

The ecological significance of foraminifera in the Kimmeridgian of Southern England

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ABSTRACT

This study investigates the nature of the benthic habitat of the foraminifera found in the Kimmeridgian of Southern England. A detailed foraminiferal study of the Black Stone Band has been carried out. Foraminifera are abundant but of low diversity. The assemblages are dominated by five genera; *Reophax*, *Ammobaculites*, *Kutsevella*, *Textularia* and *Trochammina*.

The foraminifera found were exaerobic, being perched between anoxic sediments and the dysoxic water column. They were able to withstand fluctuating oxygen levels, and are termed poikiloaerobic.

The foraminiferal and lithological evidence strongly suggests the presence of microbial mats on the surface of the sediment. This provides an answer to the long-standing enigma of the presence of a strong anoxic signal in the Kimmeridge Clay and yet an abundance of benthic foraminifera.

INTRODUCTION

This study concerns the Kimmeridge Clay Formation of the Wessex Basin in Southern England. The formation consists of grey to black clays and shales, and corresponds to the Jurassic Kimmeridgian (British) Stage. It was deposited in an epicontinental sea of varying depth, within a subsiding basin.

The palaeoecology and palaeobiology of Kimmeridgian foraminifera is poorly known, and relies heavily on taxonomic uniformitarianism. This approach assumes that the mode of life of the fossil species is similar to that of the living organism of the same genus or morphology. This approach has several weaknesses, the major problem being the assumption that evolution has stood still and that the mode of life of species have not changed over millions of years.

Until the works of Alve (1990, 1994), Bernhard & Reimers (1991), Bernhard & Alve (1996), Kaminski *et al.* (1995), and Bernhard (1996), little evidence for agglutinated foraminiferal tolerance of oxygen depleted environments had been put forward. This has caused considerable problems for foraminiferal workers as parts of the Jurassic, despite containing large numbers of agglutinated foraminifera, are extremely organic-rich, and are therefore believed to have been deposited in dysaerobic or anaerobic environments. The Kimmeridgian seas have no precise modern analogues, and any comparison with Recent environments must be made with caution.

The British Geological Survey borehole at Tisbury Wiltshire (Figure 1) is ideal for detailed micropalaeontological analysis due to the lack of

any obvious tectonic disturbance. The Black Stone Band (BSB) was chosen for particular attention because of its lateral persistence, and because of its organic-rich lithology containing extractable foraminifera. The BSB is located at the boundary between the *wheatleyensis* and *hudlestoni*

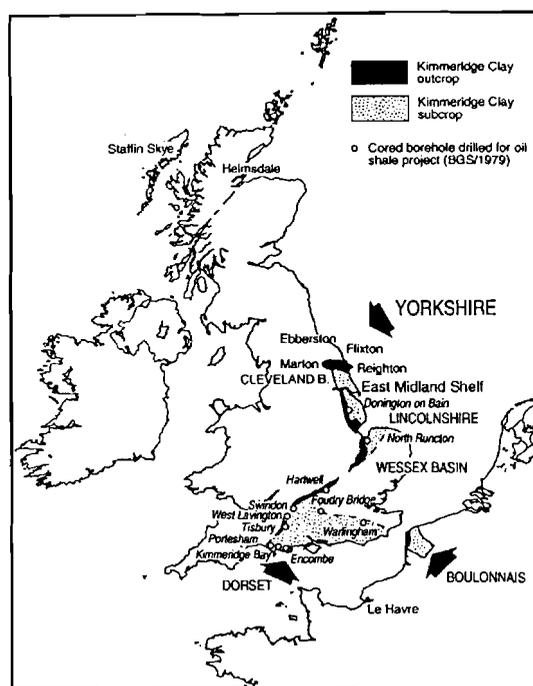


Figure 1. Locations of the Kimmeridge Clay outcrop and subcrop for the United Kingdom and France; after Herbin *et al.* (1995).

