

Photic zone palaeoenvironments of the Kimmeridge Clay Formation (Upper Jurassic, UK) suggested by calcareous nannoplankton palaeoecology

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Abstract

Nannoplankton abundance data has revealed significant and systematic population fluxes through all representative lithologies and cycle types of the Kimmeridge Clay Formation (KCF), and also through intervals in which lithology is visually homogeneous. The majority of KCF samples yielded nannofossil assemblages of low species richness (1 to 10) and marked unevenness, independent of preservational state. All samples were dominated by coccoliths of one family, the Watznaueriaceae. While assemblage unevenness is characteristic of nannofossil populations, such low species richness is atypical, particularly when compared with coeval assemblages of similar latitude. Such anomalously low nannofossil diversity may be explained as a response to nutrient-rich euphotic environments. We postulate that consistently high trophic conditions supported the eurytopic watznaueriaceans but excluded most normal open-ocean taxa. The switching of dominance within this group most likely reflects different adaptations within an r-selected ecological strategy, related to nutrient concentration. Lowest diversities were recorded in mudstone/oil-shale lithologies where *Watznaueria britannica* is the dominant species, suggesting adaptation to the highest nutrient concentrations. *Watznaueria barnesiae/fossacincta* is particularly dominant in coccolith stone bands, where diversity is slightly higher, suggesting adaptation to lower high nutrient levels. *Cyclagelosphaera margerelii* appears to be the most extremely r-selected species, exploiting unusual (very high trophic/lowered sea-level?) conditions that excluded even *W. britannica*. © 2005 Elsevier B.V. All rights reserved.

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1. Introduction

The Kimmeridge Clay Formation (KCF) of Dorset, southern England is a 620-m-thick sequence representing c. 4 myr (Kent and Gradstein, 1985) of essentially continuous Late Jurassic sedimentation. It predominantly comprises dark, organic-rich mudstones and oil-

shales, and in the North Sea the KCF sensu lato forms the most important single hydrocarbon source-rock. The formation is interrupted by infrequent, but laterally persistent, pale limestone and dolostone beds, known as ‘stone bands’. Some of these stone bands are finely laminated and are formed predominantly of coccoliths and coccospheres, providing spectacular evidence of ancient coccolithophore blooms, which have attracted much interest (Noël, 1973; Gallois, 1976; Gallois and Medd, 1979; Young and Bown, 1991; Lees et al., 2004).

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The organic matter of the KCF has been shown to be overwhelmingly algal in origin, and coccoliths as one of the major sources of carbonate (Pearson, 2000). Consequently, phytoplankton production played an important role in producing the lithological signal of changing clay, carbonate and organic matter sedimentation that constitutes the KCF record of environmental change.

Coccolithophores are a major phytoplankton group with an excellent fossil record and thus potentially provide a record of changing conditions in the photic

zone. However, interpretation requires knowledge of the ecology of individual fossil species that can only be developed by studying changes in assemblages relative to other evidence of environmental change. The objectives of this study were thus both to develop knowledge of controls on Late Jurassic coccolithophore ecology and to apply it to better constrain models of development of the KCF.

Much of the KCF displays metre- to several-metre-scale lithological cyclicity involving clays, bituminous shales, oil-shales and coccolith limestones (A-B-C-D

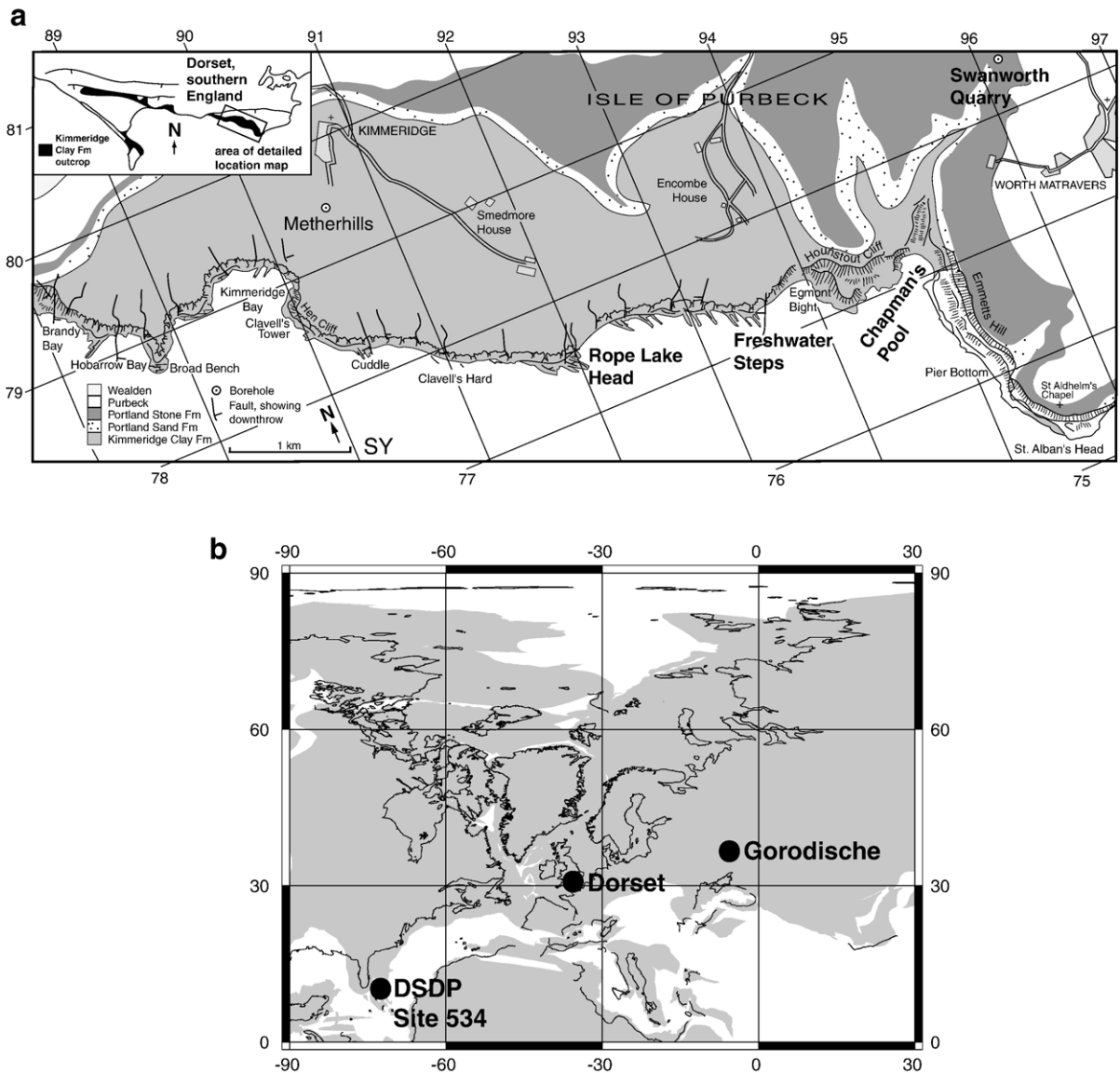


Fig. 1. (a) Map showing locations of studied boreholes (SQ1, SQ2) and coastal outcrop section (Rope Lake Head–Freshwater Steps–Chapman’s Pool), Dorset, southern England; (b) Late Jurassic reconstruction showing position of Dorset locations relative to Gorodische (Volga Basin, SE Russia) and DSDP Site 534 (Blake–Bahama Basin, western Atlantic). Plates in grey, present-day coastlines in black.

rhythms of Tyson et al., 1979). A number of models have been developed to explain these lithologies, including those of Gallois (1976), Tyson et al. (1979), Wignall (1989) and Oschmann (1990). Most of these agree fundamentally on a stratified water-column model that experienced varying degrees of (dys)oxia, but explain the lithological cyclicity with reference to different factors, including seafloor bathymetry, convective and turbulent mixing, sea-level change, and biological productivity. They all invoke the role or response of coccolithophore blooms within these cycles, although the details of interpretation differ.

A number of palaeoceanographical studies based on nanofossil analyses have been carried out in the Cretaceous (e.g. Watkins, 1989; Erba et al., 1992; Street and Bown, 2000), but there has been little work on the Late Jurassic, although Pittet and Mattioli (2002) recently reported on changes in Late Oxfordian nanofossil assemblages in relation to decreasing nutrient levels. The work presented herein documents the cm- to m-scale coccolithophore record of the KCF, and these observations form the basis for broad interpretations of the photic zone palaeoenvironments, and may help to shed some light on the anoxia vs. productivity models for this formation.

This work was carried out under the aegis of the NERC Special Topic, *Rapid Global Geological Events (RGGE) – Anatomy of a source rock*, which examined the KCF via an interdisciplinary research program focused on three continuously cored boreholes. The calcareous nanofossils of portions of two of the boreholes (Swanworth Quarry #1 [SQ1] and #2 [SQ2]; Gallois, 2000; Morgans-Bell et al., 2001) were studied here, alongside outcrop material from the coast between Rope Lake Head and Chapman's Pool (Fig. 1a). These KCF nanofloras were compared with those from a coeval section from Gorodische (Volga Basin, SE Russia) and with those from DSDP Site 534 (Blake–Bahama Basin, western Atlantic Ocean; Roth, 1978; Bralower et al., 1989) (Fig. 1b).

2. Methodology

2.1. Quantitative analysis of phytoplankton assemblages

Four hundred and eleven samples were prepared for nanofossil light microscope (LM) analysis. For samples taken from pieces of core, the core was labelled with a permanent marker at the sample intervals required, a small area ($\sim 0.5 \text{ cm}^2$) was cleaned by scraping

away the oxidised outer film, running the piece of core under water to remove the loosened sediment, and blotting it with a paper towel. Using a clean dental pick, sediment was scraped from the cleaned patch, taking care to sample a horizon of no more than 1 mm thickness, onto a licked (so as to negate surface tension) coverslip. Sample preparation then proceeded as usual for simple smear-slides (see Bown and Young, 1998, p. 17), as this preparation method ensures minimal skewing of the assemblage component proportions and reduces the chances of fossil degradation due to soaking and settling in water.

The first 300 specimens were logged on random fields of view (FOV), and the number of FOV required to reach this figure was noted. Counting was carried out on FOV of approximately equal density, to ensure consistency from sample to sample, although this was not always possible, depending on lithology. This technique is semi-quantitative but it has been shown that results are favourably comparable with more rigorous absolute preparation and counting methods (Backman and Shackleton, 1983). Photographic illustrations of all taxa logged, and their authors and references can be found in Bown (1998).

2.2. Data handling and taxonomic criteria

Seven sets of data were generated for each suite of samples:

- (1) raw counts (~ 300 specimens/sample wherever possible) and numbers of FOV needed to count these. From this, certain taxa were grouped together: *Cyclagelosphaera margerelii* here includes forms with both wide and narrow inner rim-cycles, and also protococcolith rims from all ontogenetic stages, i.e. including *Cyclagelosphaera tubulata*; *Staurolithites* spp. includes *Staurolithites lumina*, *Staurolithites quadriarcullus* and *Staurolithites* sp. (a small form with a cross which is distinguished by having well-calcified, moderately highly birefringent short-ellipse arms and poorly calcified, low-birefringence long-ellipse arms set behind the others); *Watznaueria barnesiae* and *Watznaueria fossacincta* (all lengths) were lumped together because they are believed to represent end-members of a morphological continuum (see Lees et al., 2004; Bornemann and Mutterlose, submitted for publication); *Zeughrabdotos* spp. includes *Zeughrabdotos erectus* and *Zeughrabdotos fissus*; *Watznaueria britannica* includes all lengths and all morphologies (i.e.

