



Evidence for annual records of phytoplankton productivity in the Kimmeridge Clay Formation coccolith stone bands (Upper Jurassic, Dorset, UK)

Jackie A. Lees^{a,*}, Paul R. Bown^a, Jeremy R. Young^b, James B. Riding^c

^aNannofossil Research Unit, Department of Earth Sciences, UCL, Gower Street, London WC1E 6BT, UK

^bPalaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

^cBritish Geological Survey, Kingsley Dunham Centre, Keyworth, Nottingham NG12 5GG, UK

Accepted 23 April 2004

Abstract

The Upper Jurassic Kimmeridge Clay Formation is a C_{org}-rich sequence of mudrocks that was deposited in a dysoxic basin, which served, unusually, to preserve primary coccolithophorid proportions. Strikingly contrasting within this dark-coloured formation are the white coccolith stone bands, which contain pristinely preserved coccolithophorid assemblages, preserving potentially primary coccolithophorid abundances, with minimal diagenetic alteration.

Using methodology described herein, scanning electron microscopy (SEM) observation of µm-scale laminae within selected stone bands has revealed five distinctive types of ‘microlamina’, Type 1 being barren clay, Type 2 comprising coccoliths associated with varying amounts of clay or amorphous organic matter, Type 3 being purely coccolithic, Type 4 being of putative microbial origin, and Type 5 containing frequent calcispheres. These are all described and illustrated here. Illustrated sequences of these are discussed with reference to an hypothetical model sequence, based on modern records, representing a Kimmeridgian year of coccolithophorid productivity. Annual signals are thus interpreted.

Based on the observations presented here, and including summaries of the palynomorph records from the stone bands, we comment on watznaueriacean palaeoecology, and particularly the interpretation of *Watznaueria fossacincta/barnesiae* as an opportunistic, growth-maximising taxon.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Kimmeridge Clay Formation; Upper Jurassic; coccolithophore blooms; annual deposits; watznaueriacean palaeoecology; dinoflagellates

1. Introduction

The Upper Jurassic Kimmeridge Clay Formation (KCF) is exposed along the Dorset coast of southern England, between Brandy Bay (to the west) and St.

Alban’s Head (to the east) (Fig. 1). It has also been cored through its ~ 600 m entirety (the schematic log in Fig. 2 also shows the biostratigraphy, and total organic carbon and δ¹³C_{org} plots), from the *baylei* to *albani* Ammonite Zones (AZ), in the vicinity of the type-section, at Swanworth Quarry and Metherhills (Dorset) by the Natural Environment Research Council (NERC) Rapid Global Geological Events (RGGE)

* Corresponding author. Fax: +44-20-7679-2685.

E-mail address: j.lees@ucl.ac.uk (J.A. Lees).

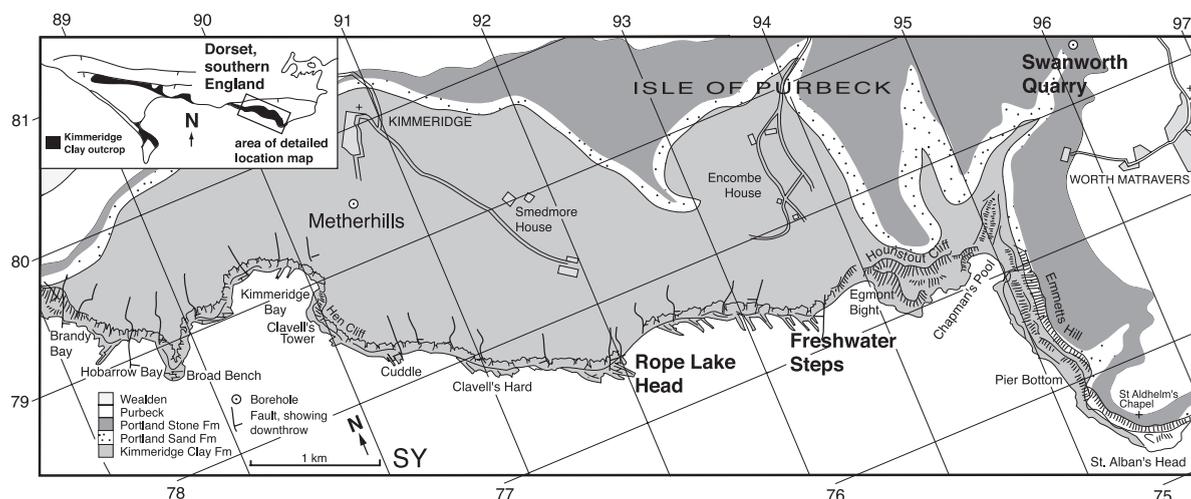


Fig. 1. Map showing the KCF outcrop, the positions of the Swanworth Quarry and Metherhills Boreholes, and the Freshwater Steps WSB and FSSB outcrop location, Dorset, southern England, UK (modified from Morgans-Bell et al., 2001, Fig. 1). National Grid 10 km squares are those used on Ordnance Survey Landranger Maps 194 and 195.

consortium (see <http://www.kimmeridge.earth.ox.ac.uk> for details) for the ‘Anatomy of a source-rock’ project. The formation comprises a 4 my, frequently laminated, marine record of phytoplankton (dinoflagellate cyst and coccolithophore) productivity and clay deposition. Furthermore, it is believed to faithfully record the primary coccolithophorid proportions and, in some parts, abundances (Lees et al., in press).

The Kimmeridgian–Tithonian KCF is the major source-rock for North Sea oil, comprising predominantly dark marls, mudstones and shales with high organic content, subordinate siltstones, and occasional pale limestone and dolostone beds, termed ‘stone bands’ (e.g. Cox and Gallois, 1981; Gallois, 2000; Morgans-Bell et al., 2001). The KCF palaeoenvironment in which these lithologies were deposited has been determined as dysoxic and predominantly eutrophic through both geochemical and palaeontological lines of evidence (e.g. Tyson et al., 1979; Myers and Wignall, 1987; Oschmann, 1988, 1990; Wignall, 1990; Pearson, 2000; Raiswell et al., 2001). Towards the top of the formation, the stone bands are coccolithic in nature; Gallois and Medd (1979) defined them as

containing >30% coccoliths in bulk sediments of >50% CaCO₃. The best-developed of these coccolith stone bands are the Rope Lake Head Stone Band (*hudlestonei* AZ), and the White, Middle White and Freshwater Steps Stone Bands (*pectinatus* AZ), all of which stand out as striking white bands in outcrop (Fig. 3). These all occur within nannofossil subzone NJ17a (first occurrence of *Stephanolithion atmetos* to the last occurrence of *Stephanolithion bigotii bigotii*) of Bown and Cooper (1998; Fig. 2).

Whilst the first quantitative study of the coccolithophores from most of the KCF (*eudoxus* to *albani* AZs) appears in Lees et al. (in press), the coccoliths of the stone bands alone have been the focus of a number of previous studies. These are of particular palaeoecological interest because, as reported by Lees et al. (in press), the nannofloral assemblages are dominated by *Watznaueria fossacincta/barnesiae* (likely end-members of a morphological continuum, which, for the purposes of this study, we did not separate), whilst the surrounding mudrocks are dominated by *Watznaueria britannica* (a morphologically distinct species). Downie (1957) was the first worker to

Fig. 2. KCF graphic log, based on the Swanworth Quarry #1 and Metherhills Boreholes, showing dinoflagellate cyst, nannofossil and ammonite biostratigraphies, lithostratigraphical bed numbers, TOC and $\delta^{13}C_{org}$ (modified from Morgans-Bell et al., 2001, Fig. 1). Dinocyst zones follow the biozonation of Riding and Thomas (1992); note that the zones approximate, rather than equate to, ammonite zone boundaries. Nannofossil biostratigraphy was determined by Lees et al. (in press) and follows the Boreal biozonation of Bown and Cooper (1998). Note that the nannofossil and dinocyst biozones correlate with the ammonite biostratigraphy but not the lithostratigraphical bed numbers.

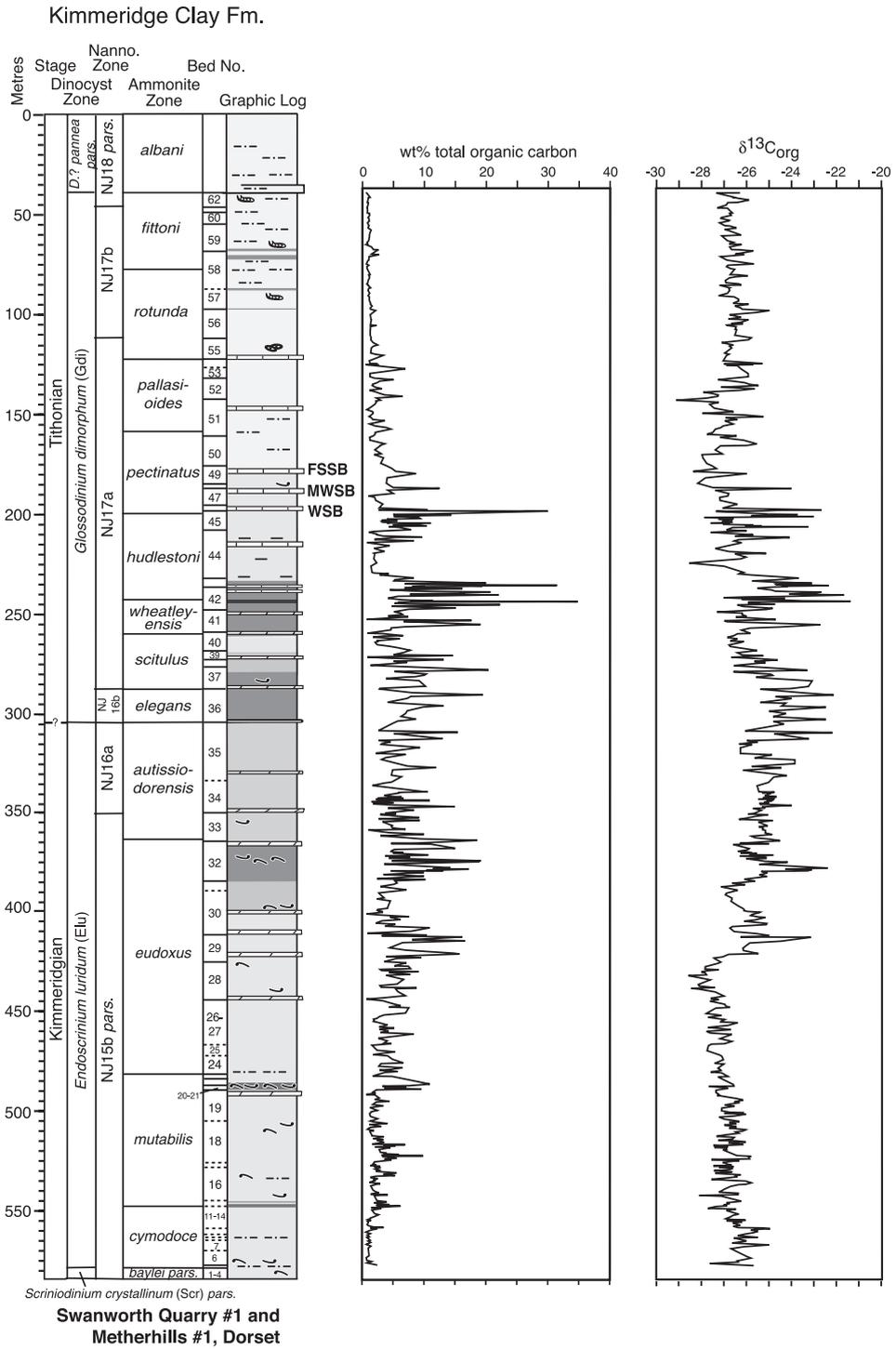




Fig. 3. View of the KCF from Egmont Point, looking west towards Freshwater Steps (foreground) and Rope Lake Head (background; see Fig. 1), showing the coccolith stone bands (white, running from bottom right to top left of background cliff).

