to deep water (Bottjer et al. 1988), in marked contrast to the Mesozoic taxa illustrated in this study, which were prominent within a range of shelf environments, including very shallow water and lagoons. Although there appears to have been a general trend amongst isocrinids towards deeper water habitats from the Cretaceous onwards (Bottjer et al. 1988), isocrinids were still present in shallow water, at least in the Eocene of Antarctica (Meyer and Oji 1993; Baumiller and Gaździcki 1996). Current palaeobiological models hold that predators eliminated populations of epifaunal suspension feeders from shallow, soft-substrate marine environments beginning in the latest Mesozoic (Aronson et al. 1997). However, Roux has questioned this in several studies (see Ameziane and Roux 1987); his alternatives have not been widely accepted. The results of the present study show that well before the late Mesozoic marine revolution, crinoids inhabited a wide range of niches and environments including very shallow waters. Today such populations can only be found in a handful of places including the Little Bahama Bank and Suruga Bay of Japan.

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Appendix 1

Field localities. SP, ST, SY, ZX, UK National grid numbers.

1. Frome Clay, Wattonensis Beds 14, Watton Cliff, Dorset, England, UK

Watton Cliff (also known as West Cliff) (SY 451 908–453 907) exposes the most complete section of fully marine sediments in the British Bathonian. The middle to upper part of the sequence consists of the largely unfossiliferous Frome Clay, which is overlain by the Boueti Bed (not sampled) and the Forest Marble Formation. The section is bounded by faults at both eastern and western sides. Callomon and Cope (1995) noted only 8 m of exposure in the eastern end of Watton Cliff, exposed beside the Eype Mouth Fault and on the beach itself. However, more recent storms (pre-2001) have revealed a far more complete section, allowing reconstruction of the section from the faulted and land-slipped sections. The sampled bed probably lies stratigraphically above the Wattonensis Beds and consists of an offshore, oyster-rich mudstone.

2. Bed Z, Blockley Station Quarry, Gloucestershire, England, UK

Blockley Brick Pit (SP 180 370) exposes a large section of Lower Jurassic shelly mudstones and limestones (Simms 2004). The base of the section is formed by Bed Z, referred to as the crinoid-belemnite bed, which consists of a well-cemented, shelly limestone with abundant belemnites, crinoids, and shell and fish debris.

3. Pecten Bed, Blockley Station Quarry, Gloucestershire, England, UK

Bed 2 of Callomon's log (see Simms 2004) is called the Blockley Shell Bed or *Pecten* Bed, a highly fossiliferous, grey to light brown mudstone series with siderite nodules in the top level of shell gravel. Bed 2 is 0.5 m thick and is an important stratigraphic marker bed. The highly diverse bivalve fauna includes *Aequipecten prisca*, *Grammatodon* sp., and *Gryphaea* sp. Although Lower Pleinsbachian, this locality and Watton Cliff are lithologically similar.

4. Frome Clay, Wattonensis Beds 3–11, Watton Cliff, Dorset, England, UK

The base of the section at Watton Cliff (SY 451 908–453 907) exposes the Wattonensis Beds, a series of alternating bryozoan and brachiopod-rich clays and thin limestones (pelmicrites) underlying the facies 1 sample. In this survey, five marl or clay beds, 3, 5, 7, 9, and 11 were sampled. Each bed varies substantially in lithology; some are more shelly and calcareous, while others are more muddy. Generally, the fauna is dominated by brachiopods (*Rugitella*, *Wattoniathyris*, *Acanthothyris*, *Tubithyris*, and *Rhynchonelloidella wattonensis*), with common bivalves (e.g., *Parallelodon*, *Trigonia*, and *Modiolus*) and belemnites. The beds are in the upper part of the *Procerites hodsoni* Zone in the *Procerites quercinus* Subzone.

5. Fullers Earth Rock, Rugitella Beds, East Cranmore, Somerset, England, UK

East Cranmore (ST 687435) exposed a temporary section of *Rugitella* Beds, and was one of the few exposures of this facies in southern England. Material was collected from an excavation for a lake in 2001. Stratigraphically, the *Rugitella* Beds lay between the Fuller's Earth Rock and the Fuller's Earth Clay. The Fuller's Earth Clays themselves are not particularly rich in fossils, although oysters are fairly common. The sampled beds consist of a series of thin, rubbly pelmicrites, which are extremely rich in bryozoans (18–20 species). Other common faunal elements include ornithellid and rhynchonellid brachiopods.