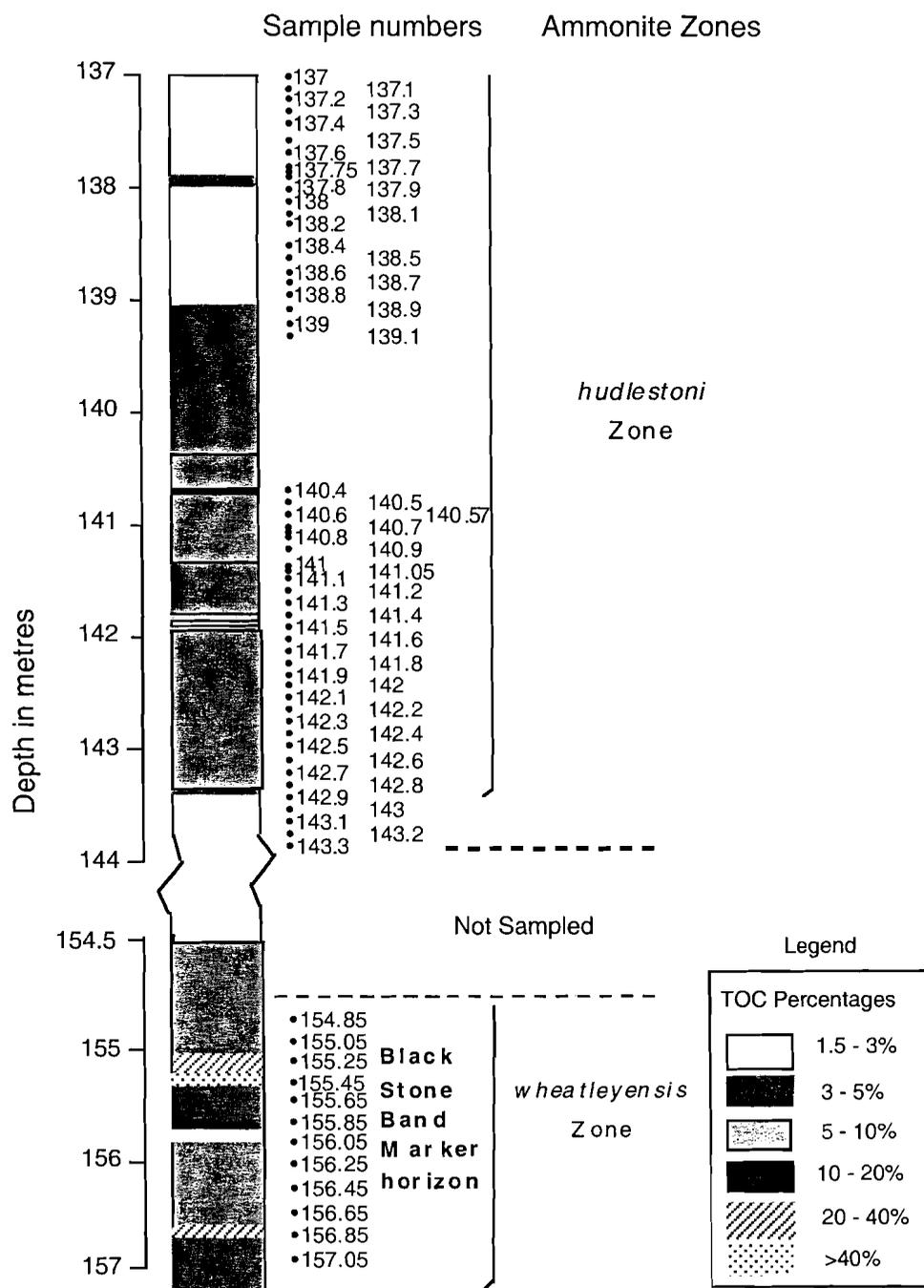


Figure 2. Log of the section of core from the Tisbury Borehole sampled in this investigation.

ammonite Zones. A further 6 m interval within the *hudlestoni* Zone, and above the BSB was also sampled (Figure 2). The aim of this project was to interpret the palaeoecology and palaeoenvironment at the time of deposition of these sedimentary successions.

Geological and Depositional Setting

During the Kimmeridgian, large areas of Southern England were covered by warm epicontinental seas, which generally deepened towards the south. Local and regional highs are thought to have been present owing to differential rates of subsidence within the continental crust (Miller, 1990). The region is

thought to have been undergoing rapid extension in the Late Jurassic (Chadwick, 1986, Chadwick *et al.*, 1989) which led to subsidence. It is also suggested that there was an eustatic sea level rise. These two factors are thought to have led to an increase in the extent of transgression and increase in accommodation space. During this period there are thought to have been a number of islands forming an archipelago that caused a restriction in the oceanic circulation within the Wessex Basin.