identify the above-named stone bands in Kimmeridge Bay, and to note their coccolithic nature. In 1973, Noël reported on the White Stone Band at Chapman's Pool, in which she described the alternating white/grey couplets typical of these deposits, and commented on the excellent preservation of the coccoliths, and the virtually monospecific assemblages visible in freshly broken rock-chips in the scanning electron microscope (SEM). Gallois and Medd (1979) demonstrated the wide correlatability of these (and other) limestone beds, using them as marker-bands from the English east to south coasts. From SEM examination of random rock-chips, they noted the absence of clay and inorganic calcite, the overall low species richness, the almost monospecific laminae (although they misidentified *W. fossacincta* as *W. britannica*: see Gallois and Medd, 1979, pl. 1, Fig. 1c,d), and the presence of both collapsed and whole coccospheres.

The apparent lack of diagenetic modification of the coccolith record in the White Stone Band allowed the first demonstration of fossil ontogenetic sequences in coccoliths (Young and Bown, 1991), the monospecific laminae providing numerous examples of broken watznaueriacean coccospheres containing protococcolith rings and early growth-stage coccoliths.

It was Gallois and Cox (1974) who first suggested that the White Stone Band formed from 'algal blooms', and Gallois (1976) who suggested that the limestone/oil-shale interlamination could have resulted from alternations between coccolithophorid and dinoflagellate 'blooms'. (Pearson (2000), found no evidence, however, to support dinoflagellate blooms, the oil-shales being dominated by amorphous organic matter (AOM).) Young and Bown (1991) supported the idea of the monospecific coccolitho-

phore laminae in the White Stone Band representing bloom deposits, based on the high frequency of early growth-stage coccoliths, analogous to observations made from cultures of *Emiliania huxleyi* in high-nutrient media. Further support for these representing coccolithophore bloom deposits is provided by Pearson (2000), who found pulses of unsorted palynomorphs in the coccolith stone bands, representing water-column instability (storminess); instability, which delivers nutrient-replenishment to surface-waters, followed by stratification, triggers modern blooms of *E. huxleyi* (Houghton, 1992). Whilst the onset of unstable water-column conditions has been hypothesised as the cause of coccolith stone band accumulation, high-amplitude storminess is believed to have terminated their deposition (Pearson, 2000).

So, previous works have reported the obvious coccolithic characteristics of the KCF coccolith stone bands, based on random samples, and suggested a scenario for their formation. However, a systematic SEM investigation of rock-chips from the above-mentioned stone bands has indicated that they are more complex than earlier reports suggest, with five different lamination types described and illustrated for the first time here. This lamina-by-lamina study was undertaken to complement the Back-scattered Electron Imagery (BSEI) and quantitative palynofacies work of Pearson (2000) and Pearson et al. (in press). The lamina-study methodology is described in detail here, and the problems encountered in carrying out such work highlighted. Sequential relationships between the described laminations are also illustrated, and interpreted as seasonal records. The palaeoecology of the Watznaueriaceae is commented upon, in light of our findings.

2. Material and methods

2.1. Nannoplankton and laminae

The nannoplankton data presented here are from chips taken from the Freshwater Steps Stone Band outcrop (Slabs 18—0–4.7 cm below the top of the stone band, 26—16.6–22.8 cm below the top, and 21—38.8–40.9 cm below the top: Plate I(1a)), the White Stone Band outcrop (Slabs 2—22.5–35.8 cm below the top of the stone band, 6—24.2–35.5 cm

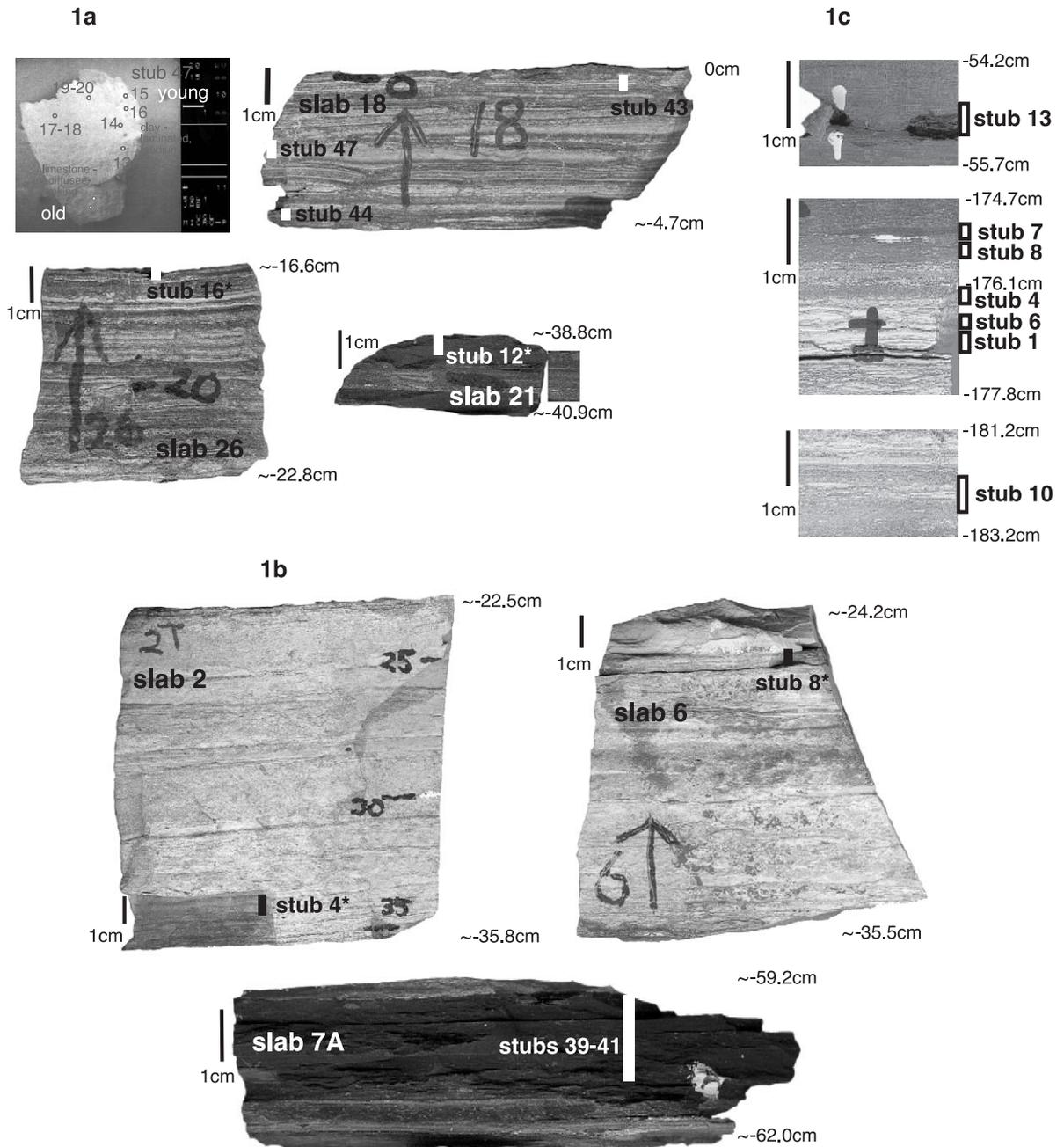


Plate I. KCF coccolith stone band stub locations. (1a) Freshwater Steps Stone band outcrop. (1b) White Stone Band outcrop. (1c) White Stone Band SQ2 core.

below the top, and 7A—the Black Band, 59.2–62.0 cm below the top: [Plate I\(1b\)](#)) and the Swanworth Quarry Borehole #2 (SQ2) White Stone Band core (Slabs

54.2–55.7 cm from the top of Box 84, Section 76a, 174.7–176.1 cm from the top, 176.1–177.8 cm from the top, and 181.2–183.2 cm from the top: [Plate I\(1c\)](#)).

The outcrop material was collected from just west of Freshwater Steps, around beach level. All sample material used in this study and the images herein are stored in the Micropalaeontology Unit at UCL. The SQ2 archive core is stored at the BGS (Keyworth). The stone bands are shown in their stratigraphical contexts in Fig. 2, and in outcrop in Fig. 3.

Pearson (2000) used BSEI to study vertical sections through the SQ1 White and Freshwater Steps Stone Band cores as part of the RGGE project. BSEI displays elemental differences in the sediment as grey-scale contrast (Bishop et al., 1992), with organic matter giving dark images and minerals composed of elements with higher atomic numbers showing brighter images (Goldstein et al., 1992). Thus, the coccolith-rich laminae appear brighter than the organic-rich laminae on back-scattered photographs. Complementarily, in the present study, it was the intention to observe the individual laminae at higher magnification, in an effort to tease out the sequential, potentially seasonal, lamina-by-lamina coccolithophore history of these deposits. The coccolith stone bands proved to be amenable lithologies for this type of study, with individual laminae being readily observable in the SEM (here we used a Zeiss DSM 940). The more common mudrocks, however, proved much less suitable, even when lamination was clearly visible in hand-specimen. Cohesion and hardness of the laminated mudrocks varied greatly. During stub preparation, the less cohesive types tended to crumble, rather than split along laminae surfaces, and the characteristically very narrow surface-areas which were consequently exposed were sprinkled with fine, non-coccolithic particles that could not be adequately removed, and which made them useless for observing in the SEM because these particles tended to become detached during/after sputter-coating of the stub, interfering with observation and causing electrical charging. The harder mudrocks tended to split with a conchoidal fracture, thus providing chips with fairly steep, concave/convex sides. Whilst these provided some information about the general nature and thickness of the laminae, they did not provide useful information on the coccolith sequences.