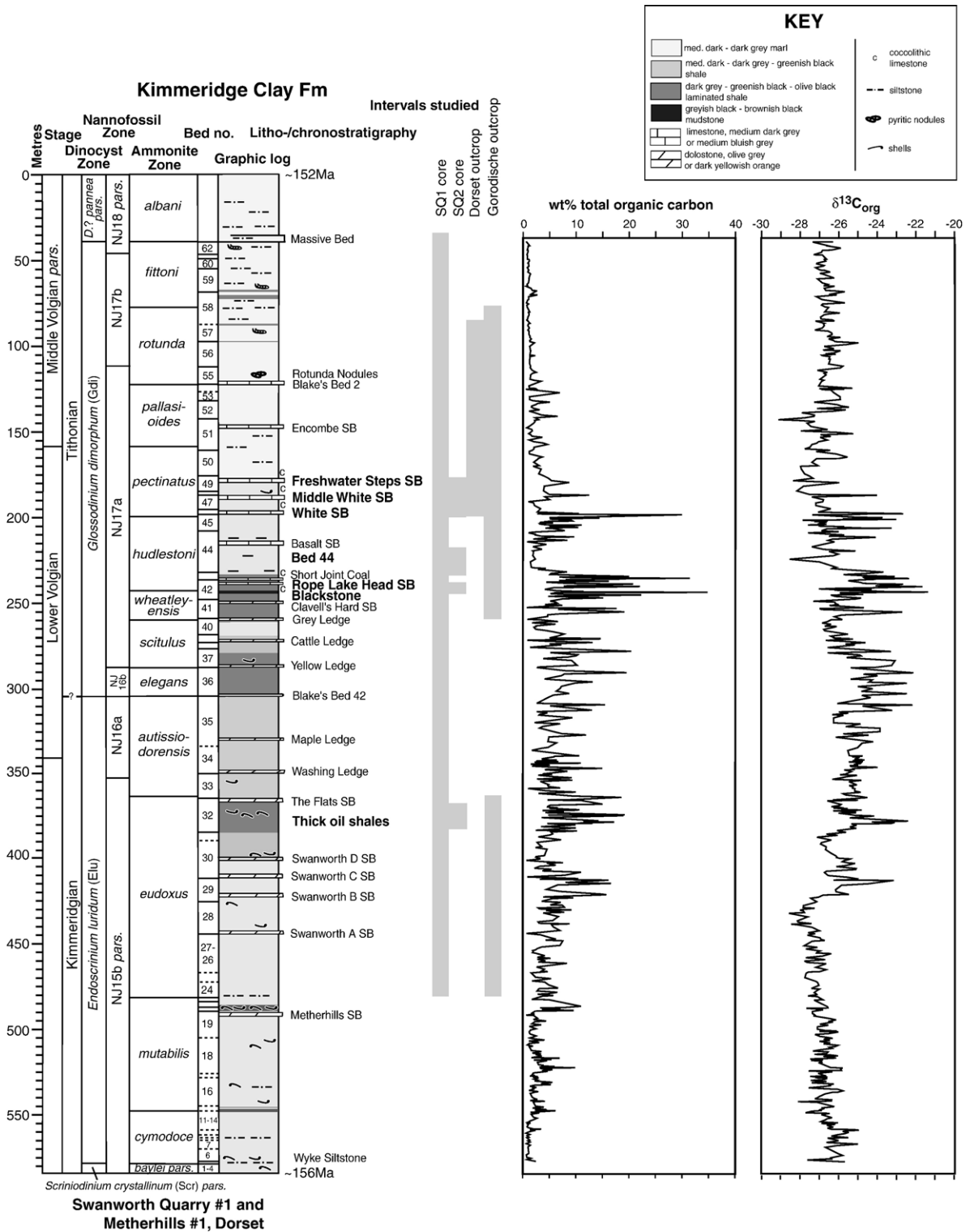


Fig. 2. Stratigraphy and lithology of the KCF, based on SQ1 and Metherhills Boreholes, showing context of studied intervals, and plotted against TOC and $\delta^{13}C_{org}$. Redrawn from Morgans-Bell et al. (2001, Fig. 6). Nannofossil zones after Bown and Cooper (1998); ages after Kent and Gradstein (1985); SB=Stone Band.

narrow and wide central-area forms) bearing a short-ellipse bar; ‘other taxa’ includes all other taxa, as specified below, as well as indeterminate (non-watznaueriacean) rims; ‘reworked’ includes *Schizosphaerella punctulata* and *Tubirhabdus patulus*;

- (2) a %relative abundance (%RA) chart was generated, plotted herein as linear plots to compare peaks/troughs in dominance of the assemblages by individual taxa. In order to cross-check the %RA data, we generated:
 - (3) nannofossil specimens/FOV data;
 - (4) a linear plot of qualitatively estimated preservation per sample, ‘good’ indicating coccoliths with very few signs of etching or overgrowth, ‘moderate’ representing coccoliths which had been moderately etched or overgrown, and ‘poor’ being coccoliths which had been severely etched/overgrown;
 - (5) a linear plot of species richness per sample. The watznaueriacean taxa were grouped as above but the non-watznaueriaceans were counted separately;
 - (6) a linear plot of number of specimens counted per sample; and
 - (7) a linear plot of the Shannon–Weiner Diversity Index for the SQ1 *eudoxus–albani* interval and the SQ2 White Stone Band, to compare with the species richness plots.

Here, the charts representing (2), and (4)–(7) are presented in Figs. 3–10, 12 and 13.

3. Material

Fig. 2 shows the stratigraphical context of the studied material, alongside the graphic log of Morgans-Bell et al. (2001). A detailed description of the stratigraphy can be found therein. Total organic carbon (TOC) and $\delta^{13}\text{C}_{\text{org}}$ data, derived from the SQ1 and Metherhills Boreholes by Morgans-Bell et al. (2001), are also shown. Unfortunately, detailed comparisons of these geochemical data with the nannofossil data presented here are not possible because our samples are predominantly from SQ2.

Samples were analysed on a variety of scales:

- (1) to discern the general pattern of nannofossil %RA changes through virtually the entire KCF, 35 samples were taken at ~10-m intervals through SQ1, from 373.62 m (upper *eudoxus* Ammonite Zone [AZ]) to 38.92 m (lower *albani* AZ);

- (2) to compare the KCF nannofloras with coeval material, 12 samples were analysed from the Gorodische outcrop, Volga Basin, SE Russia (*eudoxus–rotunda* AZs) at 1–4 samples per AZ;
- (3) to investigate the broad KCF patterns in greater detail, and test the replicability of the patterns at different scales, for specific intervals of main interest to the consortium, higher-resolution samples were taken from: the *eudoxus* oil-shale (*eudoxus* AZ) – 44 SQ2 samples at 0.5- and 5-cm intervals through dark mudstones and shales; the Blackstone interval (*wheatleyensis* AZ) – 89 SQ2 samples at ~10-cm intervals through dark mudstones with muddy limestones; the Rope Lake Head Stone Band (*hudlestoni* AZ) – 12 SQ2 samples at 5-cm intervals through dark mudstones and shales, and pale limestones; Bed 44 (*hudlestoni* AZ) – 21 SQ2 samples at ~1.5-m intervals through dark mudstones; the White Stone Band (*pectinatus* AZ) – 56 SQ2 samples at 5-cm intervals through dark shales and pale muddy limestones; the Freshwater Steps Stone Band (*pectinatus* AZ) – 22 SQ2 samples at 5-cm intervals through dark shales and mudstones, and pale limestones; and from the KCF outcrop, Rope Lake Head–Freshwater Steps–Chapman’s Pool, Dorset (*pectinatus–rotunda* AZs) – 120 samples at variable intervals (5 m–5 cm) through dark shales and pale limestones.

4. Results

For the sake of brevity, the following abbreviations are used in the text below and on Figs. 3–13: *Bd*=*Biscutum dubium*, *Cm*=*Cyclagelosphaera margerelii* (and included forms), *Sspp*=*Staurolithites* spp., *Wb+f*=*Watznaueria barnesiae*+*W. fossacincta* (and included forms), *Wbr*=*Watznaueria britannica* (and included forms), *Zspp*=*Zeugrhabdotus* spp. Taxa were considered to be significantly abundant from an arbitrary >3% level. Lithologies on Figs. 3–10, 12 and 13 are based on individual sample descriptions.

In some samples, where the number of specimens counted was very low (<50), artificial abundance peaks can occur. In these cases, dashed lines have been drawn between the best surrounding data points to provide an indication of predicted abundances.

The nannofossil abundance data shows significant and systematic population fluxes through all representative lithologies and cycle-types of the KCF, independent of preservation, and also through intervals in which lithology appears to be homogeneous. All sam-

ples yielded nannofossil assemblages of relatively low species richness (from 1 to 10) and marked unevenness. All samples were dominated by one watznaueriacean species. Assemblage unevenness is characteristic of nannofossil populations, but such low species richness is atypical, as illustrated by our comparison of the KCF with the coeval, similar-latitude Gorodische section (species richness 16 to 28), and also, for example, by comparison with DSDP Site 534 (Blake–Bahama Basin, western Atlantic), where Roth (1978) recorded diversities of 10–16.

4.1. Eudoxus oil shale (SQ2) – 0.5-m sample interval

The nannofloras are predominantly dominated by *Wbr*, infrequently giving way to *Cm* and/or *Wb+f*, which show wide variations in peak intensity. *Cm* generally dominates over *Wb+f* in the upper 75% of the section. Non-watznaueriacean taxa are generally rare and sporadic throughout. Only *Bd* and ‘other taxa’ (*Ethmorhabdus gallicus*, *Hexalithus noeliae*, *Polypodorhabdus escaigii*, *Stephanolithion bigotii bigotii*) make significant (>3%) contributions to the assemblages. The correlation between *Bd* peaks and the watznaueriacean pattern is unclear. *Bd* peaks predominantly in the upper half of this oil-shale. *Sspp* and *Zspp* exhibit %RA increases generally in the vicinity of the *Bd* and ‘other taxa’ peaks, and are more noticeably present in the upper half of this section. Species richness (0–9 taxa) generally appears to correlate with preservation. No correlation with lithology was observed (Fig. 3).

4.2. Eudoxus oil shale (SQ2) – 5-cm sample interval

Wbr is predominantly dominant, infrequently giving way mainly to *Cm*. *Cm* dominates over *Wb+f* virtually throughout this section, both again showing wide variations in peak intensity. Non-watznaueriacean taxa are confirmed as being rare and sporadic throughout but at this resolution, *Sspp* and *Zspp* are the only significant taxa (>3%). The relationship between these peaks and the watznaueriacean pattern is unclear. *Bd* and ‘other taxa’ (see above) show increased %RA generally in the vicinity of the *Sspp* and *Zspp* peaks. Species richness (1–7 taxa) correlates somewhat with preservation but the correlation is much more ambiguous at this sample resolution. An interval of ‘limestone development’ (concentrated blebby laminae, rather than limestone horizons) was noted in the core (see Fig. 4) and this appears to correspond loosely to depressed *Wb+f* and increased *Wbr* %RAs.

4.3. Blackstone (SQ2) – 10-cm sample interval

This interval has high TOC (up to 35 wt.%: Morgans-Bell et al., 2001). Dominated throughout by *Wbr*. *Cm* shows infrequent high-intensity peaks in the lower half of the section but is generally more sporadically present, and of lower %RA, than *Wb+f*, which is a relatively stable background component of the assemblages. *Zspp* and ‘other taxa’ (*Crepidolithus* sp., *E. gallicus*, *P. escaigii*, *Stephanolithion atmetos*) form significant (>3%) peaks, the former notably in the upper half of the section. There is no obvious relationship between these occurrences and the patterns presented by the watznaueriacean taxa. Other non-watznaueriacean taxa are present but only very rarely and sporadically, and without any discernible pattern. There is some correlation of species richness (0–8 taxa) with preservation, however, species richness is also variable when preservation is stable. There seems to be no correlation between lithology and nannofossil abundances (Fig. 5).

4.4. Rope Lake Head Stone Band (SQ2) – 5-cm sample interval

Dominated by *Wbr*. *Cm* generally dominates over *Wb+f*. Note that the peak in *Wb+f* in the upper half of the section (in limestone) is artificial (low numbers of counted specimens). *Zspp* and ‘other taxa’ exhibit significant (>3%) peaks, although the former is somewhat artificial. *Zspp* peaks as *Cm* declines. *Bd* and *Sspp* were not recorded in the LM. Species richness (1–5 taxa) varies whilst preservation remains stable, thus there is no obvious correlation between the two. No particular correlation with lithology is discernible, although *Cm* appears to be depressed during limestone intervals (Fig. 6).