6. Boueti Bed, Forest Marble, Herbury Point, Dorset, England, UK

Herbury Point (SY 611 810) exposes a far more fossiliferous section of the Boueti Bed than that seen at Watton Cliff. The sampled bed is exposed near the northwest tip of the point in the West Fleet lagoon. The Boueti Bed forms the base of the Forest Marble Forma-

tion, forming a marker bed as far north as the Mendips. The similarity over such a wide area of southern England suggests a hiatus in sedimentation. The richness of the fauna, and encrustation of the larger shells with bryozoans and small oysters, suggests that accumulation was over a long period of time (Sylvester-Bradley and Ford 1968), enabling suspension-feeding brachiopods to flourish (House 1993). Lithologically, the bed consists of rubbly, detrital, micritic limestone. Abundant fossils include brachiopods such as *Goniorhynchia boueti*, *Avonothyris*, *Dictyothis*, and *Digonella*, many with encrusting bryozoans and serpulids (Calloman and Cope 1995). Other common elements include the bivalves *Trigonia*, *Radulopecten*, and *Liostrea*.

7. Lower Cornbrash, Kirtlington, Oxfordshire, England, UK

Kirtlington (SP 126 252) exposes the Lower Cornbrash of the *Clydoniceras discus* Subzone, at the top of the Bathonian. One sample was taken from a marl parting in the bioclastic limestones that overlies the Forest Marble Formation. Shelly faunas include bivalves (*Modiolus*, *Pholadomya*, and *Liostrethea*), brachiopods, gastropods, and rare ammonites.

8. Forest Marble, Watton Cliff, Dorset, England, UK

Exposed at Watton Cliff, the Forest Marble Formation overlies the Frome Clay, the lowermost unit of which is the Boueti Bed. The Forest Marble Formation at this locality represents an open marine palaeoenvironment lithologically distinct from the same formation at Kirtlington. The sampled level is a massive oolitic, shelly, clean-washed, grain-supported limestone about 2 m thick with obvious cross-stratification. Although generally well lithified, irregular patches and lenses of the limestone are uncemented, allowing bulk sampling. Faunas are mixed, dominated by oysters, and with transported lagoonal and terrestrial elements (Freeman 1979). Soft sandy layers within the lithified sections were sampled.

9. Bradford Clay, Forest Marble Formation, Browns Folly, Bath and northeast Somerset, England, UK

Browns Folly Nature Reserve Site of Special Scientific Interest (ST 793 661) exposes one of the few remaining sections of the Bradford Clay overlying the Forest Marble. A section from the Combe Down Oolite to the Forest Marble can be observed (Smith 1998). The Bradford Clay occurs beneath overhangs of the overlying unit. The underlying Forest Marble consists of 4.7 m of current bedded biomicrudite that forms caverns and is locally bored and sometimes interbedded with oomicrite/biomicrite (Smith 1817). Two samples from marl partings were taken. The brachiopod *Digonella digona* was recognised.

10. Bradford Clay, Forest Marble, Old Canal Quarry, Wiltshire, England, UK

The Old Canal Quarry (ST 831 609) is now largely infilled and not suitable for resampling. It has, however, provided many fossils that are now in the BMNH. Although not collected systematically, these were studied for comparative purposes. Palmer and Fürsich (1974) described 5 m of the top of the limestone exposed at the back of the quarry. Cross-bedded oobiosparite (Forest Marble Formation) is capped by a hardground and overlain by 100 mm of a richly fossiliferous bed. The upper part of the sequence consists of blue clay with impersistent bands of oobiosparite. Common fauna includes bivalves (*Plagiostoma*, *Oxytoma*, and *Radulopecten*) and brachiopods (*Dictyothis*, *Avonithyris*, *Eudesis*, *Digonella*, and *Cryptorhynchia*). The echinoderm fauna is rich and includes the crinoid *Aiocrinites* and echinoids *Acrosalienia* and an indeterminate cidaroid.