The best results were gained from observation of the pale/dark laminations within the coccolith stone bands. These sequences are cohesive but not too hard. Al-

though it was still virtually impossible to expose single-lamina surfaces, the sections extracted, which cut through a number of laminae, had reasonably shallow angles, and ledges which were often extensive enough to be observed, classified and tracked for short distances in the SEM.

The samples were prepared in the following way: firstly, all surfaces of the rock-slab under investigation were scanned on a flat-bed scanner at 300 dpi to allow reference back to the laminae observable with the naked eye. The slab was then held securely in a vice attached to a work-bench. Gently using a hammer and a fine-point chisel on one of the edges of the slab, a chip of $\sim 1 \text{ cm}^2$ (with a variable third dimension) was detached. The freshly exposed surface was blown free of fine, unattached debris, and then glued (fresh surface upwards) to a 13-mm aluminium stub using colloidal silver. The stratigraphic direction of the laminae was noted, and the scanned-slab image annotated with the precise location the chip had been removed from (e.g. Plate I(1a)). Initially, an attempt was made to identify and number the visible laminae in the slabs, dividing them into 'clay', 'pelletal' and 'limestone' categories, so that the fine characteristics of these could be investigated in the SEM. However, this was eventually abandoned because the visible laminae could often not be equated to the laminae observed at high magnification in the SEM (see Results). The stub was coated with gold in a sputter-coater.

In the SEM, an image of the entire stub was captured and printed. The print was annotated with the stratigraphical direction (e.g. Plate I(1a)). General notes, concerning the number and types of laminae exposed, how exposed they were, and the preservational state, were taken. If the laminae were usefully exposed, observation was then conducted from one lamina to the next, as far as possible, in a stratigraphical direction. Photomicrographs were taken to illustrate portions of the best-exposed laminae, each photo plotted and numbered precisely on the stub printout (e.g. Plate I(1a)). In this way, the stratigraphical relationships between succeeding laminae were consistently recorded.

This work is inevitably slow, and so far only ~ 50 stubs have been examined. Of these, the best examples are reported on here, illustrating details of the types of laminae encountered, and the relationships between them.

2.2. Palynomorphs

Samples for palynological investigation were weighed and prepared in the standard manner, i.e. mineral acid treatment followed by oxidative maceration (Wood et al., 1996). In the White Stone Band, the presence of abundant AOM necessitated the use of strong oxidising agents in order to obtain a clean, palynomorph-rich residue. Measured aliquots of wet residue were mounted on slides in order to obtain absolute numbers of palynomorphs per gram of sediment.

3. Results

3.1. Microlamination and wavy lamination

Two immediate observations were made, concerning the coccolith stone band laminae. Firstly, the (sub-)mm-scale laminae observable with the naked eye and/or reflecting light-microscope are often composed of several μm -scale laminae, when viewed in the SEM. This meant that it was often not possible to equate the larger-scale laminae with those observable with the SEM. Furthermore, that problem has introduced some confusion to the discussion of the laminae. For the sake of clarity, the laminae observed in this study are referred to as ‘microlaminae’. These are often not the same as the larger-scale laminae referred to in other RGGE works (e.g. Pearson, 2000; Pearson et al., in press).

Secondly, problems associated with ‘wavy lamination’, first reported by O’Brien (1996, Fig. 13) from parts of the White Stone Band, were encountered. O’Brien (1996) attributed this fabric to microbial mat formation preceding coccolithophorid blooms. In addition to this, Pearson’s (2000) BSEI analyses revealed occasional disruption to laminae by trace-fossils in the White Stone Band and, in the Freshwater Steps Stone Band, microfabric-scale disruption and abrupt termination. It seems possible that the microlaminar undulation observed in this study was microbially induced because all illustrations of preserved Type 4 deposits (see below) show undulating surfaces, and the disturbances revealed by Pearson (2000) are on a larger scale. Whatever its origin, this disrupting fabric had previously been noted by Thomsen (1989) in his SEM

examination of the Lower Cretaceous Munk Marl Formation (North Sea). This means the microlaminae do not lie flat, most of them undulate and appear to be discontinuous. In practice, this meant that a single microlamina could rarely be traced far laterally with confidence. Thus, most of our relational observations are based on small areas that show an obvious relationship to/distinction from adjacent microlaminae. As a result of this, as Thomsen (1989) also pointed out, counting the microlaminae, and measuring their thicknesses, using this observation technique, is somewhat subjective and prone to a relatively large margin of error.

3.2. The coccolithophores

It is immediately noticeable in the SEM that the coccolith-bearing microlaminae are usually monospecific. Lees et al. (in press) reported on the general dominance of *Watznaueria britannica* throughout the KCF, and the increased abundances of *Watznaueria fossacincta/barnesiae* in the *huddlestonei* and *pectinatus* AZs. On/within individual microlaminae in the coccolith stone bands, the dominant taxon is *W. fossacincta/barnesiae*, with rare microlaminae of *W. britannica* or *Cyclagelosphaera margerelii*. Non-watznaueriacean taxa are present, albeit rarely, with coccoliths or collapsed coccospheres of *Zeughrabdodus*, *Staurolithites*, *Polypodorhabdus*, *Truncatosca-phus* and *Stradnerlithus* being the most commonly observed.

Preservation on individual laminae varied from moderate (e.g. Plate III(2)) to pristine (e.g. Plate III(1)), often with no apparent compaction or diagenetic infilling, spaces between and within coccospheres being abundantly evident. Imprinted microlaminae were also frequently observed, and it is assumed that the coccoliths were mechanically stripped off during stub preparation.

3.3. The palynomorphs

The pollen component of the SQ2 White Stone Band core is of relatively low diversity, with a high abundance of *Classopollis*, which suggests a warm, dry palaeoclimate (Cornet and Traverse, 1975; Filatoff, 1975; Traverse, 1988; Van Konijnenburg-van Cittert and van der Burgh, 1996). The highest numb-

ers of palynomorphs/g were recorded at the base and towards the top of the sequence.

Dinoflagellate cysts were recorded throughout the White Stone Band core in varying proportions (although they were very rarely observed in the SEM). Undifferentiated chorate cysts, *Chytroeisphaeridia chytroides*, the *Cribroperidinium globatum* group, *Kallosphaeridium* spp., *Senoniasphaera jurassica* and *Systematophora* spp. were common throughout. These associations are typical of the Upper Kimmeridgian Gd(c) and Gdi(c) dinoflagellate cyst subzones of Riding and Thomas (1988, 1992). The relatively high diversity of the dinoflagellate cyst associations indicates normal marine salinities. No evidence for salinity–stress was observed.

3.4. Microlamina types

Five types (two of which are divided into four subtypes each) of microlamina have been distinguished, characterised as follows.

Type 1—Non-coccolith-bearing clay microlaminae (Plate II(1,2)) have a characteristically flaky appearance. This type was found, perhaps predictably, most commonly in the visibly darker layers of the stone bands.

Type 2—Coccolith/imprint-bearing matrix (clay or AOM) microlaminae. This type has been subdivided based on the apparent abundance of imprints/coccoliths preserved, and all subtypes are associated with the dark/pale laminations visible in hand-specimen: Subtype 2a—clay matrix with sparse, usually monospecific, watznaueriacean imprints/coccoliths (Plate II(3,4)); Subtype 2b—jumbled, frequent/common, usually monospecific, watznaueriacean coccoliths (rarely coccospheres) encased in a clay matrix (Plate II(5–8)); Subtype 2c—common, usually monospecific, watznaueriacean imprints/coccoliths (rarely/frequently coccospheres) resting on clay but not encased by it (Plate II(9,10)); and Subtype 2d—frequent/common, usually monospecific, watznaueriacean imprints in an AOM matrix (Plate II(11)). This matrix has a characteristically smooth appearance, dissimilar to that of the flaky clay. Untyped (because this is not likely to be a primary depositional feature), but interesting to note, coccolith imprints have also been observed on fine-grained pyrite, particularly associated with the Black Band of the White Stone

Band (Plate II(12): in this illustration, the pyrite is a flake, presumably detached from part of a larger fossil). Similar coccolith impressions in the walls of dinoflagellate cysts, and in AOM after palynological preparation, have previously been commented on by Downie (1957) and Batten (1985), and in radiolarian tests by De Wever et al. (1986).

Type 3—Purely coccolithic microlaminae. This type has been subdivided based on qualitative relative proportions of watznaueriacean to other taxa, irrespective of preservational state. Subtype 3a—monospecific watznaueriacean coccospheres/coccoliths (Plate III(1,2)), mainly associated with limestone-dominated pale/dark laminae bundles visible in hand-specimen; Subtype 3b—monospecific watznaueriacean coccospheres/coccoliths with rare coccoliths/coccospheres of non-watznaueriacean taxa (Plate III(3–5)) mostly associated with clay-dominated dark/pale laminae bundles visible in hand-specimen; Subtype 3c—monospecific watznaueriacean coccospheres/coccoliths with frequent/common coccoliths/coccospheres of non-watznaueriacean taxa (Plate III(6–10)), as with Subtype 3a, mainly associated with limestone-dominated visible bundles. This subtype is also frequently, but not obviously always, associated with faecal pellets; Subtype 3d—*Truncatoscapus* and *Stradnerlithus* coccoliths (Plate III(11)). Only one such microlamina has been observed so far, associated with limestone-dominated pale/dark bundles.

Type 4—Spicular mat microlaminae of putative microbial origin (Plate III(12); Plate IV(1,2)). We originally thought that this type may have been composed of the degraded remains of *Truncatoscapus*/*Stradnerlithus* (cf. Subtype 3d), since the spicular appearance is reminiscent of the long lateral rims of these taxa. However, it is likely that the rims of *Truncatoscapus*/*Stradnerlithus* would have broken into their constituent granular elements, rather than remaining as spicules, on disintegration of the rest of the coccolith. Also, it has been noted that both *Stradnerlithus* and *Truncatoscapus* generally appear reasonably robust in SEM photomicrographs (e.g. Bown and Cooper, 1998, p. 60, pl. 4.4, Figs. 3 and 8), and the general state of preservation of the stone bands is relatively good, and, as observed below, where the spicular mats are under- and overlain by *Watznaueria* bloom deposits (Types 3a–c), these are pristinely preserved, and so the Type 4 mats are most