4.5. Bed 44 (SQ2) – 1.5-m sample interval

Predominately dominated by *Wbr*, but interrupted in the lower half of the section by *Cm*. *Cm* generally dominates over *Wb+f*. All the other taxa have significant (>3%) peaks. *Bd* and *Sspp* peaks flank the broad *Cm* peak. *Zspp* has a marked peak following the *Cm* peak. Some reworked taxa were identified (*Crepidolithus* spp., *Crucirhabdus primulus*, *Schizosphaerella punctulata*, *Tubirhabdus patulus*) in the middle part of the section, coincident with the *Zspp* peak. ‘Other taxa’ (*Diazomatolithus gallicanus*, *E. gallicus*, *P. escaigii*, *S. atmetos*) are more noticeable in the upper half of the section, and are also coincident with *Zspp* peaks. Spe-

cies richness (1–10 taxa) varies whilst preservation remains stable, thus there is no obvious correlation between the two. There is no correlation with lithology (Fig. 7).

4.6. White Stone Band (SQ2) – 5-cm sample interval

Wb+f generally dominates, although in the lower quarter of the section these apparently occasionally

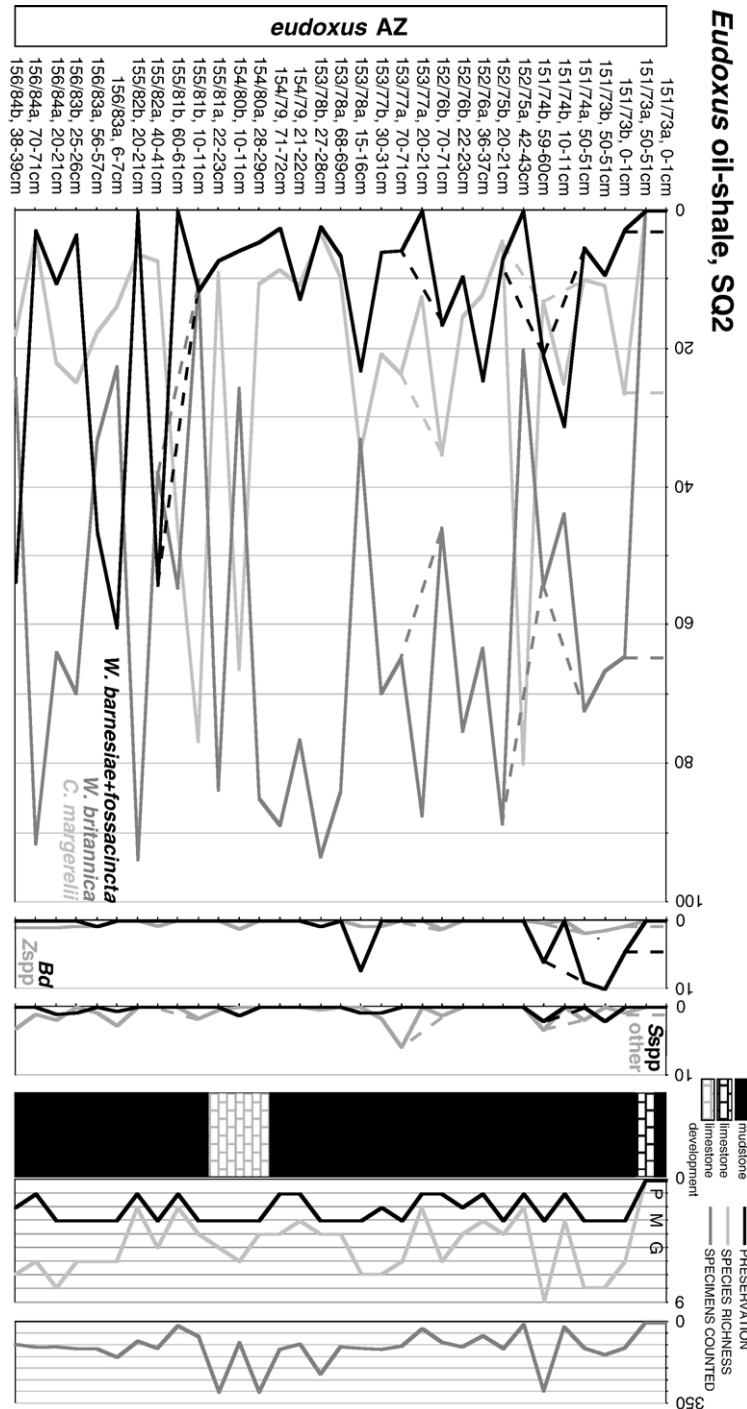


Fig. 3. *Eudoxus* oil-shale, SQ2, 0.5 m interval. Linear %RAs plotted against lithology, preservation, species richness and specimens counted. 'Limestone development' refers to alternating dark/pale colour laminations; P=poor, M=moderate, G=good preservation. Sea-level rose throughout this interval (Taylor et al., 2001).

Eudoxus oil-shale, SQ2

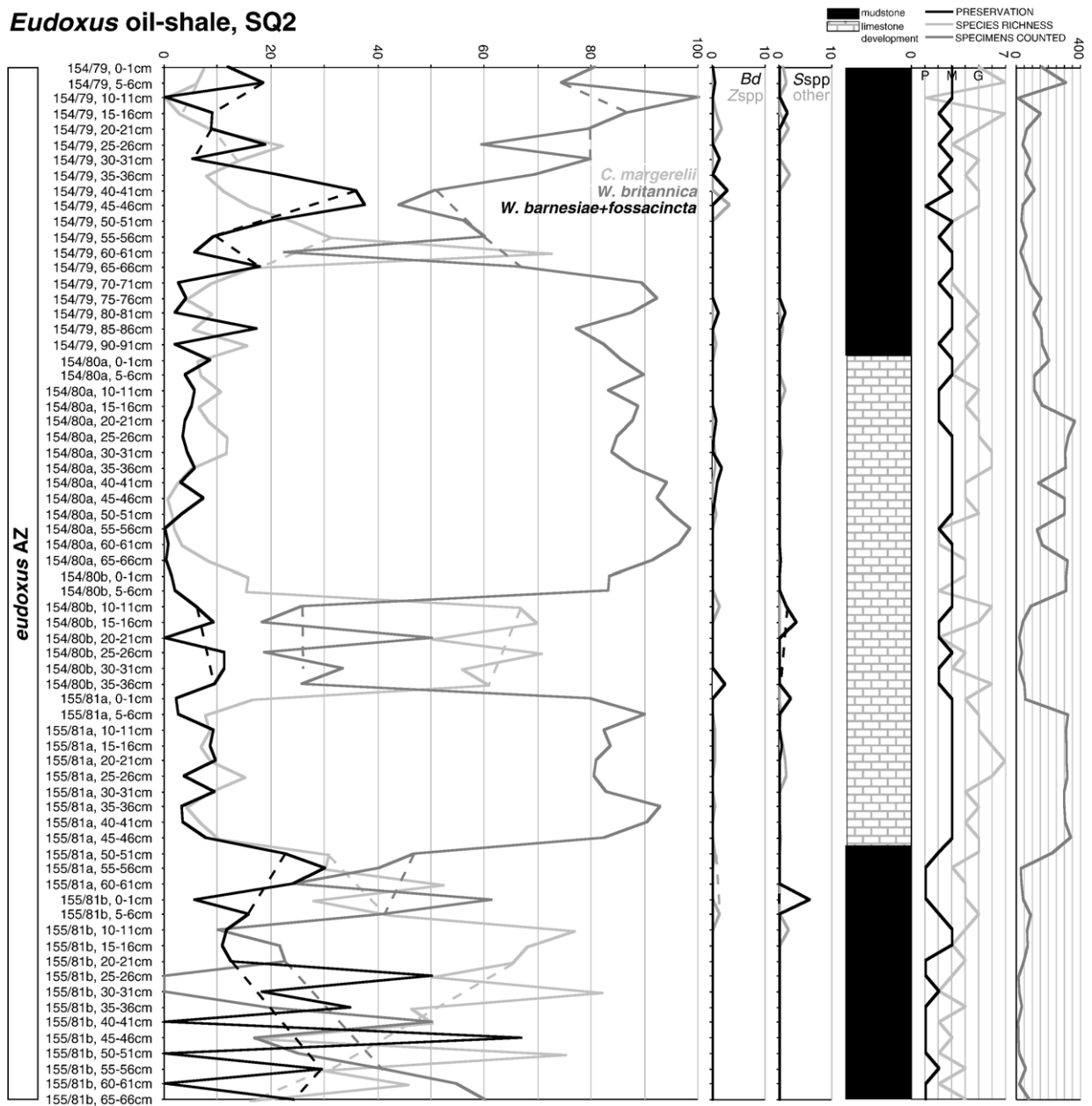


Fig. 4. *Eudoxus* oil-shale, SQ2, 5 cm interval. See Fig. 3 caption for explanation. Sea-level rose throughout this interval (Taylor et al., 2001).

give way to *Wbr* or *Cm* (the latter being somewhat artificial, correlating with low numbers of counted specimens). In the upper half of the section, *Wb+f* only just show greater %RA than *Wbr*. *Cm* is consistently present in the background. All other non-watznaueriacean taxa (including *Discorhabdus ignotus*) are very poorly represented. There is very little correlation between species richness (1–7 taxa) and preservation: species richness is generally stable through intervals of

fluctuating preservation. *Wb+f* predominate through the limestone lithologies, whilst *Wbr* is depressed (Fig. 8).

4.7. Freshwater Steps Stone Band (SQ2) – 5-cm sample interval

Wb+f dominates throughout. *Cm* is extremely rare and sporadic, whilst *Wbr* is consistently present in the

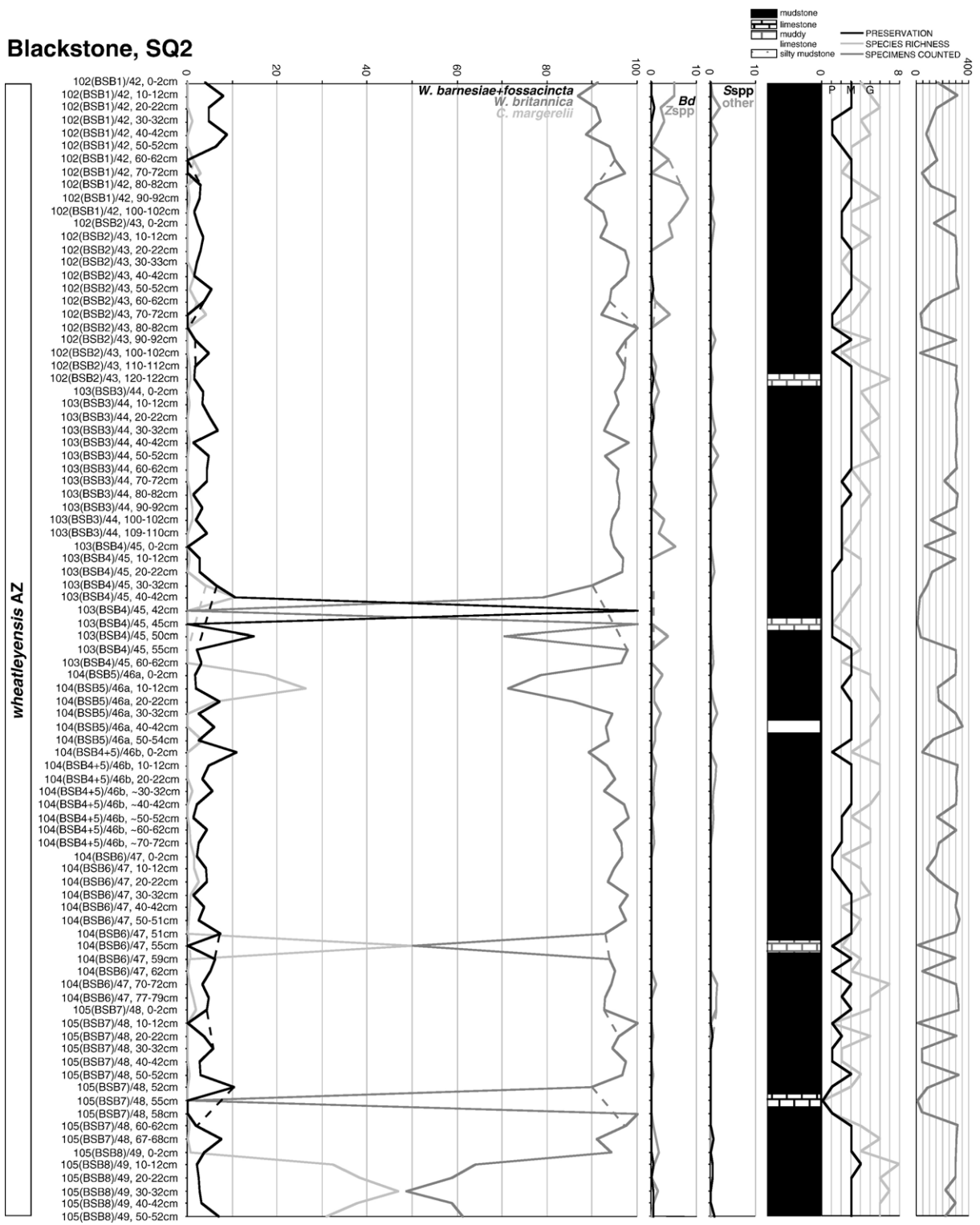


Fig. 5. Blackstone, *wheatleyensis* AZ, SQ2, ~10 m interval. See Fig. 3 caption for explanation. Sea-level rose to a peak during this interval (Taylor et al., 2001).