11. Bradford Clay, Forest Marble, Springfield, Wiltshire, England, UK

The Springfield exposure (ST 831 609) was visible in the summer of 1972 but is now inaccessible. Fossils now in the BMNH, although not collected systematically, were studied for comparative purposes. Palmer and Fürsich (1974) mentioned that 5 m of the limestone as well as 2.5 m of the overlying clay were temporarily exposed. In addition, the contact between the limestone and the overlying Bradford Clay could be followed in vertical section for about 100 m towards the north. This locality has an identical lithology and fauna to those described above.

12. Forest Marble, Sunhill Bradford Bed Gloucestershire, England, UK

Sunhill Quarry (ZX 145 178) is now largely unexposed and not suitable for resampling. Fossils now in the BMNH, although not collected systematically, were studied for comparative purposes. Elliott (1973) described cream-coloured beds with lenticles of shells irregularly interleaved with shelly limestones that contain micritic portions showing bioturbation. Common fauna includes serpulids and oysters, other bivalves (*Plagiostoma*, *Liostrea*, *Trigonia*, and *Radulopecten*) and gastropods. Brachiopods (*Eudesia*, *Dictyothis*, *Epithyris*, and *Rhynchonelloidella*) were common.

13. Sharps Hill Formation, Northleach, Gloucestershire, England, UK

The Northleach site (grid number undisclosed) is now largely infilled and much of the echinoderm-bearing material has been removed; thus, it is not suitable for resampling. Samples of the bioclastic limestones have been stored intact in the collections of the BMNH. The fossiliferous level consists of a monospecific assemblage of the crinoid *Aiocrinites* sp. overlying a locally developed clay band (Paul D. Taylor, personal communication 2005).

14. Hampen Marly Formation, Hampen Cutting, Gloucestershire, England, UK

Hampen Railway Cutting Site of Special Scientific Interest (SP 063 205) (1 km long and 15 m deep) exposes one of the most complete sections through the Middle Bathonian. It exposes a section southwest to northeast of Fullers Earth through the Taynton Limestone Formation, to the Hampen Marly Formation and White Limestone Formation. The Hampen Marly Formation overlies the Taynton Limestone and consists of grey-green silty mudstones and marls with ooids alternating with impure limestones (Sumbler and Barron 1996). The presence of matrix-supported ooids suggests an association with shoal systems nearby. The locality is close to the Morton Axis, where more shallow-water facies predominate and the Hampen Marly Formation grades towards into the Rutland Formation. Two samples were collected from beds typical of the Hampen Marly Formation (Sumbler and Barron 1996); bed 50 consists of grey clay with ooids and shell fragments, while Bed 43 (*Ostrea* Bed) consists of grey-brown, partly-indurated, silty marl. Common fauna include the bivalves *Praeexogyra*, *Modiolus*, *Protocardia*, and *Trigoniids*.

15. Sharps Hill Formation (Eyford member), Hampen Cutting, Gloucestershire, England, UK

The Eyford Member of the Sharps Hill Formation at Hampen (above) consists of yellow and brown, fine-grained sandstones and grey clays passing upwards into well-bedded bioclastic and oolitic limestones. Grey clays were sampled, but proved too silty to process. The fauna includes oysters and rhynchonellids.

16. Eyford Member, Sharps Hill Formation, Huntsmans Quarry, Gloucestershire, England, UK

Huntsmans Quarry (SP 126 252) exposes the Eyford Member of the Sharps Hill Formation. This member is 4.9 m thick and is overlain by the Taynton Limestone Formation. It is the lateral equivalent of the Charlbury Formation. The lithology consists of bioclastic limestones and cross-bedded, burrowed sandstones containing concentrations of bivalve fragments towards the base of the beds. The fauna includes disarticulated *Trigonia impressa* and *Plagiostoma subcardiiforme*, together with *Pholadomya*, *Pleuromya*, and *Modiolus*.