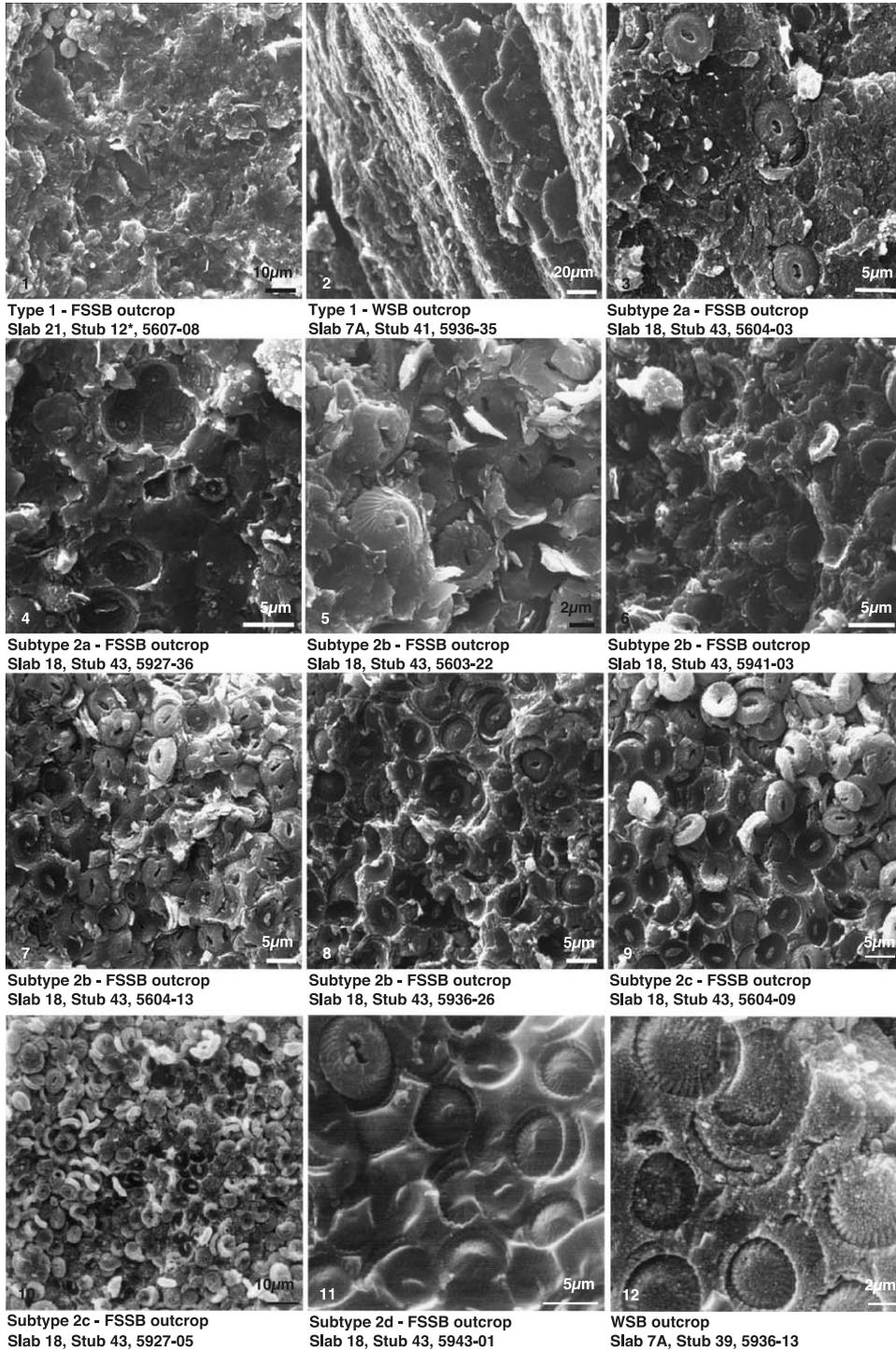


Plate II. Microlamina Types 1 and 2 (1–11), and imprinted pyrite ‘lamina’ (12), KCF.

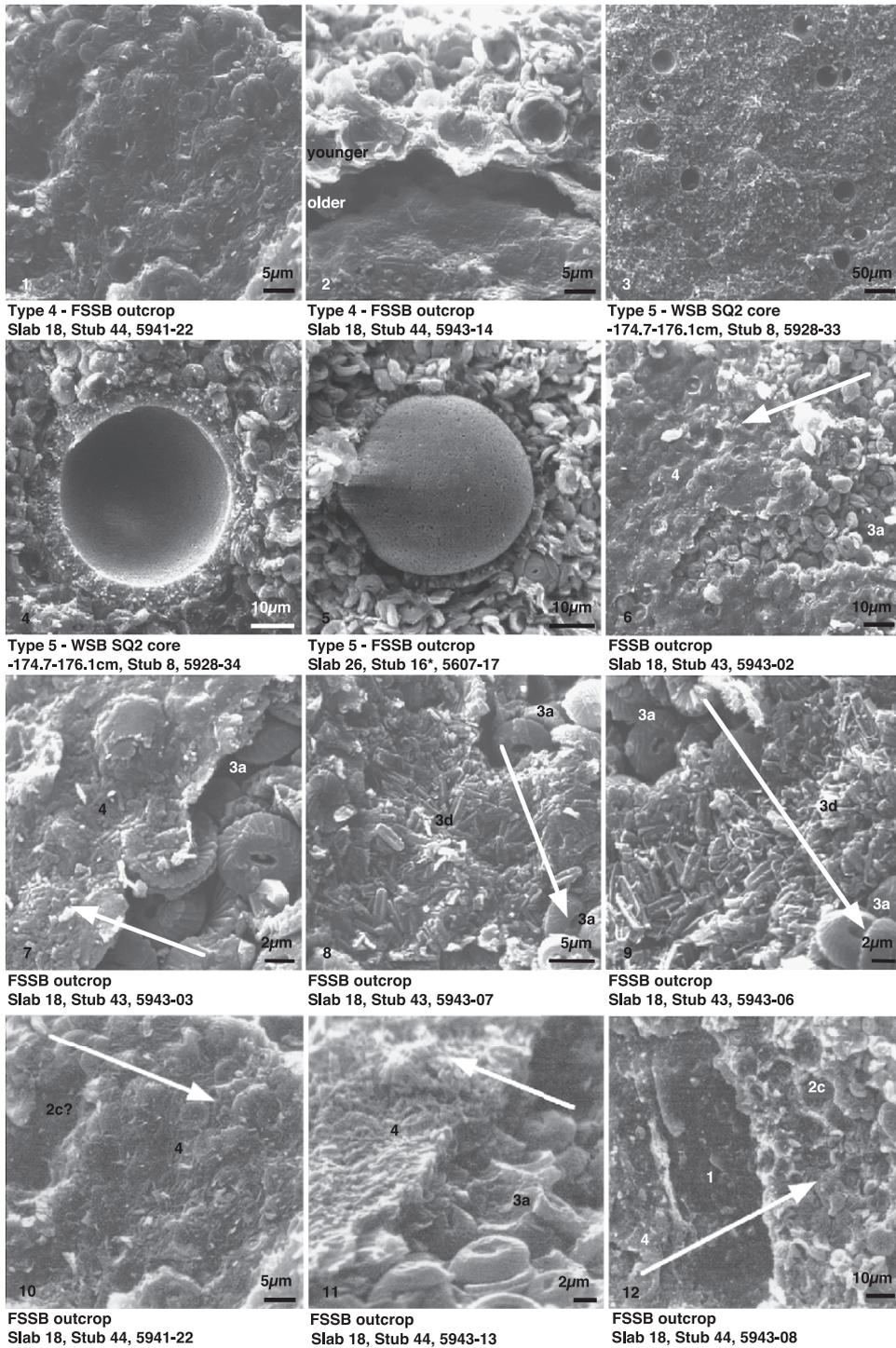


Plate IV. Microlamina Types 4 and 5 (1–5), KCF. Time-series relationships between microlamina types (6–12). Arrows indicate direction of younging.

likely to represent well-preserved deposits. Furthermore, even at high resolution (Plate IV(7,11)), no discernible coccolithic features are apparent.

O'Brien (1996) found wavy lamination in the White Stone Band, suggestive of bacterial mat formation, and peaks in the isorenieratene-derived biomarkers (chlorobiacean bacteria-specific) have been found associated with TOC peaks in the White Stone Band (Van Kaam-Peters et al., 1998; Sælen et al., 2000; Van Dongen et al., 2003). Röhl et al. (2001, p. 32) have reported “an irregular filamentous network” surrounding coccolith-rich faecal pellets in thin-sections of the well-preserved Lower Toarcian Posidonia Shale; etching of dark laminae in bituminous limestone laminites of Orbagnoux (Upper Kimmeridgian, Southern Jura, France) has revealed filamentous bacterial structures (Tribovillard, 1998, p. 127, pl. 1, Fig. e); whilst Von Knorre and Krumbein (2000) suggested that bacteria can act as nucleation sites for precipitation of calcite with varying crystallographic habit. These rare mats are associated with limestone-dominated pale/dark bundles visible in hand specimen.

Type 5—Frequent-calcisphere-bearing matrix microlaminae (Plate IV(3–5)). This type is mainly associated with clay-dominated dark/pale bundles observable in hand-specimen.

3.5. Microlamina associations

Due to wavy bedding, and the small area and limited number of microlaminae represented by each SEM stub sample, it is not a simple matter to follow one microlamina to the next. However, wherever possible, clear, direct relationships between succeeding microlaminae were recorded. The most unambiguous relationships between microlamina types are reported below. On Plates IV and V, arrows indicate the direction of younging.

3.6. Freshwater Steps Stone Band (FSSB) outcrop, slab 18

Stub 43—A sequence of Sub/types 3a–4 was seen in this limestone-dominated pale/dark bundle (Plate IV(6,7), the latter being a close-up of the same microlamina), in which a very thin spicular mat (Type 4) blankets the underlying accumulation of *Watznaueria fossacincta/barnesiae* coccoliths and coccospheres,

and preserves a sparse record of coccolith imprints on its surface, reminiscent of the Type 2a microlamina. A short way above this, a purely coccolithic (Subtypes 3a–3d–3a) succession (Plate IV(8,9), showing the same microlaminae in different locations) was found. The Subtype 3d microlamina, comprising *W. fossacincta/barnesiae* coccoliths and coccospheres, appears to be thicker than that of the spicular mat (Type 4). Note that the preservational state of the associated *W. fossacincta/barnesiae* coccoliths beneath both the Sub/types 4 and 3d microlaminae is very good.

Stub 44—A very thin spicular mat (Type 4) overlies a questionable clay/coccolith (Subtype 2c) microlamina (Plate IV(10)). Due to the blanketing effect of the mat, it was not possible to determine the exact nature of the underlying deposit: it is obviously *Watznaueria fossacincta/barnesiae* coccolith/coccosphere-rich but there also appears to be some clay associated with it. This succession is from a clay-dominated dark/pale bundle. Some way above this, a purely coccolithic microlamina (Subtype 3a) underlies a thin, spicular mat (Type 4) microlamina (Plate IV(11))—note that preservation of the underlying *W. fossacincta/barnesiae* coccoliths is again very good. Slightly above that, a spicular mat (Type 4) lies beneath barren clay (Type 1), which itself is overlain by a clay/coccolith (Subtype 2c) microlamina (Plate IV(12)). A short way above this, a spicular mat (Type 4) underlies a purely coccolithic (Subtype 3a) microlamina (Plate IV(2)).