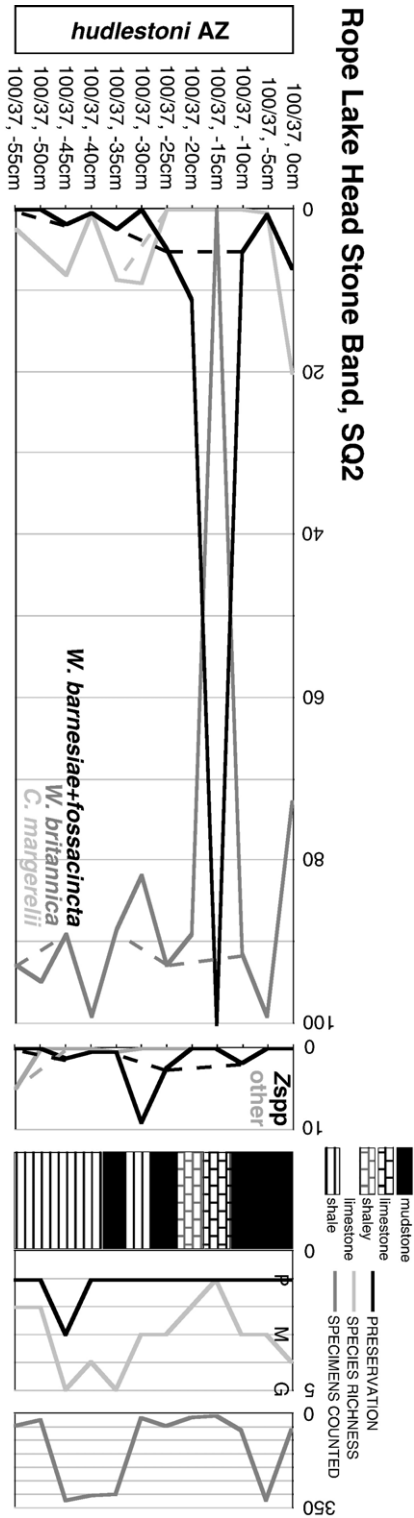


Fig. 6. Rope Lake Head Stone Band, *hudlestoni* AZ, SQ2, 5 cm interval. See Fig. 3 caption for explanation. Sea-level peaked in this interval (Taylor et al., 2001).

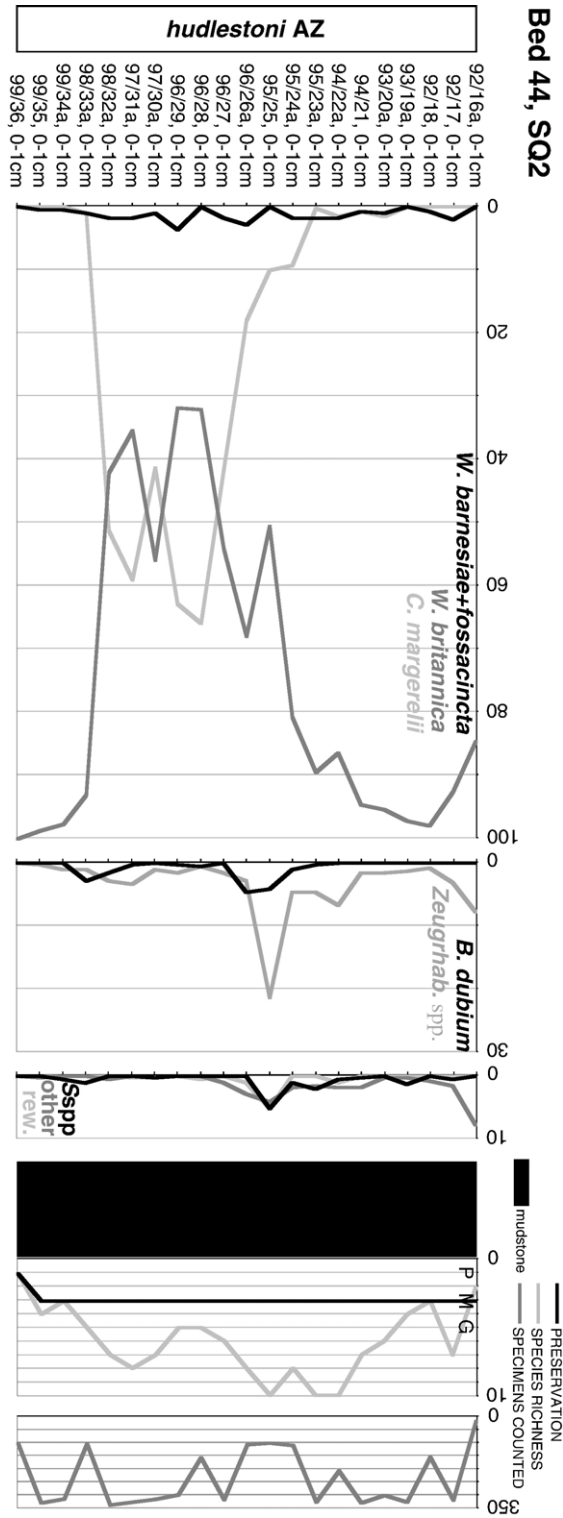


Fig. 7. Bed 44, *hudlestoni* AZ, SQ2, ~1.5 m interval. See Fig. 3 caption for explanation. Sea-level fell then rose within this peak interval (Taylor et al., 2001).

background. *Zspp* is noticeable, and forms a significant (>3%) peak, in the upper half of the section, peaking as *Wbr* slightly increases and *Wb+f* slightly decreases. *Bd*

was not recorded in the LM, whilst all other non-watznaueriacean taxa (including *P. escaigii*) have insignificant occurrences. Generally, preservation is sta-

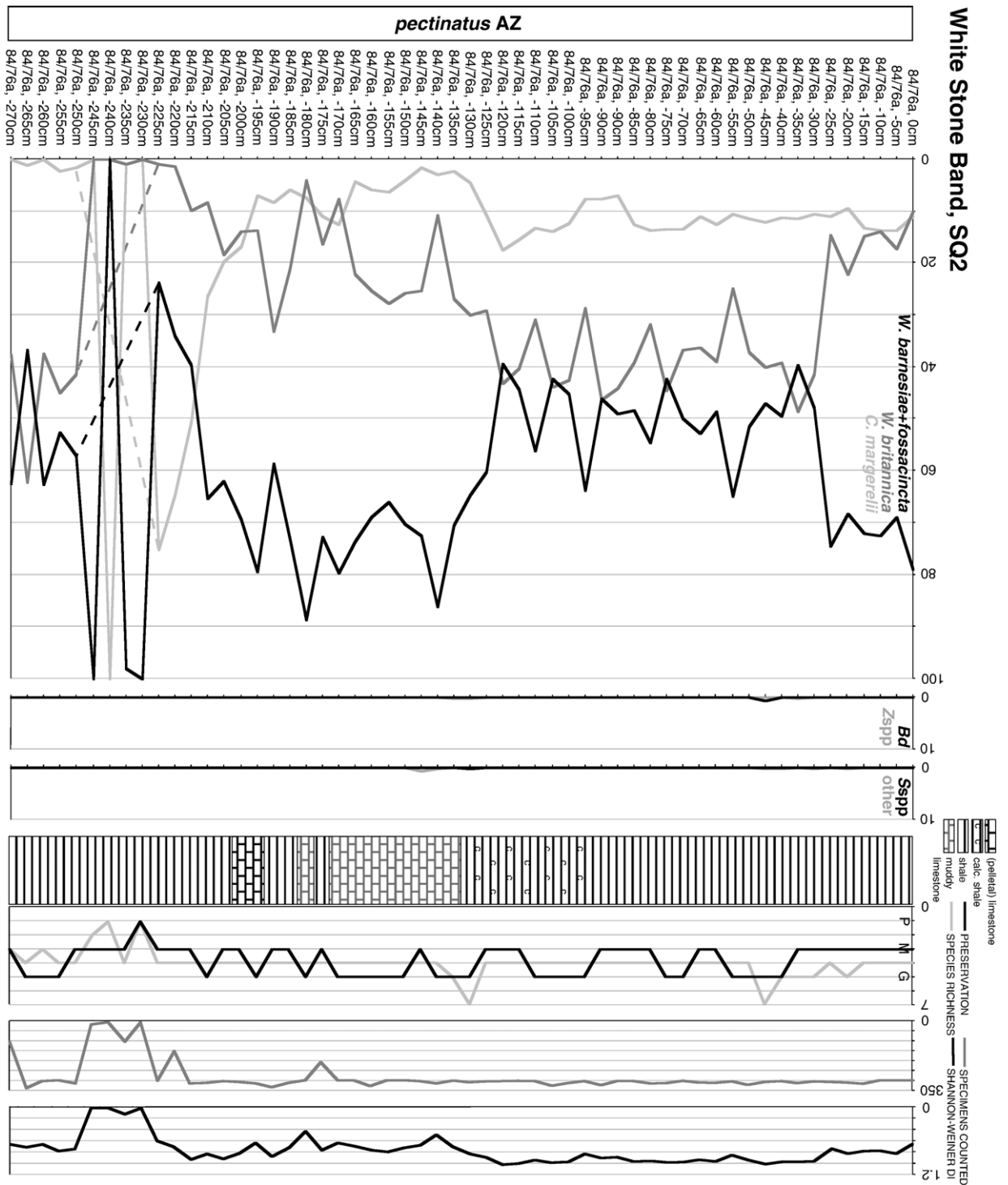


Fig. 8. White Stone Band, *pectinatus* AZ, SQ2, 5 cm interval. See Fig. 3 caption for explanation. Far right: Shannon-Weiner Diversity Index. Sea-level rose then fell during this interval (Taylor et al., 2001).