17. Sharps Hill Formation, Hornsleaslow Quarry, Gloucestershire, England, UK

Hornsleaslow Quarry (SP 131 322) exposes the Fullers Earth-Sharps Hill transition and, although described by some authors as the Sharps Hill Formation, it is more correctly identified (Underwood and Ward 2004) as the Fullers Earth Formation. Richardson (1929), Channon (1950), Torrens (1969) and Ager et al. (1973) logged the succession. The quarry exposes 12.5 m of massive cross-bedded oolites of the Chipping Norton Formation containing lenses of grey-green clay rich in vertebrate remains (Metcalf et al. 1992). This is overlain by 1.6 m of the Fullers Earth Formation, which consists of grey clays with gastropods such as *Aphanoptyx* sp. and *Nerinea* sp., and the oyster *Praeexogyra hebridica*. Other bivalves include *Pseudopecten*, *Modiolus*, and *Protocardia*. Isolated coral colonies indicate a more restricted palaeogeography (although fully marine) with low energy deposits, and the high diversity of marine taxa suggest that this may have been an embayment (Sellwood and McKerrow 1974). It is mapped continuously with the Fullers Earth, apparently without intervening limestones.

18. Stonesfield Slate, Stonesfield, Oxfordshire, England, UK

Samples in museums have been collected from various localities from around the village of Stonesfield. Although not collected systematically, these collections, especially in the BMNH, have been studied for comparative purposes. This lithology was described by Underwood and Ward (2004) as quasilaminated sandy and oolitic limestones with a restricted mollusc fauna.

19. Argiles de Lion, Sword Beach, Calvados, Basse-Normandy, France

The Lion Clays cap the Langrune Limestone Formation, and consist of clays with impersistent thin limestones rich in brachiopods and molluscs. These clays are latest Bathonian in age and overlie the Langrune Formation.

20. Caillasses de la Basse-Ecarde, Juno Beach, Calvados, Normandy, France

The low cliff section at St Aubin-sur-Mer (ZX 1537 1274) exposes a sequence containing sponge bioherms (Rose and Pareyn 2003). This is a section protected by French Law in which collecting is strictly prohibited. The sequence sits on the Ranville Limestone, a pink, well-cemented, cross-bedded, limestone capped by a hardground surface with cemented oysters (Rose and Pareyn 2003). The overlying sequence of Caillasses de Saint-Aubin consists of four sedimentary units, each terminated by a discontinuity. Units 1 and 2 of Rose and Pareyn (2003) are lenticular beds of marly limestone that lie within hollows eroded in the Ranville Limestone. The lenticles are rich in brachiopods (notably rhynchonellids), crinoids (*Apiocrinus elegans*) and rolled corals (*Isastrea*). Unit 3 is another marly limestone rich in brachiopods (*Goniorhynchia* and *Digonella*) and gastropods, and capped with bored hardground surface. Unit 4 begins with

a conglomerate of pebbles derived from the underlying bed, overlain by a marly limestone rich in brachiopods, bryozoans (*Ceriacava*, *Ripisoecra*, and *Terebellaria*, which are also found in the Forest Marble Formation; Taylor 1978) and echinoids; it is terminated by hardground. Above the units in which brachiopods dominate lies a bed dominated by calcareous sponge bioherms 1–2 m high with their growth apparently arrested by the arrival of cross bedded calcareous sands. The sampled supra-reef beds are a continuous sequence of marly limestones passing up into cross-bedded bioclastic limestones with abundant bryozoans succeeds the reef beds.

21. Bath Rags, Ford Road Cutting, Wiltshire, England, UK

Ford Road cutting (ST 854 747) is one of the few exposures in the Avon area and reveals the Upper Rags Member of the recently-defined Charlfield Oolite Formation (Wyatt and Cave 2002). The Charlfield Oolite is comprised of strongly cross-bedded units deposited in high energy, tidally dominated conditions of the carbonate ramp. This locality represents a lull in the shoal system. The lithology consists of flaggy oolitic medium/course grained shell fragmental thinly-bedded limestones with marl partings.

22. Calcaire des Pichotts, Belle Houlefort, Boulogne, France

This classic Upper Bathonian (*Clydoniceras discus* Zone) section (ZX 145 178) is now largely infilled and built on, and thus not suitable for large-scale resampling, but some oolites were collected. The oolites form much of the overburden to the Palaeozoic inlier, and consist of shallow marine limestones with interbedded clays containing brackish and freshwater ostracods and some charophytes. The topmost bed is the Calcaire des Pichotts, a fossiliferous, oolitic limestone of the Lower Cornbrash. Beneath this are a series of calcareous marls and clays with abundant rhynchonellids, and a shelly limestone equivalent to the upper part of the Forest Marble Formation.