3.7. White Stone Band (WSB) outcrop, Slab 7a (Black Band)

Stub 39—This clay-dominated, blebby/pelletal succession contains a clay/coccolith (Subtypes 2b–2a–2c) sequence (Plate V(1)), showing decreasing, then significantly increasing, amounts of *Watznaueria fossacincta/barnesiae* coccoliths. Subtype 2a (sparse imprints/coccoliths) appears to be relatively thin compared to Subtype 2b (frequent imprints/coccoliths).

Stub 40—An alternating sequence of barren and coccolith-poor clay (Sub/types 1–2b–1–1–2b) was observed in this dark, blebby/pelletal succession (Plate V(2)), illustrating increasing, decreasing, then increasing amounts of *Watznaueria fossacincta/barnesiae* coccoliths. The clays appear to be thicker than the coccolithic microlaminae. Some way above this,

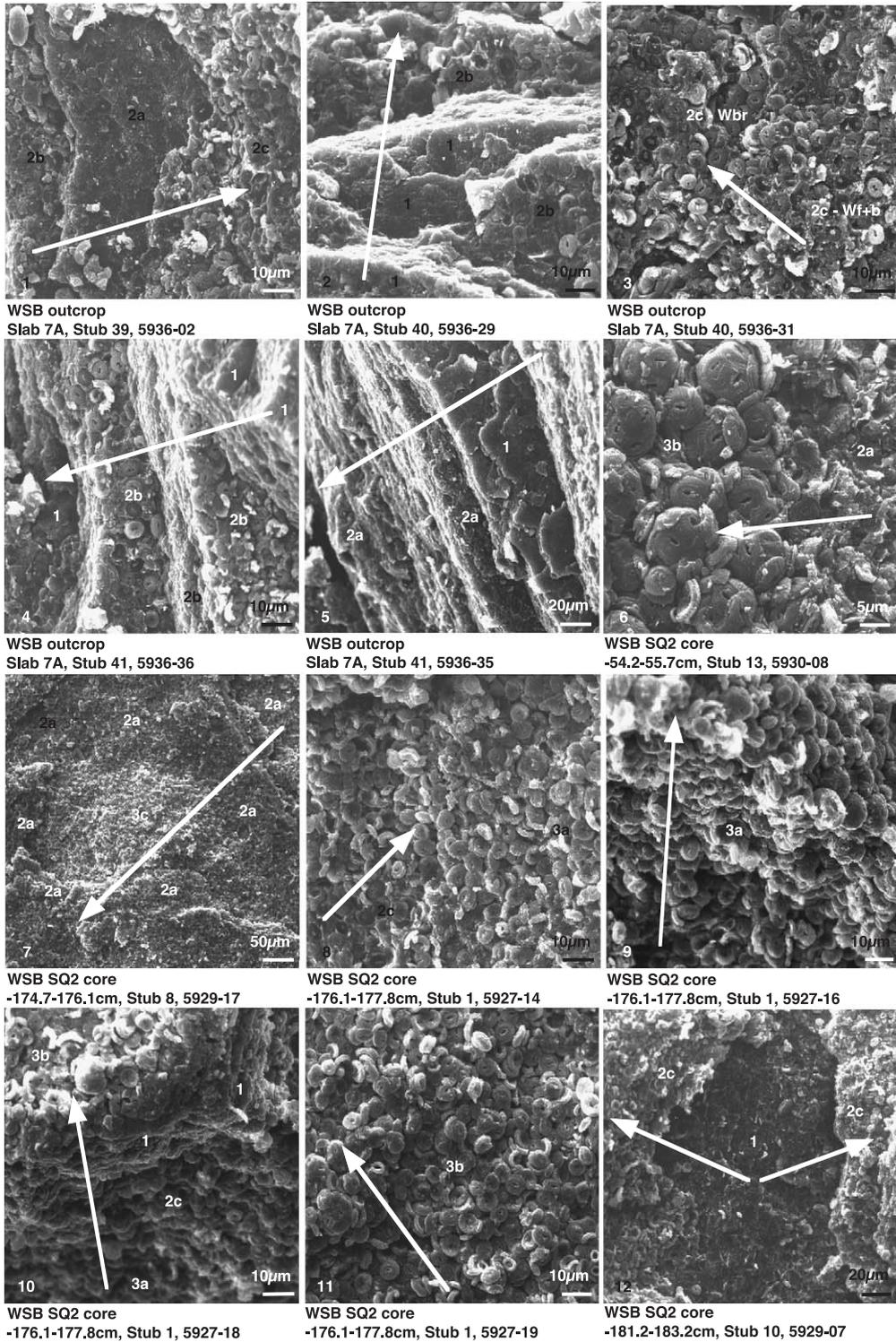


Plate V. Time-series relationships between microlamina types. Arrows indicate direction of younging.

rare, clay-rich *Watznaueria britannica* (Subtype 2c) microlaminae were observed to overlie similar (Subtype 2c) *W. fossacincta/barnesiae* microlaminae (e.g. Plate V(3)).

Stub 41—In this clay-dominated, blebby/pelletal sequence, an alternating barren and coccolith-poor clay (Sub/types 1–1–2b–2b–2b–1) succession was recorded (Plate V(4)), where clay is dominant but with occasional, relatively insignificant *Watznaueria fossacincta/barnesiae* coccolith deposition, and in which the clay and coccolith microlaminae appear to be of relatively equal thickness. A little way above this, another barren and coccolith-poor (Sub/types 1–2a–2a) sequence occurs (Plate V(5)), showing that clay deposition barely gave way to *W. fossacincta/barnesiae* coccolith accumulation. The clay in this example appears to be thinner than the coccolith-bearing microlaminae. A number of *Watznaueria britannica* Subtype 2c microlaminae were also observed, mid-way through the stub succession.

3.8. WSB SQ2 core, –54.2–55.7 cm

Stub 13—Plate V(6) illustrates a sequence of coccolith-poor clay (Subtype 2a) to purely coccolithic (Subtype 3b: *Watznaueria fossacincta/barnesiae* and *Cyclagelosphaera margerelii*) across the edge of a faecal pellet in this dark shale. Coccospheres are abundant in the pellet.

3.9. WSB SQ2 core, –174.7–176.1 cm

Stub 8—This dark, blebby/pelletal succession recorded examples of faecal pellet sequences, particularly coccolith-poor clay to purely coccolithic (Subtypes 2a–3c: e.g. Plate V(7)). Also, a calcisphere-rich (Type 5) microlamina (Plate IV(3,4)) was observed. It has proved difficult to determine which types of microlamina calcispheres are associated with: Plate IV(3,4) shows calcispheres mechanically shorn off at their midpoints, the visible lower parts surrounded by coccolith-rich clay (Subtype 2c) microlaminae. Plate IV(5) shows a more complete calcisphere surrounded by a purely coccolithic (Subtype 3a) deposit. However, because the calcispheres are large relative to the microlaminae, it is possible they sank through microlaminae on deposition, so the coeval microlamina might be impossible to determine. If sinking was not

the case, then shallow depressions made by calcisphere bases in a particular microlamina type might indicate the coeval microlamina type, but these have so far not been observed.

3.10. WSB SQ2 core, –176.1–177.8 cm

Stub 1—A composite succession of coccolith-rich clay to pure coccoliths to coccolith-rich clay to barren clay to pure coccoliths (Sub/types 2c–3a–2c–1–3b) was recorded from this limestone-dominated pale/dark bundle (Plate V(8–11)), the *Watznaueria fossacincta/barnesiae*-dominated Subtype 3a microlamina being tens of μm thick, and both Subtypes 3a and 3b bearing abundant coccospheres.

3.11. WSB SQ2 core, –181.2–183.2 cm

Stub 10—An example of barren clay (Type 1) underlying coccolith-rich clay (Subtype 2c) was found in this limestone-dominated pale/dark bundle (Plate V(12)), indicating a marked increase in coccolith accumulation.

4. Discussion

4.1. Remarks on coccolithophore preservation

Lees et al. (in press) have argued that the KCF preserves primary relative abundances of coccolithophorids, with unusually low species richness and diversity being generally unaffected by preservation, but rather governed by palaeoecological factors. The best preservation is found in the coccolith stone bands, qualitatively estimated here as moderate to pristine (compare Plate III(5) with Plate III(8,9), respectively), and it is in these that monospecific microlaminae can be commonly observed. Since the dominant taxa are all medium-sized Watznaueriaceae, they have essentially the same ultrastructure and so must have similar preservation potential, a point also made by Pittet and Mattioli (2002) in a study that used quantitative data of the six most abundant taxa in Upper Oxfordian sediments to determine palaeoenvironmental changes associated with deep-shelf environments. Consequently, individual microlaminae in the stone bands must record primary proportions, and the different types of

microlaminae described above cannot be a product of differential preservation.

Although Pearson (2000) recorded examples of disruptions and abrupt terminations in the coccolith stone bands, her BSEI analyses also revealed numerous repeated sequences of microfabric types. This evidence, in tandem with the coccolith preservation, the presence of stabilising putative microbial mats, and the ability to trace mm-scale laminae for many metres in outcrop, has led us to believe that the coccolith stone bands constitute a near-complete record of coccolithophorid productivity, such that the majority of adjacent microlaminae preserve actual time-series relationships, mostly unaffected by post-depositional disturbance or diagenesis.

Despite their good preservational state, the length of time represented by the coccolith stone bands is still a matter of debate, since it is clear, from this study and that of Pearson (2000), that one coccolith-rich/organic-rich lamina couplet (as visible with the naked eye) does not necessarily represent one year's accumulation. Added to this is the variable sedimentation rate, as demonstrated by the fluctuations in thickness of the coccolith component, postulated as relating to water-column instability (Pearson, 2000).

4.2. Climatic indications

The palynomorph data herein suggests that the onshore climate was generally warm and dry during coccolith stone band accumulation. However, several lines of evidence suggest climatic instability during these intervals. Francis (1984) suggested annual seasonality for the semi-arid Late Jurassic, indicated by tree-ring growth parameters. Chambers (2000) recorded an increase in kaolinite through the White Stone Band (he did not analyse the Freshwater Steps Stone Band), possibly indicative of increased humidity. Pearson (2000) attributed intervals of high abundances of unsorted palynomorphs to storminess. These suggest that the coccolithophore blooms were triggered by a combination of increased runoff and water-column turbulence, the former possibly refreshing nutrient levels (including micronutrients) and decreasing salinity in the surface-waters, and the latter disrupting water-column stratification, elevating oxygen levels, and recycling nutrients from deeper levels. These would have been punctuated by arid intervals,

which returned the water-column to a stratified, oxygen-poor state.