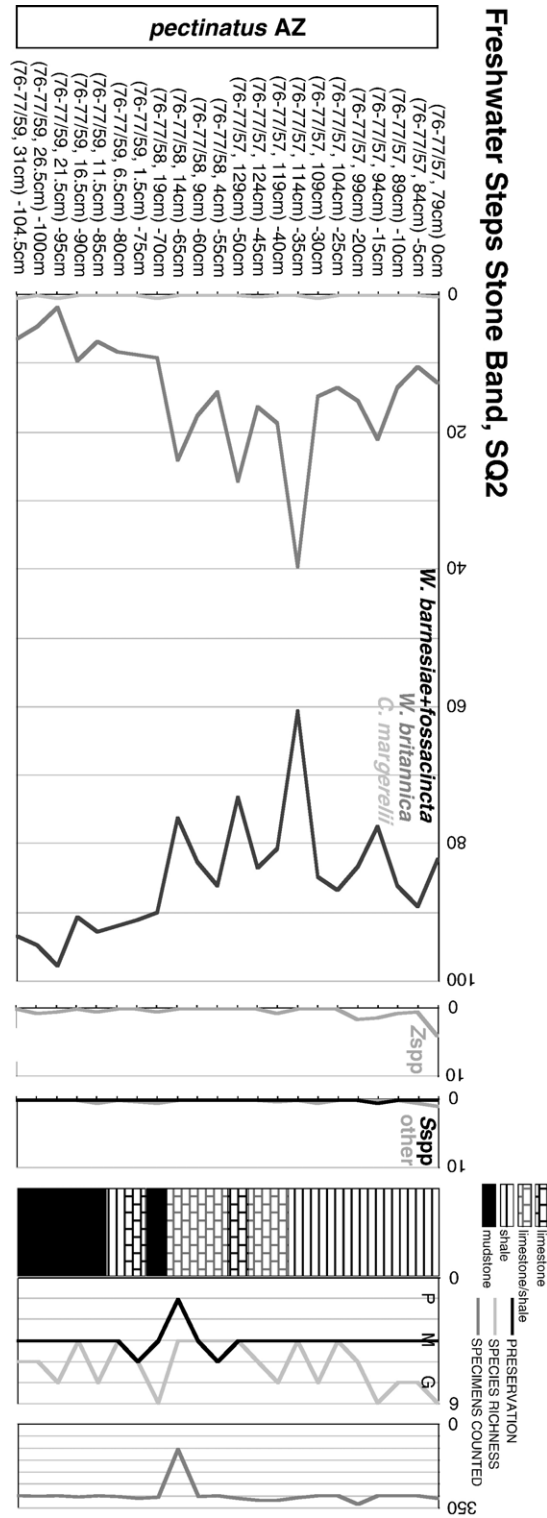


Fig. 9. Freshwater Steps Stone Band, *pectinatus* AZ, SQ2, 5 cm interval. See Fig. 3 caption for explanation. Sea-level rose to a peak, then fell during this interval (Taylor et al., 2001).

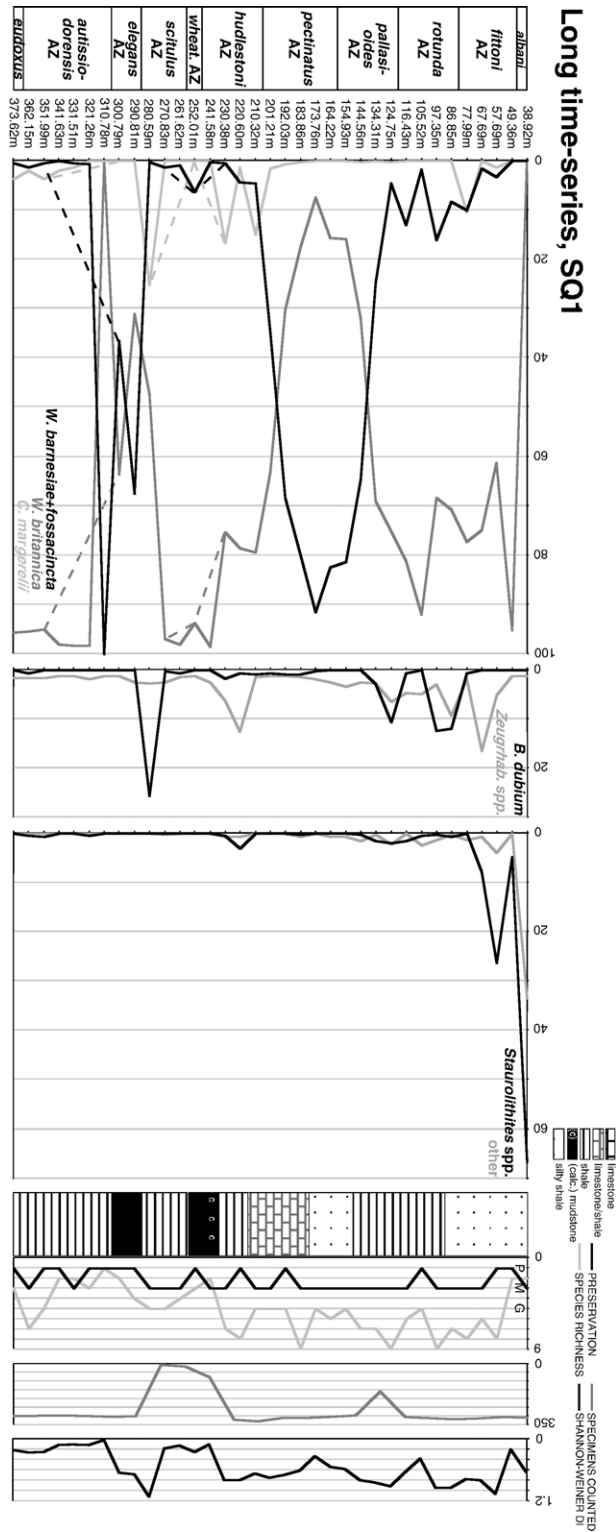


Fig. 10. Long time-series, *eudoxus-albani* AZs, SQ1, ~10 m interval. See Fig. 3 caption for explanation. Far right: Shannon-Weiner Diversity Index.

Ammonite Zone (AZ)	Species richness/AZ		Dominant watznaueriacean/AZ		Secondary watznaueriacean dominance/AZ		Significant (>3%) non-watznaueriacean taxa/AZ					
	5Q1	5Q2	5Q1	5Q2	5Q1	5Q2	5Q1	5Q2	KCF outcrop	Gorodische outcrop		
<i>albani</i>	2	x	x	x	x	x	x	x	x	x	x	
<i>fittoni</i>	2-8	x	x	x	Wbr	Wb+f	x	x	Sspp, Zspp, other	x	x	
<i>rotunda</i>	5-9	x	7-10	13-15	Wbr	Wb+f	x	x	Sspp, Zspp, other	x	x	
<i>pallasioides</i>	5-9	x	3-9	15-16	Wbr&Wb+f	Wbr	x	Wb+f	Bd, Zspp	x	Sspp, Zspp, other	all
<i>pectinatus</i> (White, Freshwater Steps)	5-9	1-7	3-8	17	Wb+f	Wb+f	Wbr	Wbr	Bd, Zspp	x	Sspp, Zspp	Bd, Zspp, other
<i>huddlestoni</i> (Hope Lake Head SB, Bed 2-8)	2-8	1-10	x	13	Wbr	Wbr	x	Wb+f	none (WSB), Zspp (FSSB)	x	none	Bd, Zspp, other
<i>wheatleyensis</i> (Blackstone)	3	0-8	x	15	Wbr	Wbr	x	Wb+f	Zspp, other (FSSB), all (Bed 44)	x	x	Zspp, other
<i>scitula</i>	4-5	x	x	15	Wbr	Wbr	x	Wb+f	Zspp, other	x	x	Zspp, other
<i>elegans</i>	2-4	x	x	x	Wbr&Wb+f	x	x	Wb+f	Bd	x	x	Zspp, other
<i>aufssiodorensis</i>	1-7	x	x	x	Wbr	x	x	Cm	none	x	x	x
<i>eudoxus</i> (oil shale)	3	0-9	x	16-28	Wbr	Wbr	x	Cm	none	x	x	x
									Bd, other (0.5m), Sspp, Zspp (5cm)	x	x	all

Fig. 11. Summary comparison of data between SQ1, SQ2 Boreholes, KCF and Gorodische outcrops.

Long time-series, Dorset outcrop

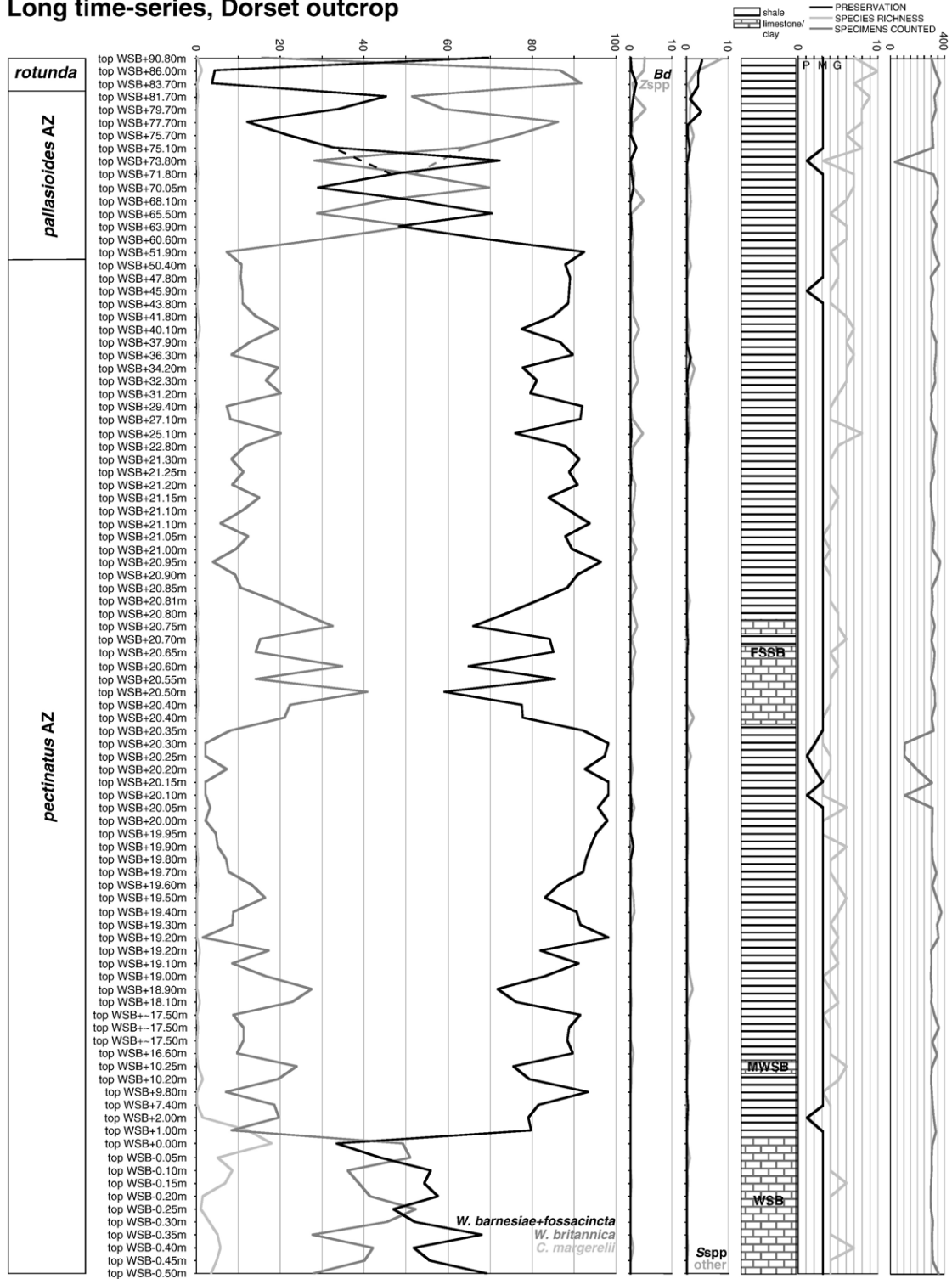


Fig. 12. Long time-series, *pectinatus*–*rotunda* AZs, Dorset outcrop (Rope Lake Head–Freshwater Steps–Chapman’s Pool), 5 cm–5 m interval. See Fig. 3 caption for explanation. Sea-level rose then fell during the *pectinatus* AZ, rose through the *pallasioides* AZ, fell at the base of the *rotunda* AZ, then began to rise again (Taylor et al., 2001).