23. Calcaire de Langrune, Sword Beach, Calvados, Normandy, France

This site comprises an extensive section of coastal cliff near Luc-sur-Mer. A log for this “protected” section is given by Rose and Pareyn (2003). Samples were collected at intervals along the section. The Langrune Limestone (Unit 5 of Rose and Pareyn 2003) is 8–10 m thick, and consists of a well-cemented, bioclastic, oolitic, cross-bedded limestone rich in shelly debris, and capped by a hardground. The diverse, but fragmentary, fauna consists of bivalves, brachiopods, gastropods, and bryozoans.

24. Caillasses de la Basse-Ecarde, Sword Beach, Calvados, Normandy, France

The lower section of the coastal cliff near Luc-sur-Mer (ZX 153 127) was studied by Rose and Pareyn (2003). The base of the sequence consists of the Ranville Limestone, which consists of a micro-atoll about 50 m in length, formed by siliceous sponge bioherms 2–3 m high, capped by a bored hardground surface. It can be seen on the foreshore at low tide about 150 m east of the beach access point. Pseudosynclines are interpreted as being analogous to the bioherms described further along the coast at St Aubin by Fürsich and Palmer (1979). The overlying sequence consists of three separate lithologies consisting of lenses of yellow marls, oncoids and echinoderm-rich lenses.

Three samples are collected from yellow marls, which are rich in brachiopods (*Digonella*, *Kallirhynchia*, *Avonothyris*, and *Dictyothyris*). One sample was collected from the oncoid lenses and bioclastic limestones. Oncoid lenses have concentrically encrusted clasts. The encrusting organisms include algae, serpulids, and bryo-

zoans. Echinoderm lenses are thin (< 0.15 m), discontinuous horizons with articulated specimens of crinoids and echinoids which have been recorded photographically.

25. Taynton Limestone, Huntsmans Quarry, Gloucestershire, England, UK

Huntsmans Quarry (SP 126 252) exposes 3.5 m of Taynton Limestone (Calloman and Cope 1995). The lithology consists of white, medium-course-grained, oolitic limestones; in places these are shell-fragmental with cross bedding and have some marl partings. Blocks were collected and sampled by acid etching. The fauna includes fragmentary brachiopods and bivalves.

26. Sevenhampton Rhynchonellid Bed, Taynton Limestone, Hampen Cutting, Gloucestershire, England, UK

A clay parting was sampled at the base of the Taynton Limestone exposed at Hampen Cutting (SP 063 205).

27. Rutland Formation, Woodeaton Quarry, Oxfordshire, England, UK

Woodeaton Quarry (SP 535 122) exposes an inlier of the White Limestone and Rutland formations (Palmer 1972). In 2001, the quarry was enlarged and additional units below the Rutland Formation were exposed. Beds sampled from this site include lenses four-five of sandy, grey clay and black clay with many aragonitic bivalves, and common tetrapod remains. Other sampled collected include beds Six and Seven. Bed Six consists of fine-grained shell detrital biomicrite with moderately diverse shelly fauna. Bed seven, consists of grey clay with a moderately diverse shelly fauna including *Isgonomon* and *Trigonia*.

28. Forest Marble Formation, Kirtlington Old Cement Works, Oxfordshire, England, UK

Kirtlington Old Cement Works Site of Special Scientific Interest (SP 126 252) exposes an extensive section of the more lagoonal part of the Forest Marble Formation. The lithologies consist of oyster-rich oolitic limestones and clays containing both marine organisms (indicating marine influence) and non-marine faunas (including mammals (Freeman 1979), dinosaurs and freshwater ostracods. Forest Marble Formation clays contain lignite and both freshwater and marine ostracods, representing fringing swamps close to an area of deposition (McKerrow 1994; McKerrow and Kennedy 1973). Two horizons were sampled, one comprising a grey clay and the other an oolitic shell rich clay with scattered ooids, corals and terrestrial fossils.