4.3. Predicted annual depositional sequence for the stone bands, incorporating all common microlamina types

The Black Sea provides a modern example of an ecologically restricted (seasonally eutrophic, anoxic, low salinity) environment, at an intermediate latitude, in which *Emiliania huxleyi* has dominated coccolithophorid assemblages through the Holocene (e.g. Aksu et al., 2002), and so which in some respects is analogous to the KCF palaeoenvironment, although dinoflagellate cyst evidence suggests normal marine salinities for the KCF basin, as described above. Measurements of phytoplankton productivity in the modern Black Sea (pre-anthropomorphic eutrophication) have shown the following sequence of events: an intense winter–early spring diatom bloom; occasional summer coccolithophorid and dinoflagellate blooms; and autumn coccolithophorid blooms (Sorokin, 1983; Bologna, 1986; Benli, 1987; all referred to in Eker-Develi and Kideys, 2003). Generally, in modern temperate environments, summer water-column stratification engenders low coccolithophorid productivity and high diversity, followed by late summer blooms as stratification is broken down and nutrients are replenished (e.g. Houghton, 1992). It should be noted that diatoms, which in modern environments generally outcompete coccolithophores in high-nutrient environments where silica is available (Egge and Aksnes, 1992), have not been recorded from Jurassic sediments (Philippe et al., 1994), and so the KCF coccolithophores may have had no competition for the first available nutrients in the KCF basin. Using these modern observations, and the likely climatic conditions described above, as a guide, we could perhaps predict that a typical annual record in the stone bands during unstable climatic conditions would comprise: barren clay (Type 1, winter, coccolithophore productivity nil, due to non-conductive light, water clarity, temperature and/or too much water-column instability); monospecific coccolithophorid bloom (Type 3a, spring, exploiting replenished nutrients and increased oxygen from storm-induced water-column instability); increased diversity and moderate productivity (Types

3b–d, summer, exploiting declining nutrient concentrations, increasing water-column stratification as seasonal aridity is re-established); monospecific coccolithophorid bloom (Type 3a, autumn, as humidity increases, water-column destabilises, nutrients replenished); decreasing productivity, relatively increasing clay (Types 2c–a, late autumn–winter, water-column too unstable), and back into barren clay (Type 1, winter). In summary, the sequence would be 1–3a–3b/3c/3d–3a–2c/2b/2a–1.

During only moderately unstable intervals, blooms may not have developed, and then perhaps early coccolithophore productivity increased gradually, in response to moderate nutrient, and possibly oxygen, replenishment and increased light levels perhaps, with a concomitant relative decrease in clay. Therefore, a sequence of Types 1–2a–2b–2c–(3b/c/d)–2c–2b–2a–1 might be predicted. Incomplete sequences have been observed from the varved Holocene sediments of the Black Sea: the typical annual sequence comprises a pale lamina formed by summer–autumn *Emiliania huxleyi* blooms, with subordinate dinoflagellates, and a dark lamina formed by late winter–spring diatom and silicoflagellate blooms, interspersed with terrestrially derived sediment (e.g. Hay et al., 1990, 1991; Arthur et al., 1994). Incomplete varves lack the *E. huxleyi* bloom laminae (Hay et al., 1990).

The Type 1 (barren clay) microlaminae that occur between coccolith-bearing microlaminae are most likely to be analogous to those found in modern deposits, representing seasonal (i.e. winter) non-coccolithophorid productivity, since we know that coccolithophores were continually present in the KCF basin during stone band accumulation (and also during mudrock accumulation; Lees et al., in press), and since preservation of the coccoliths is generally good. So, the clay microlaminae must represent primary palaeoenvironmental signals, indicative of a period during which conditions (light levels, water turbulence, trophic level) were not conducive to coccolithophore productivity. Since the balance between clay-rich and clay-poor laminae is predominantly driven by the seasonal coccolith dilution effect, it is potentially possible that the barren clay microlaminae could be used to delimit annual depositional records in the KCF stone bands. This is not pursued further here.

4.4. The evidence for an annual record

Of the illustrations shown in Plates IV and V, a number fit into the theoretical succession of microlamina types outlined above. Plate IV(8,9) shows Types 3a–3d–3a (*Watznaueria fossacincta/barnesiae* bloom–*Truncatoscaphus/Stradnerlithus*? bloom–*W. fossacincta/barnesiae* bloom), which might be interpreted as a spring–summer–autumn sequence. In the very rare example of a *Truncatoscaphus/Stradnerlithus* microlamina (Type 3d), they are sandwiched between purely monospecific *Watznaueria* (Type 3a) deposits, i.e. such microlaminae occur within watznaueriacean bloom intervals, and in potentially bloom abundances, and are thus interpreted as summer deposits. It should be noted that *Truncatoscaphus* and *Stradnerlithus* have often been seen in bloom abundances on well-preserved laminae in other strata (e.g. Goy, 1981; Lambert, 1987), indicating that they were probably opportunistic and bloom-forming, although they tend to be overlooked in light-microscope studies since they are small and inconspicuous in the cross-polarised light which is predominantly used in routine data-gathering. Examples of Types 3a–4 (*Watznaueria fossacincta/barnesiae* bloom–spicular mat), as shown in Plate IV(11), and of Types 4–3a, illustrated in Plate IV(2), imply that Type 4 occurs after or before either a spring or autumn bloom. There is evidence indicating that Type 4 may be an autumn deposit: Plate IV(6,7) shows Type 2a-like imprints on the spicular mat, suggesting a post-bloom coccolithophore productivity decrease; and Plate IV(12) shows Types 4–1–2c, also suggestive of low to nil productivity following spicular mat deposition. Also, the questionable observation of a Type 2c–4 sequence (Plate IV(10)) links spicular mats to decreasing coccolith/increasing clay input. These may further support the suggestion that these are microbial mats, forming particularly thick (more preservable?) colonies at the end of the annual coccolithophore productivity cycle.

Gradual increases in productivity from nil are suggested by Type 1–2a–2a (Plate V(5): early–late winter), Type 1–2c (Plate V(12): winter–early spring), and a rapid transition from winter clay to a spring/summer bloom by Type 2a–3b (Plate V(6)) sequences. The Type 2c–3a–2c–1–3b sequence (early spring clay + coccoliths–monospecific spring bloom–?autumn/spring clay + coccoliths–winter/summer nil pro-

ductivity–summer bloom) shown in Plate V(8–11) may indicate an incomplete late winter–spring–autumn–winter–summer cycle. Possibly incomplete annual records (i.e. non-bloom or too unstable years) are also exemplified in Plate V(2) (Types 1–2b–1–1–2b) and Plate V(4) (Types 1–1–2b–2b–2b–1).

Essentially, there is coccolithophorid evidence for seasonal change in the coccolith stone bands. It is apparent, however, that this record does not include year-on-year *Watznaueria* blooms, and is probably complicated by variations in weather conditions, particularly by more-or-less ‘stormy’ years, affecting the distribution of available nutrients and oxygen in the surface-waters. This is in agreement with the findings of Pearson (2000).

4.5. Comparison of putative stone band seasonal records with fossil and modern records

Preservation of likely annual cycles of coccolithophore productivity in the sedimentary record is rare. The KCF coccolith stone bands exhibit the tell-tale signs of intact and collapsed coccospheres, preserved small and delicate forms, and laminae dominated by just one or a few species, in common with other fossil examples (e.g. Goy, 1981; Lambert, 1987; Thomsen, 1989; Bown, 1993; Krhovsky, 1995; Da Gama, 2000; Ravilius, 2002). The coccolith stone bands, however, differ markedly from these previous studies in that they record an almost monospecific signal. This must be due to the palaeoecological restrictions in force in the KCF basin, which allowed only the most opportunistic species to survive under such eutrophic, dysoxic, or otherwise limiting, conditions, even though higher-diversity assemblages are known elsewhere and other species do occasionally occur. In this way, the KCF coccolith stone bands have more in common with modern Black Sea deposits than any other modern analogue. There, the seasonal nannofloras are dominated by *Emiliania huxleyi*, the most opportunistic, ecologically r-selected extant taxon, due to the palaeoecologically restrictive low salinities (17–18‰). These are finely interlaminated with fine-grained organic-rich terrigenous material (Bukry, 1974), taken to represent an apparently simple annual varve couplet (e.g. Hay et al., 1990).

Thomsen (1989), however, provided a detailed illustration of the complexity of such deposits, his

example being the dark, finely laminated Munk Marl Bed (Tuxen Formation, Barremian, Lower Cretaceous, Central Graben, North Sea). He showed the Munk Marl to be composed of alternating laminae which comprised either nannofossils or clay, the former being 15–70 µm thick, the latter, 3–15 µm thick. Some of his laminae were monospecific (nine taxa displaying this type of distribution), and his uppermost layer was found to contain a succession of different nannofloras in bloom proportions. His inferred tripartite annual productivity cycles typically began with a *Watznaueria barnesiae*-dominated, and ended with a *Micrantholithus obtusus*-dominated, lamina, the middle part being represented by one dominant, and a number of less abundant other, coccolith species, the whole interpreted as representing seasonal variation in the nanoplankton population (spring–summer–autumn). These annual successions were repeated, separated by barren, or virtually so, clay laminae, until the pattern was interrupted and different species took over. Whilst these patterns are consistent with modern examples from normal marine environments, where seasonally dominant forms vary from year to year at temperate latitudes (Okada and McIntyre, 1979; Reid, 1980; Ziveri et al., 1993), they are mostly dissimilar to those seen in the KCF coccolith stone bands, wherein *Watznaueria fossacincta/barnesiae* accounts for virtually all coccolithophorid productivity. However, the occurrence of rare to frequent non-watznaueriacean taxa in certain microlaminae (Types 3b and 3c), and sometimes in bloom proportions (Type 3d) may indicate a seasonal (summer) change in nutrient levels, but generally not enough to allow non-watznaueriacean taxa to flourish. In the Pouzdrany Marl (Lower Oligocene, West Carpathian Flysch Belt, Czech Republic), Krhovsky (1995) determined a pattern of scattered coccoliths and diatom fragments among terrigenous grains, representing a winter deposit (dark lamina), followed by pale laminae recording a diatom bloom at the base, overlain by a small reticulofenestrid bloom (early spring high productivity), and topped off with a highly diverse nannoflora, including holococcoliths (summer). Again, this is generally dissimilar to the coccolith stone band record. However, the annual patterns from this example and that of the Munk Marl indicate that spring was characterised by coccolithophorid blooms (the ability to bloom

being an indication of ecological r-selection for growth maximisation; Kilham and Kilham, 1980) which likely were triggered by eutrophication events, other taxa only finding conditions amenable as nutrient levels fell. This may also have been the case during coccolith stone band accumulation.

So, although the KCF coccolith stone bands share certain features in common with modern and ancient annual records of coccolithophore productivity, there is really no modern or fossil analogue. The coccolith stone bands are unique in being virtually monospecific, the nannofloras having apparently no competition from diatoms (although the productivity dynamics between coccolithophores and dinoflagellate cysts is unclear), and being deposited in a normal-marine-salinity environment but living in an apparently eutrophic, oxygen-poor water-column.