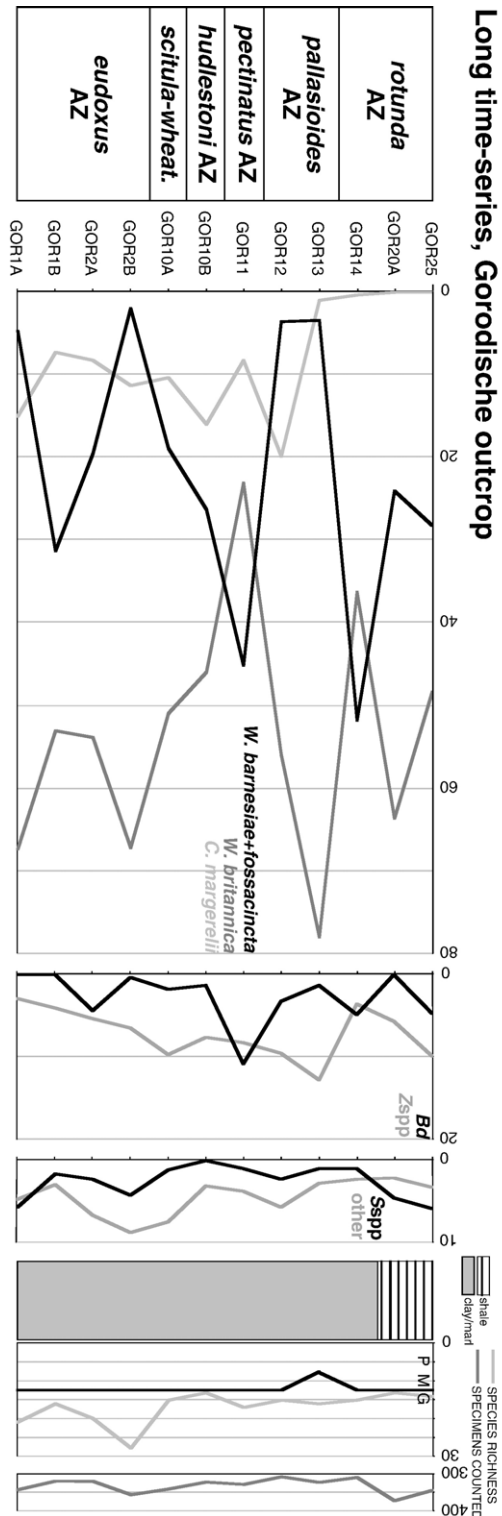


Fig. 13. Long time-series, *eudoxus-rotunda* AZs, Gorodische outcrop, 1–4 samples per AZ interval. See Fig. 3 caption for explanation.

ble through intervals of fluctuating species richness (3–6 taxa), thus there is no particular correlation between the two. No particular correlation with lithology is observable (Fig. 9).

4.8. Long time-series *eudoxus* to *albani* interval (SQ1) – 10 m sample interval

Wbr dominates except through the *elegans* (affected by preservation) and lower *pectinatus*–*pallasioides* AZs, wherein *Wb+f* dominates, or is equally dominant (Fig. 10). *Cm* is sporadically present and constitutes an irregularly peaky background component of the assemblage. Significant (>3%) non-watznaueriacean taxa per AZ are listed in Fig. 11. *Bd* appears to peak as *Wb+f* declines. *Sspp* seems to peak with, or after, *Zspp*. *Zspp* appear to increase in %RA flanking the main peak in *Wb+f* and also generally seem to peak with a decline in *Wb+f*. ‘Other taxa’ (*Cretarhabdus conicus*, *Crucirhabdus primulus*, *E. gallicus*, *Lotharingius crucicentralis*, *S. atmetos*, *S. bigotii bigotii*) are very poorly represented, and have enigmatic distributions, but become more noticeable in the upper half of the section. Species richness is shown in Fig. 11. There is some correlation between preservation and species richness but only in the lower third of the section (*eudoxus*–*wheatleyensis* AZs). There is no consistent correlation with lithology apparent.

4.9. Long time-series *pectinatus* to *rotunda* interval (Dorset outcrop) – c. 5 m to 5 cm sample interval

Wb+f dominates in the *pectinatus* AZ, is equally dominant (with *Wbr*) in the *pallasioides* AZ, whilst *Wbr* dominates in the *rotunda* AZ. Otherwise, *Wbr* constitutes a peaky but consistently present background taxon. *Cm* has a very low %RA virtually throughout, but shows some significant peakiness at the base of the section (White Stone Band, *pectinatus* AZ). Fig. 11 lists the significant (>3%) non-watznaueriacean taxa. *Sspp* are only really noticeable at the top of the section (*pallasioides* and *rotunda* AZs), where they appear to peak as *Wb+f* increases. *Zspp* are relatively consistently present, although enigmatically distributed, and only peak significantly (>3%) in the upper half of the section (*pallasioides* and *rotunda* AZs). ‘Other taxa’ (*Ansulaphaera covingtonii*, *E. gallicus*, *P. escaigii*, *S. atmetos*, *Truncatoscaphus intermedius*) are also rare and sporadically distributed but peak significantly (>3%) in the *rotunda* AZ. Generally, preservation is stable through intervals of fluctuating species richness, thus there is no particular correlation between the two. Species richness

per AZ is shown in Fig. 11. There is no obvious correlation with lithology (Fig. 12).

4.10. Long time-series *eudoxus* to *rotunda* interval (Gorodische outcrop) – AZ sample interval

Although *Wbr* generally dominates the assemblages (~50%), the nannofloras are relatively more even than in the Dorset area. In the *eudoxus*, *pectinatus* and *rotunda* AZs, *Wb+f* either dominate or have more intense peaks. *Cm* is generally subordinate to *Wb+f*, except between these *Wb+f* peaks, especially in the *pallasioides* AZ. All non-watznaueriacean taxa exhibit significant (>3%) peaks at one time or another (listed in Fig. 11). *Bd* peaks in the *pectinatus*–*rotunda* AZs, around the interval of *Wb+f* peaks. *Sspp* peak in the *eudoxus* and *rotunda* AZs, mainly coincident with troughs in *Wb+f* and somewhat mirroring *Cm*. *Zspp* peak in the *eudoxus* and *scitula* through *rotunda* AZs. They are relatively consistently represented, and tend to peak on the flanks of the *Wb+f* peaks. ‘Other taxa’ (*Anfractus* spp. including *Anfractus harrisonii* and *Anfractus* sp., *Axopodorhabdus cylindricus*, *Chiastozygus leptostaurus*, *Crepidolithus* cf. *C. perforata*, *Discorhabdus corollatus*, *E. gallicus*, *Hexalithus cuvillieri*, *Octocyclus decussatus*, *Podorhabdus grassei*, *P. escaigii*, *Retecapsa* cf. *R. schizobrachiata*, *S. atmetos*, *S. bigotii bigotii*, *Stephanolithion brevispinus*, *Stradnerolithus comptus*, *S. fragilis*, *S. geometricus*, *Triscutum* sp., *T. intermedius*, *Truncatoscaphus senarius*) are also consistently present and relatively well-represented. They show a pattern similar to that of *Zspp*. Species richness does not appear to be affected by preservation, and is shown in Fig. 11, per AZ. Notably, the *pectinatus* AZ is dominated by *Wb+f* here as it is in Dorset, although there is no limestone development in the Gorodische samples (Fig. 13).

5. Discussion

The KCF nannofloras represent a record of changing surface-water environments, and this is apparent even through intervals where change is not expressed lithologically. This is most obviously exemplified by the dominance of *Wb+f* in the *pectinatus* AZ in both Dorset and at Gorodische, in differing lithologies. Changes in the nannofloras are most likely related to changing nutrient concentrations, since there is no external evidence for significant temperature, salinity or water–mass circulation implications (see Section 5.2). Several problems remain, however, in interpreting our data, the most important being a lack of data

concerning the productivity dynamics between the dinoflagellate and coccolithophore phytoplankton groups, and the other being the universal predominance of watznaueriacean taxa, to the virtual exclusion of other taxa, including those which might elsewhere be interpreted as fertility-sensitive. Additionally, it must always be remembered that ecological interrelations between taxa are liable to be complicated products of multiple environmental influences, rather than linear responses to single influences, so enigmatic fossil records are almost to be predicted. Consequently, the palaeoenvironmental hypotheses set out below are tentative and require further investigation.

5.1. Nannofossil preservation

Dissolution and overgrowth can change nannofloral assemblage compositions and relative proportions. Here, coccolithophore preservation was assessed on a qualitative scale in all LM slides logged. Fine details of preservation have also been observed in SEM samples (see Lees et al., 2004). All extremes of preservation were observed, from highly etched samples, particularly in the dark lithologies, to pristine preservation in the stone bands, in which rare, delicate, weakly calcified coccolith taxa were present, along with articulated coccospheres containing internal protococcolith rings (Young and Bown, 1991).

In more typical nannofossil assemblages, the validity of using such intervals of variable preservation for palaeoceanographical interpretation would be questioned. However, the KCF assemblages are exceptional, in that the dominant coccoliths in all cases belong to the same family, the Watznaueriaceae (which includes *Watznaueria* and *Cyclagelosphaera*). All these coccolith species have identical rim construction and thus identical preservation potential. The %RA signals between these taxa, therefore, must be a primary signal and cannot have been modified by preservation or diagenesis.

It has been argued that the composition of the preserved nannofossil record is generally remarkably resistant to alteration by preservational changes (Thierstein and Roth, 1991). Even where significant variations in preservation in Mesozoic assemblages have been recorded, the assemblages usually only show abundance fluctuations between *Watznaueria* and all other taxa (Thierstein and Roth, 1991). The abundance of *Watznaueria* has previously been used as a preservation index, based on the assumption that assemblages strongly affected by dissolution will be enriched in this solution-resistant genus (Roth and Bowdler, 1981).

However, there is increasing evidence that *Watznaueria* abundances reflect primary environmental factors, at least in moderately to well-preserved sediments (Watkins, 1989; Erba, 1992; Erba et al., 1992; Williams and Bralower, 1995; Street and Bown, 2000; Cobiainchi, 2002; Negri et al., 2003). The exceptionally rich watznaueriacean assemblages observed in the KCF are a good example of this, since even in exquisitely preserved samples from the stone bands (Lees et al., 2004), the Watznaueriaceae are overwhelmingly dominant. This dominance must be a primary palaeoecological signal rather than a secondary preservational effect, and even in samples which have been affected by deleterious preservation (e.g. in the *eudoxus-elegans* AZs), the %RAs of the dominant species can be assumed to be close to primary proportions. Furthermore, the nannofossil diversities throughout the KCF cannot be explained by preservation because there is generally no correlation between preservation estimates and species richness, and because well-preserved, monospecific assemblages of intact coccospheres have been observed on microlaminar surfaces in the coccolith stone bands (Lees et al., 2004).

5.2. Significance of low-diversity nannofloras

All KCF nannofossil assemblages are extremely low in species richness and are dominated by a very few species. Not even in isolated samples do diversities approach those observed in coeval strata from boreal (e.g. Gorodische) or low latitudes (e.g. DSDP Site 534). Since preservation can be largely discounted as an explanation, and since the KCF basin was not oceanographically isolated, this must represent a primary surface-water signal.

Extant coccolithophores have a widespread oceanic distribution, living in the photic zone and being most diverse at low latitudes (Brand, 1994). Seasonally stable, oligotrophic, tropical and subtropical mid-ocean gyre environments support the highest diversities, but standing crops are low, reflecting low reproduction rates and K-selected strategies (environment-specific specialist). Higher trophic conditions, due to upwelling or deep seasonal mixing, often support high standing-crops dominated by one or a few r-selected species. Continental shelf environments also tend to be unstable and more eutrophic in nature and support distinctive assemblages, including some taxa that do not live in open-ocean environments.

The dominance of watznaueriacean coccolithophores in the KCF is comparable to extant assemblages that are often dominated by one or two genera of the family

Noelaerhabdaceae, particularly *Emiliania huxleyi*, but also *Gephyrocapsa*. *E. huxleyi* has the broadest ecological tolerances of any living species and has been interpreted as r-selected (growth maximising or opportunistic), in terms of its ecological strategy. The ubiquitous and abundant occurrence of *Watznaueria* through much of the Mesozoic also indicates a broad palaeoecological range, and it is almost certainly r-selected (see also Mutterlose, 1996; Street and Bown, 2000; Cobianchi, 2002; Negri et al., 2003). In addition, it has been suggested that the placolith morphology, possessed by both *Emiliania* and *Watznaueria*, is associated with an r-selected strategy (Young, 1994).