29. White Limestone, Ardley Member, Kirtlington, Oxfordshire, England, UK

This sample was collected at Kirtlington Old Cement Works (ZX 153 127), from the White Limestone Formation that underlies the Forest Marble Formation. Palmer (1979) and Sumbler (1984) divided the formation into three members, the lowest Shipton, Ardley and Bladon members. The Ardley Member was sampled at Kirtlington. It was interpreted as a shallow, subtidal palaeoenvironment by Palmer (1979), analogous to deposits forming in modern Florida. This deposit was probably more palaeoenvironmentally restricted than the Forest Marble Formation and could probably better be referred to as a calcareous lagoon (Underwood and Ward 2004). The lithology consists of clays and micritic limestones.

30. Sharps Hill Formation, Oakham Quarry, Warwickshire, England, UK

Oakham Quarry (SP 282 307) exposes the Sharps Hill and overly-

ing Chipping Norton Formations. The sampled section was 0.9 m, and consisted of very shelly marls and impure limestones. A very low diversity bivalve fauna was recovered.

31. Causses du Quercy Limestones, Dordogne Valley, France

Numerous small road cuts along the N20 and N140 between Brive la Gaillarde and the Dordogne valley expose one of the most complete sections through the Upper Bathonian of the Dordogne valley. These sections are principally composed of micritic limestones and marly limestones with small partings of clays and marls. Samples from four marl partings were collected.

32. Doue Oncolite, Doue Valley, southwest France

A path along the western slope of the Doue valley exposes an oncolitic, oolitic limestone. Large samples were collected and were found to be largely devoid of shelly fauna with exception of well-preserved *Trigonia* and other bivalves.

33. Blisworth Limestone, Ketton, Castle Cement Quarry, Rutland, England, UK

Castle Cement Quarry, Ketton (SK 980 060) exposes a sequence of Bathonian lagoonal sediments. The sequence is underlain by the Bajocian Lincolnshire Limestone, with a palaeokarst surface at the top. Above the Rutland Formation is the Middle Bathonian Blisworth Limestone, now seen in full section due to an extension of the quarry. This is a buff-coloured, fine-grained, shelly limestone (non oolitic) with marl interbeds. Common faunas from the Blisworth Limestone Formation include bivalves (*Praeexogyra hebridica*, *Modiolus*, *Pleuromya*, *Pholadomya*, and *Protocardia*), corals, brachiopods, gastropods, and serpulids; the echinoids *Clypeus* and *Acrosalenia* are rare, but present. The upper part of the formation becomes more oyster-rich and far more argillaceous.

34. Rutland Formation, Ketton, Castle Cement Quarry, Rutland, England, UK

The greater part of the sequence exposed at Ketton is from the Rutland Formation (a simplified log was published by Dawn 2003). The Rutland Formation consists of mudstones and thin limestones, and represents a largely non-marine sequence. The stratigraphy consists of the Stamford Member and the rhythmic sequence. The Stamford Member (above the karstic Lincolnshire Limestone) consists of non-marine silts tones with rooted horizons virtually devoid of animal fossils.

The rhythmic sequence consists of a series of stacked regressive-transgressive progradational sequences. Generally, the cycles start with laminated shelly clay, with a marine-brackish fauna (Hudson and Dawn 2002) dominated by bivalves, including *Praeexogyra hebridica*, *Modiolus imbricatus*, *Cuspidaria ibbetsoni*, *Myopholas acuticosta*, and *Protocardia lycetti*. Up to six "coastal" cycles (Dawn 2003) are recognised, each starting with a flooding surface, followed by black-grey clays rich in brackish bivalve faunas; the first rhythm contains *Lingula*. The abundant shelly fauna at the base of each cycle is interpreted as living in brackish (brachyhaline) conditions (Hudson and Dawn 2002) comparable to the *Cuspidaria-Modiolus-Praeexogyra* association (Fürsich 1994). The gradual deposition of mud caused progressive shallowing, until plant beds could root forming intertidal flats. These roots are truncated at the top of each cycle, indicating flooding. The fourth rhythm has abundant oysters (*Praeexogyra hebridica*). Subsequent layers become coarser-grained and more massive, and progressively less shelly. It is proposed that this area was a coastal plain (Dawn 2003).