4.6. Implications for watznaueriacean palaeoecology

The KCF basin hosted unusually low-diversity (usually monospecific) coccolithophorid assemblages, compared to coeval nannofloras from similar palaeolatitudes, and this is most likely related to the trophic state and oxygen-depleted nature of the water-column (Lees et al., in press). The broader KCF assemblages are dominated by *Watznaueria* or *Cyclagelosphaera*, demonstrating that they were capable of exploiting palaeoenvironments that were hostile to other taxa. These genera were globally distributed throughout their stratigraphical ranges (Jurassic–earliest Paleocene), *Watznaueria* especially being ubiquitous and abundant in Mesozoic nannofloras, further illustrating their wide palaeoecological tolerance. In this, they show analogy to the extant coccolithophore *Emiliania huxleyi*, with which they also share similar basic placolith morphology. Young (1994) has indeed argued that placolith-bearing coccolithophores are predominantly r-selected and characteristic of higher trophic conditions at the present day. Furthermore, these taxa are stratigraphically long-ranging and morphologically conservative, characteristics of generalist rather than specialist taxa. In the stone bands, there is clear evidence that *Watznaueria fossacincta/barnesiae* at least formed seasonal blooms (Subtypes 3a–c), up to tens of μm thick. Consequently, this taxon at least is likely to be r-selected, whilst the demonstrably broad ecological tolerances of *Cyclagelosphaera* and *Watz-*

naueria britannica, and the fact that they share similar placolith morphology with *W. fossacincta/barnesiae* and *E. huxleyi*, suggests that the whole watznaueriacean plexus probably was r-selected. As suggested above, however, blooms would have been dependent on water-column conditions.

Watznaueriacean palaeoecology will be dealt with in more detail in a separate paper, however, it should be noted that *Watznaueria barnesiae* has been used increasingly as a proxy for oligotrophy in Cretaceous palaeoceanographical studies (e.g. Erba, 1992; Erba et al., 1992; Williams and Bralower, 1995; Herrle, 2003). However, a link between mesotrophy and *W. barnesiae* has recently been made by Pittet and Mattioli (2002), whilst they further suggested that *Watznaueria britannica* occupied a higher level (towards eutrophic) on the trophic continuum. The present study, and that of Lees et al. (in press), show that *Watznaueria fossacincta/barnesiae* and *W. britannica* are both dominant in ostensibly eutrophic palaeoenvironments, from which other taxa are virtually excluded. Furthermore, *W. fossacincta/barnesiae* has herein been shown to bloom in the coccolith stone band environment (usually an indication of eutrophy). These, when compared to the rest of the KCF, appear to represent the most extreme environment since they show the maximum exclusion of other taxa (Lees et al., in press), so perhaps represent peak eutrophy in the KCF. This implies that *W. fossacincta/barnesiae* occupied a more eutrophic position on the trophic continuum than *W. britannica*, thus contradicting the findings of Pittet and Mattioli (2002). More seriously, since the ability to bloom is an ecological strategy typical of r-selected, growth-maximising species, such opportunistic taxa should not be cited as proxies for oligotrophic surface-water conditions without qualification.

5. Conclusions

KCF coccolith stone band laminae visible with the naked eye in hand-specimen are generally divisible into several microlaminae when viewed in the SEM. These microlaminae are generally undulating and apparently discontinuous, possibly due to microbial mat formation. Consequently, lateral tracking of individual microlaminae is problematical, and estimates of thickness are difficult to make.

Five types of microlamina, two of them subdivided into four subtypes each, have been described. Type 1 is coccolith-barren clay. Subtypes 2a–c represent an increasing coccolith component versus a relatively decreasing clay component, whilst 2d comprises AOM with a coccolith component. Subtypes 3a–c are purely coccolithic, 3a being monospecific, and 3b–c dominated by one watznaueriacean taxon but with varying proportions of other watznaueriacean or non-watznaueriacean taxa. Subtype 3d comprises a *Truncatoscapus/Stradnerlithus* accumulation/bloom. Type 4 appears as a spicular mat, and putatively has a microbial origin. Type 5 is a calcisphere-rich microlamina. Types 1–3 are interpreted in terms of seasonal coccolithophorid flux. Type 4 is rare and possibly only preserved where a substantial thickness has built up. The ecological origin of Type 5 is enigmatic.

Annual records of coccolithophore productivity exist in the KCF coccolith stone bands, with consecutive sequences of microlamina types indicating seasonal changes.

Most individual coccolith-bearing KCF stone band microlaminae are dominated by a single watznaueriacean species (even when preservation is pristine, and so this is a primary palaeoenvironmental feature), predominantly *Watznaueria fossacincta/barnesiae* (apparently members of a morphological continuum), but occasionally by *Watznaueria britannica* or *Cyclagelosphaera margerelii*. Certain microlaminae are composed of *W. fossacincta/barnesiae* in bloom abundances, demonstrably comparable to modern *Emiliana huxleyi* blooms, indicating that this species has an r-selected palaeoecological strategy. Non-watznaueriacean taxa were generally ecologically excluded from this dysoxic, eutrophic basin. The dark lithologies of the rest of the KCF are dominated by *W. britannica*. Thus, the different watznaueriacean taxa had differential palaeoecological strategies, apparently primarily determined by nutrient and oxygen availability. The ability to bloom in response to hypothesised water-column instability and concomitant eutrophication suggests that *W. fossacincta/barnesiae* occupied the more eutrophic end of a trophic continuum, with *W. britannica* and *C. margerelii* being less eutrophic. This would suggest that the coccolith stone bands represent more eutrophic conditions than the mudrocks of the rest of the KCF. This calls into question the assumption that *Watznaueria barnesiae*

in Cretaceous sediments can be used a proxy for oligotrophic surface-waters, or suggests that it changed its ecological strategy through time.

There is no direct modern or fossil analogue for the KCF stone bands, although they show certain similarities to modern laminated Black Sea varves, in being an annual representation of an ecologically restricted environment.

Acknowledgements

JAL gratefully acknowledges receipt of one year of PDRA funding from the NERC (Grant No. GST021351, 1996–1997). JBR publishes with the permission of the Executive Director, BGS (NERC). Thank you to Drs. Emanuela Mattioli and John Marshall for their incisive and erudite reviews, to Dr. Sarah Pearson (ex-Southampton) for stimulating RGGE discussions and allowing us access to her unpublished work, and Dr. Helen Morgans-Bell (Oxford) for help in all things RGGE-related. Various solicited opinions concerning the spicular and calcisphere laminae were gratefully received from Drs. Juergen Schiebe and Simon Brassell (Indiana), Jenny Pike (Cardiff), and Profs. Richard Tyson (Newcastle) and Helmut Willems (Bremen).

References

- Aksu, A.E., Hiscott, R.N., Kaminski, M.E., Mudie, P.J., Gillespie, H., Abrajano, T., Yasar, D., 2002. Last glacial–Holocene paleoceanography of the Black Sea and Marmara Sea: stable isotopic, foraminiferal and coccolith evidence. *Marine Geology* 190, 119–149.
- Arthur, M.A., Dean, W.E., Neff, E.D., Hay, B.J., King, J., Jones, G., 1994. Varve calibrated records of carbonate and organic carbon accumulation over the last 2000 years in the Black Sea. *Global Biogeochemical Cycles* 8, 195–217.
- Batten, D.J., 1985. Coccolith moulds in sedimentary organic matter and their use in palynofacies analysis. *Journal of Micropaleontology* 4, 111–116.
- Benli, H., 1987. Investigations of plankton distribution in the southern Black Sea and its effects on particle flux. In: Degens, E.T., Izdar, E., Honjo, S. (Eds.), *Particle Flux in the Ocean*. Mitteilungen der Geologisch-Paläontologischen Institut, vol. 62. Universität Hamburg, pp. 77–87.
- Bishop, A.N., Kearsley, A.T., Patience, R.L., 1992. Analysis of sedimentary organic materials by scanning electron microscopy:

- the application of backscattered electron imagery and light element x-ray microanalysis. *Organic Geochemistry* 18, 431–446.
- Bologa, A.S., 1986. Planktonic primary productivity of the Black Sea: review. *Journal Thalassia Jugoslavia* 2, 1–22.
- Bown, P.R., 1993. New holococcoliths from the Toarcian–Aalenian (Jurassic) of northern Germany. *Senckenbergiana Lethaea* 73, 407–419.
- Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropaleontological Society Series, Chapman & Hall, The University Press, Cambridge, UK, pp. 34–85.
- Bukry, D., 1974. Coccoliths as paleosalinity indicators—evidence from Black Sea. *The Black Sea—Geology, Chemistry, and Biology*. AAPG Memoir 20, 353–363.
- Chambers, M.H., 2000. A high resolution chemostratigraphy and mineralogical study of the UK onshore Kimmeridge Clay. PhD thesis, University of Reading, UK. Unpublished.
- Cornet, B., Traverse, A., 1975. Palynological contributions to the chronology and stratigraphy of the Hartford Basin in Connecticut and Massachusetts. *Geoscience and Man* 11, 1–33.
- Cox, B.M., Gallois, R.W., 1981. The stratigraphy of the Kimmeridge Clay of the Dorset type area and its correlation with some other Kimmeridgian sequences. IGS Report No.80/4. 44 pp.
- da Gama, R., 2000. Calcareous nannoplankton palaeoecology from the Cenomanian–Turonian of Tarfaya, Morocco. MSc thesis, UCL, London, UK. Unpublished.
- de Wever, P., Geyssant, J.R., Azéma, J., Devos, I., Duée, G., Manivit, H., Vrielynck, B., 1986. La coupe de Santa Anna (Zone de Sciacca, Sicile): une synthèse biostratigraphique des apports des macro-, micro- et nannofossiles du Jurassique supérieur et Crétacé inférieur. *Revue de Micropaléontologie* 29, 141–186.
- Downie, C., 1957. Microplankton from the Kimmeridge Clay. *Quarterly Journal of the Geological Society of London* 112, 413–434.
- EGGE, J.K., Aksnes, D.L., 1992. Silicate as regulating nutrient in phytoplankton competition. *Marine Ecology Progress Series* 83, 281–289.
- Eker-Develi, E., Kideys, A.E., 2003. Distribution of phytoplankton in the southern Black Sea in summer 1996, spring and autumn 1998. *Journal of Marine Systems* 39, 203–211.
- Erba, E., 1992. Middle Cretaceous calcareous nannofossils from the western Pacific (Leg 129): evidence for paleoequatorial crossings. *Proceedings of the Ocean Drilling Program. Scientific Results* 129, 189–201.
- Erba, E., Castradori, D., Guasti, G., Ripepe, M., 1992. Calcareous nannofossils and Milankovitch cycles: the example of the Albian Gault Clay Formation (southern England). *Palaeogeography, Palaeoclimatology, Palaeoecology* 93, 47–69.
- Filatoff, J., 1975. Jurassic palynology of the Perth Basin, Western Australia. *Palaeontographica Abteilung B Palaophytologie* 154, 1–113.
- Francis, J.E., 1984. The seasonal environment of the Purbeck (Upper Jurassic) fossil forests. *Palaeogeography, Palaeoclimatology, Palaeoecology* 48, 285–307.
- Gallois, R.W., 1976. Coccolithic blooms in the Kimmeridge Clay and origin of North Sea oil. *Nature* 259, 473–475.
- Gallois, R.W., 2000. The stratigraphy of the Kimmeridge Clay Formation (Upper Jurassic) in the RGGE project boreholes at Swanworth Quarry and Metherhills, south Dorset. *Proceedings of the Geologists' Association* 111, 265–280.
- Gallois, R.W., Cox, B.M., 1974. Stratigraphy of the Upper Kimmeridge Clay of the Wash area. *Bulletin of the Geological Survey of Great Britain* 47, 1–16.
- Gallois, R., Medd, A.W., 1979. Coccolith-rich marker-bands in the English Kimmeridge Clay. *Geological Magazine* 116, 247–334.
- Goldstein, J.I., Newbury, D.E., Echlin, P., Joy, D.C., Romig, A.D., Lifshin, E., 1992. *Scanning electron microscopy and x-ray microanalysis. A Text for Biologists, Materials Scientists, and Geologists*, 2nd edn. Plenum Press, New York, p. 820.
- Goy, G., 1981. Nannofossiles calcaires des schistes carton (Toarcien inférieur) du Bassin de Paris. *Documents de la RCP* 459, 1–86 (éditions BRGM).
- Hay, B.J., Honjo, S., Kempe, S., Ittekkot, V.A., Degens, E.T., Konuk, T., Izdar, E., 1990. Interannual variability in particle flux in the southwestern Black Sea. *Deep-Sea Research I* 37, 911–928.
- Hay, B.J., Arthur, M.A., Dean, W.E., Neff, E.D., Honjo, S., 1991. Sediment deposition in the late Holocene abyssal Black Sea with climatic and chronological implications. *Deep-Sea Research I* 38, 1211–1235.
- Herrle, J.O., 2003. Reconstructing nutricline dynamics of mid-Cretaceous oceans: evidence from calcareous nannofossils from the Niveau Paquier black shale (SE France). *Marine Micropaleontology* 47, 307–321.
- Houghton, S.D., 1992. Thermocline control on coccolith diversity and abundance in Recent sediments from the Celtic Sea and English Channel. *Marine Geology* 83, 313–319.
- Kilham, P., Kilham, S.S., 1980. The evolutionary ecology of phytoplankton. In: Morris, I. (Ed.), *The Physiological Ecology of Phytoplankton*. University of California Press, Berkeley, CA, pp. 571–597.
- Krhovsky, J., 1995. Comparison of calcareous nannoplankton factor assemblages and seasonally variable assemblages fixed in fecal pellets: the Early Oligocene of the South Moravia flysch belt. In: Flores, J.-A., Sierro, F.J. (Eds.), *Proceedings of the 5th INA Conference, Salamanca 1993*. Universidad de Salamanca/INA, Spain, pp. 125–141.
- Lambert, B., 1987. Nannofossiles calcaires de l'Albien supérieur et du Vranconnien du Cameroun méridional. *Cahiers de Micropaléontologie* 2, 33–96.
- Lees, J.A., Bown, P.R., Young, J.R., in press. Late Jurassic coccolithophores record eutrophy: gross palaeoenvironmental characteristics of the Kimmeridge Clay Formation photic zone. *Journal of Nannoplankton Research* 26.
- Morgans-Bell, H.S., Coe, A.L., Hesselbo, S.P., Jenkyns, H.C., Weedon, G.P., Marshall, J.E.A., Tyson, R.V., Williams, C.J., 2001. Integrated stratigraphy of the Kimmeridge Clay Formation (Upper Jurassic) based on exposures and boreholes in south Dorset, UK. *Geological Magazine* 138, 511–539.
- Myers, K.J., Wignall, P.B., 1987. Understanding Jurassic organic-rich mudrocks—new concepts using gamma-ray spectrometry and palaeoecology. Examples from the Kimmeridge Clay of Dorset and the Jet Rock of Yorkshire. In: Leggett, J.K., Zuffa, G.G. (Eds.), *Marine Clastic Sedimentology Concepts and Case Studies*. Graham and Trotman, London, UK, pp. 172–189.
- Noël, D., 1973. Nannofossiles calcaires de sédiments jurassiques

- finement laminés. *Bulletin du Muséum National d'Histoire Naturelle* 75, 95–156 (3^e série).
- O'Brien, N.R., 1996. Shale lamination and sedimentary processes. In: Kemp, A.E.S. (Ed.), *Palaeoclimatology and Palaeoceanography from Laminated Sediments*. Special Publication-Geological Society, vol. 116, pp. 23–36.
- Okada, H., McIntyre, A., 1979. Seasonal distribution of modern coccolithophores in the western North Atlantic Ocean. *Marine Biology* 54, 319–328.
- Oschmann, W., 1988. Kimmeridge Clay sedimentation—a new cyclic model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 65, 217–251.
- Oschmann, W., 1990. Environmental cycles in the late Jurassic northwest European epeiric basin: interaction with atmospheric and hydrospheric circulations. *Sedimentary Geology* 69, 313–332.
- Pearson, S.J., 2000. High resolution environmental change in the Late Jurassic Kimmeridge Clay Formation. PhD thesis, University of Southampton, UK. Unpublished.
- Pearson, S.J., Marshall, J.E.A., Kemp, A.E.S., in press. The White Stone Band of the Kimmeridge Clay, an integrated high-resolution approach to understanding environmental change. *Journal of the Geological Society, London, Special Volume*.
- Philippe, H., Sorhannus, U., Baroin, A., Perasso, R., Gasse, F., Adoutte, A., 1994. Comparison of molecular and paleontological date in diatoms suggests a major gap in the fossil record. *Journal of Evolutionary Biology* 7, 247–265.
- Pittet, B., Mattioli, E., 2002. The carbonate signal and calcareous nannofossil distribution in an Upper Jurassic section (Balingen–Tieringen, Late Oxfordian, southern Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology* 179, 71–96.
- Raiswell, R., Newton, R., Wignall, P.B., 2001. An indicator of water-column anoxia: resolution of biofacies variations in the Kimmeridge Clay (Upper Jurassic, U.K.). *Journal of Sedimentary Research* 71, 286–294.
- Ravillious, K., 2002. Controls on mid-Cretaceous marine sedimentation in the Tarfaya Basin, southern Morocco. PhD thesis, UCL, London, UK. Unpublished.
- Reid, F.M.H., 1980. Coccolithophorids of the North Pacific Central Gyre with notes on their vertical and seasonal distribution. *Micropaleontology* 26, 151–176.
- Riding, J.B., Thomas, J.E., 1988. Dinoflagellate cyst stratigraphy of the Kimmeridge Clay (Upper Jurassic) from the Dorset coast, southern England. *Palynology* 12, 65–88.
- Riding, J.B., Thomas, J.E., 1992. Dinoflagellate cysts of the Jurassic System. In: Powell, A.J. (Ed.), *A Stratigraphic Index of Dinoflagellate Cysts*. British Micropaleontological Society Publication Series. Chapman & Hall, London, UK, pp. 7–97.
- Röhl, H.-J., Schmidt-Röhl, A., Oschmann, W., Frimmel, A., Schwark, L., 2001. The Posidonia Shale (Lower Toarcian) of SW-Germany: an oxygen-depleted ecosystem controlled by sea-level and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165, 27–52.
- Sælen, G., Tyson, R.V., Telnæs, N., Talbot, M.R., 2000. Contrasting watermass conditions during deposition of the Whitby Mudstone (Lower Jurassic) and Kimmeridge Clay (Upper Jurassic) formations, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* 163, 163–196.
- Sorokin, Y.I., 1983. The Black Sea. In: Ketchum, B.H. (Ed.), *Ecosystems of the World 26. Estuaries and Enclosed Seas*. Elsevier, Amsterdam, pp. 253–292.
- Thomsen, E., 1989. Seasonal variation in boreal early cretaceous calcareous nannofossils. *Marine Micropaleontology* 15, 123–152.
- Traverse, A., 1988. *Paleopalynology* Hyman Unwin, Boston.
- Tribovillard, N.-P., 1998. Cyanobacterially generated peloids in laminated, organic matter rich limestones: an unobtrusive presence. *Terra Nova* 10, 126–130.
- Tyson, R.V., Wilson, R.C.L., Downie, C., 1979. A stratified water column environmental model for the Type Kimmeridge Clay. *Nature* 277, 377–380.
- van Konijnenburg-van Cittert, J.H.A., van der Burgh, J., 1996. Review of the Kimmeridgian flora of Sutherland, Scotland, with reference to the ecology and in situ pollen and spores. *Proceedings of the Geologists' Association* 107, 97–105.
- van Dongen, B.E., Schouten, S., Sinninghe-Damsté, J.S., 2003. Preservation of carbohydrates through sulfurization: the primary cause of the accumulation of organic matter in a Jurassic euxinic shelf sea. *Geologica Ultraiectina* 224, 107–145.
- van Kaam-Peters, H.M.E., Schouten, S., Köster, S., Sinninghe-Damsté, J.S., 1998. Controls on the molecular and carbon isotopic composition of organic matter deposited in a Kimmeridgian euxinic shelf sea: evidence for preservation of carbohydrates through sulfurization. *Geochimica et Cosmochimica Acta* 62, 3259–3283.
- von Knonre, H., Krumbein, W.E., 2000. Bacterial Calcification. In: Riding, R.E., Awramik, S.M. (Eds.), *Microbial Sediments*. Springer-Verlag, Berlin, pp. 25–32.
- Wignall, P., 1990. Benthic palaeoecology of the Late Jurassic Kimmeridge Clay of England. *Special Papers in Palaeontology* 43, 1–75.
- Williams, J.R., Bralower, T.J., 1995. Nannofossil assemblages, fine fraction stable isotopes, and the palaeoceanography of the Valanginian–Barremian (Early Cretaceous) North Sea Basin. *Palaeoceanography* 10, 815–839.
- Wood, G.D., Gabriel, A.M., Lawson, J.C., 1996. Palynological techniques—processing and microscopy. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, vol. 1, pp. 29–50.
- Young, J.R., 1994. Functions of coccoliths. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, UK, pp. 63–82.
- Young, J.R., Bown, P.R., 1991. An ontogenetic sequence of coccoliths from the Late Jurassic Kimmeridge Clay of England. *Palaeontology* 34, 843–850.
- Ziveri, P., Rio, D., Thunell, R., 1993. Seasonal distribution of calcareous nannoplankton in an upwelling region: results from sediment trapping and water sampling in the San Pedro Basin, southern California Bight. *INA Newsletter* 15, 103 (abstract).