Virtually monospecific assemblages of *Emiliania huxleyi* are well-documented from the Black Sea (e.g. Hay, 1988; Hay et al., 1990, 1991), where salinity may well be the dominant diversity-limiting factor, although these waters are also high in nutrients. Previous models of the KCF basins have addressed both these factors, and most dismiss salinity as a major control; Tyson et al. (1979) particularly argued that the development of a significant, long-term, widespread halocline in the broad, epeiric Kimmeridgian sea was highly unlikely. Palynological data (J. Riding, personal communication, 1999) also suggests relatively normal surface-water salinities; the dinoflagellates are normal marine and counts of freshwater/brackish algal taxa such as *Botryococcus*, *Micrhystridium*, etc., are low. There is also little to support unusual salinities from other fossil groups (e.g. Wignall, 1990).

Gröcke et al. (2003) determined a slight cooling trend in the latest Jurassic (c. mid-*pectinatus* to mid-*fittoni* AZs) in the Volga Basin, correlatable with postulated cooling based on nannofossil abundances (Mutterlose in Ruffell et al., 2002). In some agreement, $\delta^{18}\text{O}$ data from belemnite rostra indicate relatively stable palaeotemperatures through the Kimmeridgian (16–19 °C), with a slight decline (15–17 °C) in the Volgian (Riboulleau et al., 1998). Our data does not appear to show any obvious correlation with this trend, however, and so temperature is dismissed as a significant controlling factor on the KCF assemblages.

The KCF basin was open to surface-water-mass exchange with both the Volga Basin to the north-west and the North Atlantic to the south-east, all locations having taxa in common, particularly the biostratigraphical marker species. As illustrated in Chambers et al. (2000, Fig. 3), the KCF and Volga Basins were located on a broad shelf, the relief comprising an archipelago of low massifs. Consequently, we do not believe that restricted circulation was the cause of the patterns we have recorded.

The possibility of surface-waters enriched (at least periodically) in nutrients, is, however, a concept almost universally embraced by KCF-environment modellers, and it is this scenario which we believe best fits the nannofossil data. Low diversity assemblages, dominated by one, r-selected taxon, would be supported by consistently (or at least seasonally) higher-trophic surface-water conditions, and if these conditions were extreme enough, then they might feasibly exclude most other taxa. Nutrient supply could primarily be sourced from terrestrial runoff, but effective recycling of organic matter in the KCF basin may have amplified this source, and individual species of nannoplankton may have been adapted to exploiting a deeper nutricline. Models explaining anoxia and organic-matter preservation in the KCF basin provide plausible mechanisms for surface-water replenishment of nutrients. Tyson et al. (1979) postulated that rhythmic lithological variation was the result of vertical movement of the $\text{O}_2/\text{H}_2\text{S}$ interface in a temporarily stratified water-column; when it reached a level where convective or turbulent mixing processes could provide its nutrients to the euphotic zone, coccolith blooms could have resulted, such as those responsible for the stone bands. However, this mechanism is too broad to account for all the different patterns of coccolithophore %RA through the differing lithologies of the KCF.

Using modern nannoplankton distributions as an analogue, it would appear that the anomalously low nannofossil diversity in the KCF can best be explained by sustained (long-term) elevated-nutrient (relative to open-ocean) euphotic zone environments, which supported the eurytopic watznaueriaceans (along with dinoflagellates) but excluded most open-ocean taxa.

However, it cannot be ruled out that sea-level was a factor in the patterns we have observed. Sea-level fluctuated throughout KCF deposition. According to Taylor et al. (2001), based on 3rd-order sequence stratigraphic cycles determined from the KCF, there is a pattern of: incremental rises from the *baylei* through *mutabilis* AZs, with falls marking the base of each AZ; sustained deepening of the basin through the *eudoxus* and *autissiodorensis* AZs; incremental rises through the *elegans/scitulus* and *wheatleyensis* AZs, with a small fall marking the base of the latter AZ. Sea-level peaked in the lower *huddlestoni* AZ (Rope Lake Head Stone Band), followed by incremental falls: a fall follows the *huddlestoni* peak; a rise through the upper *huddlestoni* into the *pectinatus* AZ was followed by a fall at the end of the latter, with

stepwise rises and falls to the *albani* AZ. We discuss the ramifications of this below.

5.3. KCF palaeoenvironments and coccolithophore palaeoecology

The KCF nanofossil assemblages are all dominated by the family Watznaueriaceae, with varying proportions of three taxa: *Watznaueria britannica* (*Wbr*), *W. barnesiae*+*fossacincta* (*Wb+f*) and *Cyclagelosphaera margerelii* (*Cm*). The dominance of this family is a well-known feature of Mesozoic assemblages. In broad terms, *Wbr* tends to characterise Jurassic assemblages and *Wb+f*, Cretaceous assemblages; *Cm* is not as consistently dominant, but rather forms stratigraphically restricted acme intervals in both the Jurassic, Cretaceous and post-Cretaceous/Tertiary boundary Danian. It seems apparent that all these taxa occupied a heightened-trophic environment (relative to the open ocean) during KCF deposition. The significant variations in abundance between the species likely then reflect different adaptations within an r-selected ecological strategy. (A summary and further discussion concerning the palaeoecology of *Watznaueria* is provided by Lees et al., 2005.)

The KCF nanofossil signal is mainly characterised by the interplay of *Wbr* and *Wb+f*, and occasionally of *Cm*. The lowest species richness and diversity are generally recorded during intervals of *Wbr* dominance. *Wbr* dominates the organic-rich lithologies (e.g. the *eudoxus* oil-shale and Blackstone: Figs. 3–4 and 5, respectively). Limestone lithologies of the *pectinatus* AZ (e.g. the White and Freshwater Steps Stone Bands: Figs. 8 and 9, respectively) are associated with high *Wb+f*. Peaks of *Cm* dominance occur sporadically throughout KCF lithologies but not in the upper coccolith stone bands (e.g. the Middle White and Freshwater Steps Stone Bands: Fig. 10, *pectinatus* AZ).

Therein lies the dilemma in our interpretation of the assemblages: are higher nutrient concentrations indicated by lowest diversities (and potentially higher dinoflagellate productivity), as in the dark lithologies of the KCF, or by highest productivity, as suggested by Pearson et al. (2004) for the stone bands? The dark lithologies, with the lowest diversity assemblages, are herein generally interpreted as representing the highest trophic levels of the KCF environments. These environments probably supported enhanced organic-matter production, most likely by dinoflagellates (e.g. Saelen et al., 2000). The coccolith flux has been diluted by organic matter and clay, but may also have suffered some dissolution; diversity reduction cannot be entirely dis-

missed but it is generally not apparent from comparison of preservation estimates with species richness. Although preservation may have affected diversity, the dominance of *Wbr* is not in doubt, and this species may thus be interpreted as occupying the higher end of the watznaueriacean trophic spectrum. In support of this interpretation, perhaps, Chambers et al. (2000) found a correlation between coccolith Ca (presumably from *Wbr*) abundance and occurrences of Na, P and K at the base of the *wheatleyensis* AZ. They postulated that these nutrients triggered ‘blooms’ (preserved as faecal pellets).

In the *eudoxus* oil-shale (Fig. 4) and, to a lesser extent, the Blackstone (Fig. 5, *wheatleyensis* AZ), the rapid switches between *Wbr* and *Cm* suggest that these species may have been similarly adapted to higher-trophic conditions. Although these particular data sets are hampered by low specimen counts, causing some artificial peaks, if we invoke the argument that the taxa had similar preservation potential, then a comparison between the two intervals indicates that *Cm* was more abundant during the *eudoxus* interval (when sea-level was rising) than during the *wheatleyensis*/Blackstone interval (peak sea-level). This implies that *Cm* might be a more proximal taxon than *Wbr*. Potentially in support of this, Taylor et al. (2001) recorded a fall in sea-level within the *hudlestoni* AZ highstand; in Bed 44 (Fig. 7), there is an interval dominated by *Cm*. *Cm* was identified as the dominant species in a Kimmeridgian lagoonal/ramp environment in the French Southern Jura by Tribouillard et al. (1992), suggesting tolerance for extreme nearshore conditions. Bown (2005) has suggested that the very few survivors of the Cretaceous/Tertiary boundary nanoplankton mass extinction were unusual and/or neritic(-tolerant) taxa, and *Cyclagelosphaera* was one of those. These factors lead us to tentatively suggest that *Cm*, not *Wbr*, might be the prime opportunist in the plexus, and thus tolerant of the highest trophic levels.

Although slightly higher diversities are recorded in the coccolith stone bands than elsewhere in the KCF (White, Middle White, Freshwater Steps: Fig. 10), these are still very low, clearly indicating ecological exclusion of most open-ocean taxa, and so again suggest an elevated trophic environment. However, here *Wb+f* is the dominant taxon, and coccolith productivity dominated over dinoflagellate production and clay accumulation, at least intermittently (for example, see individual laminae in Lees et al., 2004), perhaps suggesting a preference for lowered, but still high, trophic levels, but probably more importantly, increased water-column turbulence. At high resolution,

there is quite a strong correlation between abundant *Wb+f* and the limestone lithologies, with sharp rises and declines marking the bottom and top of the White Stone Band (Fig. 8). At lower resolution, however, *Wb+f* dominates over much broader intervals than just the stone bands, suggesting that environments favourable to its success did not always result in limestone deposition (Fig. 10). On the finer-scale at least, the *Wb+f* signal appears to be related to well-oxygenated episodes in the KCF water-column: in the stone bands, putative bloom accumulations are associated with faecal pellets from pelagic grazers and, at lower resolution, the coccolith stone bands show clear signs of bioturbation, implying amelioration of otherwise anoxic water-column conditions.

The most even assemblages observed were recorded in Bed 44 (Fig. 7), an interval of relatively low TOC in the sediments (Morgans-Bell et al., 2001). Coccolith diversity was still low, and the dominance of *Wbr* and *Cm* may suggest higher-trophic environments, based on our interpretations herein. However, there is also relatively systematic variability, and relatively significant peaks, in other, lower-abundance taxa, which is not seen so clearly elsewhere in the KCF. This is particularly interesting as it includes taxa that, in Lower Cretaceous studies, have been recognised as putative surface-water fertility-indices (*Biscutum* and *Zeughrabdoutus*). In particular, a *Cm* peak is straddled by peaks in *Bd* and *Zspp*. Although these records are not directly comparable with Cretaceous ones, where different *Biscutum* and *Zeughrabdoutus* species often show abundances in excess of those of *Watznaueria* in eutrophic settings (e.g. Roth and Bowdler, 1981), they may indicate that these genera were able to exploit these higher-nutrient environments under particular conditions, similarly to their Cretaceous morphological counterparts, during Bed 44 deposition.

Whilst all three watznaueriacean species dominate at some stage within these low-diversity assemblages, indicating an ability to thrive in stressful, heightened-trophic surface-waters, there is evidence to suggest that they occupied slightly different positions along a trophic preference continuum. Arguably, *Wbr* dominated in the highest trophic environments, which supported the lowest diversities, and *Wb+f* dominated in lower high-trophic environments, with *Cm* taking advantage of particular conditions in the highest trophic/?lowest sea-level environments. Pittet and Mattioli (2002) reached a similar conclusion regarding the relative trophic positions of *Wbr* and *Wb+f*, based on analysis of a lower latitude, deep shelf, Oxfordian section, although their reasoning was largely based

on nannofossil abundance and sedimentological observations without recourse to interpretation based on diversity.

It is acknowledged that interpretation of the diversity data is not unambiguous. Intervals of very low diversity *may* have been affected by preservation, and species richness *is* extremely low throughout. Therefore, our interpretations of the precise nature of the ecological adaptations of the watznaueriacean coccoliths should be viewed with caution. In many respects, bloom behaviour (in modern settings prompted by increased nutrient concentrations related to water-column turbidity) is best demonstrated for *Wb+f* on the coccolith stone band microlaminae (Lees et al., 2004), and integrated sedimentological (microfacies) and palynological research by Pearson (2000) suggested that it was the *stone bands* that represented periods of highest productivity, generated by storm-induced water-column mixing bringing euxinic water into the photic zone (Pearson et al., 2004). This is in agreement with Lees et al. (2004), but contradictory to our current interpretations!

Finally, it is interesting to note that the KCF time-interval represented the final period of dominance for *Wbr*, prior to its decline across the Jurassic/Cretaceous boundary, and subsequent replacement by *Wb(±f)*. The observations herein thus represent the interplay between declining and ascendant species. Similar successions of interfamilial replacement are clearly demonstrated through the Neogene and Quaternary by the Family Noelaerhabdaceae, although the causes of these shifts are not yet understood (Young, 1990). In the Late Jurassic, it is unclear whether the decline of *Wbr* was evolutionary, reflecting interspecific competition, or ecological, corresponding to broad palaeoceanographical changes; i.e. whether *Wbr* was replaced ecologically by *Wb(+f)*, or whether the ecological niche it inhabited disappeared or was no longer occupied by coccolithophores. Interestingly, *Wbr* did not become extinct at this time but was rare through the Early Cretaceous, only becoming conspicuous again in the mid-Cretaceous, reappearing globally just prior to OAE1a (Bown et al., 1998; Bown, personal observations, 2003) before final extinction in the earliest Cenomanian (e.g. Burnett, 1998). *Cm* was a long-ranging taxon which, although rarely dominant through the Cretaceous, did show distinct acme intervals, and a number of these were associated with periods of organic-rich sediment deposition, for example, the Blatterton (Barremian) and Fischechiefer (Early Aptian) in the North Sea Basin (Bown et al., 1998). Notably, this genus/species survived the Cretaceous/Tertiary boundary mass extinction (which wiped out ~93% of all

nannoplankton species; Bown et al., 2004) and was locally abundant immediately afterwards along with neritic, opportunistic forms (Bown, 2005), supporting the interpretation of this species as an ultimate opportunistic taxon.

6. Conclusions

Relative abundances and low diversities in the KCF are considered to provide robust environmental signals, unaffected by preservation. The Watznaueriaceae all have similar rim architecture, and thus original proportions would not be susceptible to differential preservation, and because virtually monospecific abundances of exceptionally well-preserved coccolithophores have been observed on individual laminae in the SEM.

The entire KCF is characterised by low coccolithophorid species richness and distinctive unevenness. It differs markedly from coeval sections, such as Gorodische and DSDP Site 534, where diversity is higher and the assemblages more even.

By analogy with modern, low-diversity nannoplankton assemblages, KCF euphotic environments are interpreted as continuously highly-trophic, possibly eutrophic, and the watznaueriacean taxa as ecologically r-selected.

The KCF is alternately dominated by either *W. britannica* or *W. barnesiae*+*fossacincta* or, to a lesser degree, *C. margerelii*. Dark, organic-rich lithologies are generally dominated by *W. britannica* or *C. margerelii*. These were deposited under anoxic bottom-water conditions (e.g. little/no evidence of bioturbation), in which dinoflagellates are suspected of being the major phytoplankton primary producer (very few coccolithophore blooms), which would indicate an elevated high trophic level and a stratified water-column (evidenced by water-column anoxia, lowest coccolithophore diversities, and because modern dinoflagellates dominate in stable, stratified, high-nutrient environments). The coccolith stone bands are dominated by *W. barnesiae*+*fossacincta*. These were deposited under oxygenated conditions (evidence of bioturbation), in which coccolithophores appear to have been the major phytoplankton primary producer, at least seasonally (evidence from seasonal blooms), thus possibly indicating a reduced, yet still high, trophic level (cf. modern bloom dynamics). Consequently, we tentatively postulate that *W. britannica* and *C. margerelii* occupied a higher trophic position than *W. barnesiae*+*fossacincta*, *C. margerelii* being the most r-selected and responding to possibly more extreme nitrification intervals and/or lowered sea-levels.

Biscutum dubium, *Staurolithites* spp. and *Zeughrabdotus* spp. show relatively significant (c. 3–10%) abundance peaks throughout the KCF, which appear to be linked to switchovers between the dominant watznaueriaceans. This may indicate that these taxa respond to fertility signals in similar ways to their morphological counterparts in Cretaceous sediments.

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References

- Backman, J., Shackleton, N.J., 1983. Quantitative biochronology of Pliocene and early Pleistocene calcareous nannofossils from the Atlantic, Indian and Pacific oceans. *Marine Micropaleontology* 8, 141–170.
- Bornemann, A., Mutterlose, J., submitted for publication. Size analyses of the coccolith taxa *Biscutum constans* and *Watznaueria barnesiae* from the Late Albian 'Niveau Breistroffer' (SE France): taxonomic and palaeoecological implications. *Geobios*.
- Bown, P.R. (Ed.), 1998. *Calcareous Nannofossil Biostratigraphy*, British Micropalaeontological Society Publications Series. Chapman and Hall/Kluwer Academic Publishers, London.
- Bown, P.R., 2005. Selective calcareous nannoplankton survivorship at the Cretaceous/Tertiary boundary. *Geology* 33 (8), 653–656.
- Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*, British Micropalaeontological Society Series. Chapman and Hall/Kluwer Academic Press, London, pp. 34–85.
- Bown, P.R., Young, J.R., 1998. Techniques. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*, British Micropalaeontological Society Series. Chapman and Hall/Kluwer Academic Press, London, pp. 16–28.
- Bown, P.R., Rutledge, D.C., Crux, J.A., Gallagher, L.T., 1998. Lower Cretaceous. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*, British Micropalaeontological Society Series. Chapman and Hall/Kluwer Academic Press, London, pp. 86–131.
- Bown, P.R., Lees, J.A., Young, J.R., 2004. Calcareous nannoplankton evolution and diversity through time. In: Thierstein, H.R., Young, J.R. (Eds.), *Coccolithophores—From Molecular Processes to Global Impact*. Springer, Berlin, pp. 481–508.
- Bralower, T.J., Monechi, S., Thierstein, H.R., 1989. Calcareous nannofossil zonation of the Jurassic/Cretaceous boundary interval and correlation with the geomagnetic polarity timescale. *Marine Micropaleontology* 14, 153–235.

- Brand, L.E., 1994. Physiological ecology of marine coccolithophores. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, pp. 39–49.
- Burnett, J.A. (with contributions from Gallagher, L.T. and Hampton, M.J.), 1998. Upper Cretaceous. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropalaeontological Society Series, Chapman and Hall/Kluwer Academic Press, London, pp. 132–199.
- Chambers, M.H., Lawrence, D.S.L., Sellwood, B.W., Parker, A., 2000. Annual layering in the Upper Jurassic Kimmeridge Clay Formation, UK, quantified using an ultra-high resolution SEM–EDX investigation. *Sedimentary Geology* 137, 9–23.
- Cobianchi, M., 2002. I nannofossili calcarei del Giurassico medio e superiore del Bacino di Belluno (Alpi Calcaree Meridionali). *Atti Ticinensi di Scienze della Terra* 43, 3–24.
- 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.
- Gallois, R.W., 1976. Coccolithic blooms in the Kimmeridge Clay and origin of North Sea oil. *Nature* 259, 473–475.
- Gallois, R., 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., Medd, A., 1979. Coccolith-rich marker-bands in the English Kimmeridge Clay. *Geological Magazine* 116, 247–334.
- Gröcke, D.R., Price, G.D., Ruffell, A.H., Mutterlose, J., Baraboshkin, E., 2003. Isotopic evidence for Late Jurassic–Early Cretaceous climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology* 202, 97–118.
- Hay, B.J., 1988. Sediment accumulation in the central western Black Sea over the past 5100 years. *Paleoceanography* 3, 491–508.
- 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.
- Kent, D.V., Gradstein, F.M., 1985. A Cretaceous and Jurassic geochronology. *Bulletin of the Geological Society of America* 96, 1419–1427.
- Lees, J.A., Bown, P.R., Young, J.R., Riding, J.B., 2004. Evidence for annual records of phytoplankton productivity in the Kimmeridge Clay Formation coccolith stone bands (Upper Jurassic, Dorset, UK). *Marine Micropaleontology Special Issue* 52, 29–49.
- Lees, J.A., Bown, P.R., Mattioli, E., 2005. Problems with proxies? Cautionary tales of calcareous nannofossil palaeoenvironmental indicators. *Micropaleontology* 51 (4), 333–343.
- 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.
- Mutterlose, J., 1996. Calcareous nannofossil palaeoceanography of the Early Cretaceous of NW Europe. *Mitteilungen der Geologisches—Paläontologisches Institut, Univ. Hamburg* 77, 291–313.
- Negri, A., Cobianchi, M., Luciani, V., Fraboni, R., Milani, A., Claps, M., 2003. Tethyan Cenomanian pelagic rhythmic sedimentation and Pleistocene Mediterranean sapropels: is the biotic signal comparable? *Palaeogeography, Palaeoclimatology, Palaeoecology* 190, 373–397.
- Noël, D., 1973. Nannofossiles calcaires de sédiments jurassiques finement laminés. *Bulletin du Muséum National d'Histoire Naturelle 3e serie* 75, 95–156.
- Oschmann, W., 1990. Environmental cycles in the Late Jurassic north-west 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. Unpubl. PhD thesis, Univ. of Southampton, UK.
- Pearson, S.J., Marshall, J.E.A., Kemp, A.E.S., 2004. The White Stone Band of the Kimmeridge Clay Formation, an integrated high-resolution approach to understanding environmental change. *Journal of the Geological Society (London)* 161, 675–683.
- 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.
- Riboulleau, A., Baudin, F., Daux, V., Hantzpergue, P., Renard, M., Zakharov, V., 1998. Évolution de la paléotempérature des eaux de la plate-forme russe au cours du Jurassique supérieur. *Comptes Rendus de l'Académie des Sciences, Paris. Sciences de la Terre et des Planetes* 326, 239–246.
- Roth, P.H., 1978. Cretaceous nannoplankton biostratigraphy and oceanography of the northwestern Atlantic Ocean. *Initial Reports of the DSDP* 44, 731–760.
- Roth, P.H., Bowdler, J.L., 1981. Middle Cretaceous calcareous nannoplankton biogeography and oceanography of the Atlantic Ocean. *SEPM, Special Publication* 32, 517–546.
- Ruffell, A.H., Price, G.D., Mutterlose, J., Kessels, K., Baraboshkin, E., Gröcke, D.R., 2002. Palaeoclimate indicators (clay minerals, calcareous nannofossils, stable isotopes) compared from two successions in the Late Jurassic of the Volga Basin (SE Russia). *Geological Journal* 37, 17–33.
- Saelen, G., Tyson, R.V., Telnaes, 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.
- Street, C., Bown, P.R., 2000. Palaeobiogeography of Early Cretaceous (Berriasian–Barremian) calcareous nannoplankton. *Marine Micropaleontology* 39, 265–292.
- Taylor, S.P., Sellwood, B.W., Gallois, R.W., Chambers, M.H., 2001. A sequence stratigraphy of the Kimmeridgian and Bolonian stages (Late Jurassic): Wessex–Weald Basin, southern England. *Journal of the Geological Society (London)* 158, 179–192.
- Thierstein, H.R., Roth, P.H., 1991. Stable isotopic and carbonate cyclicity in Lower Cretaceous deep-sea sediments: dominance of diagenetic effects. *Marine Geology* 97, 1–34.
- Tribouillard, N.-P., Gorin, G.E., Belin, S., Hopfgartner, G., Pichon, R., 1992. Organic-rich biolaminated facies from a Kimmeridgian lagoonal environment in the French Southern Jura mountains — a way of estimating accumulation rate variations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 99, 163–177.
- 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.

- Watkins, D.K., 1989. Nannoplankton productivity fluctuations and rhythmically-bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous). *Palaeogeography, Palaeoclimatology, Palaeoecology* 74, 75–86.
- Wignall, P.B., 1989. Sedimentary dynamics of the Kimmeridge Clay: tempest and earthquakes. *Journal of the Geological Society (London)* 146, 273–282.
- 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. *Paleoceanography* 10, 815–839.
- Young, J.R., 1990. Size variations of Neogene *Reticulofenestra* coccoliths from Indian Ocean DSDP cores. *Journal of Micropalaeontology* 9, 71–86.
- Young, J.R., 1994. Functions of coccoliths. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, 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.