It has been suggested by Parrish *et al.* (1982), Partington (1983) and Miller (1990) that the climate of the post-*hudlestoni* zone was arid to semi-arid. This would have caused sediment starvation within

the basin, thereby creating low deposition rates, leading to condensation of sequences. It is thought that the above processes led to stagnation of the water column, and the deposition of organic-rich sediments.

Sedimentology

The sediments of the core section are shales. On visual inspection these shales can only be differentiated by colour (Figure 2), which reflects the amount of organic carbon and pyrite contained in the rock. A rough guide to this is as follows: light grey (1-3% TOC), graphite grey (4-8% TOC), black or near black (>9% TOC).

When cleaned, samples with the highest TOC, $\geq 40\%$, are seen to be brown, and less dense than samples with lower TOC values. During acidification, as a precursor to elemental analysis, it could be seen through differing amounts of effervescence, that some samples contained greater quantities of calcium carbonate than others, although this could not be seen through visual inspection alone.

History of research

Upper Jurassic foraminiferal taxonomy has been studied by Barnard (1953), Lloyd (1958, 1959, 1962), Cordey (1962), Dain (1972), Nørling (1972), Barnard, Cordey & Shipp (1981), Barnard & Shipp (1981), Løfaldi & Nagy (1981, 1983), and Neagu & Neagu (1995).

Work on the palaeoecology of Jurassic foraminifera has been conducted by Løfaldi & Nagy (1983), Nagy (1985, 1992), Nagy *et al.* (1984, 1988, 1990, 1995), Nagy & Johansen (1989), Bernhard (1986), and by Gregory (1989). Jurassic foraminiferal stratigraphic work has been undertaken by Dain (1972), and Løfaldi & Nagy (1980), and by Nagy *et al.* (1990).

Stratigraphical analysis on the Kimmeridgian has been conducted by Arkell (1933), Gallois & Cox (1974), and by Cox & Gallois (1981). Models of the Kimmeridgian seas have been proposed by Hallam (1975), Tyson *et al.* (1979), Oschmann (1988, 1990), Miller (1990), and by Wignall (1991).

METHODS

Processing for foraminifera.

The Tisbury core was sampled at 10 cm intervals taking samples of between 3 g and 8 g, but predominately between 4-6 g. Samples were dried in an oven at 60°C for 48 hours, then placed in a solution of sodium hexametaphosphate (Calgon) for 24 hours. The concentration found to be most effective, and causing least damage to the foraminiferal tests, was 2.5 g/l of water. Calgon softens the clay, enabling it to be washed away using water. Full disaggregation occurs only in the clays with the least organic carbon content. The disaggregated samples were then sieved over a 63 μm sieve. This process was repeated until full disaggregation had occurred.

At least 250 foraminiferal tests were picked from the >63 μm fraction, or until all tests were removed from the residue. A test was picked only if it was deemed to consist of more than 50% of the original test, and therefore could be said to represent a 'whole' specimen.

TOC

Organic carbon was measured using a Carlo Erba Instruments EA1108 Elemental analyser. Both unacidified and acidified samples were analysed and corrections calculated using techniques proposed by Wilkinson (1991).

Palynology & Thin Sections

Samples of between 2 g and 4 g were taken and a standard palynological procedure was used, though no oxidation technique was used on the samples. This was undertaken to allow the foraminiferal test linings to be studied. Standard thin sections were ground to 30 microns.

Definitions concerning Oxygen Levels

Oxygen is one of the most important factors affecting metazoan communities. Low levels inhibit foraminiferal abundance, diversity and affect taxonomic composition. The lack of this element leads to a lessening of microbial decay, and therefore can lead to organic carbon build-up.

It must be recognised here that there are two categories of descriptive terms. One that describes the faunal communities resulting from different levels of oxygen content in the environment (Table 1), and the other which defines the levels of oxygen content itself in environment (Table 2).

Table 1. A definition of terms relative to faunas.

TERM	DEFINITION
Aerobic	Normal benthic fauna, no oxygen restriction.
Dysaerobic	Impoverished benthic fauna, low oxygen levels.
Anaerobic	No benthic fauna present.
Exaerobic	Only fauna that are able to perch between anoxic and dysoxic conditions.
Poikilo-aerobic	Faunas that are able to withstand fluctuating oxygen levels, generally low diversity assemblages.

Taken from Allison *et al.* (1995)

Table 2. Terms that describe oxygenation

TERM	DEFINITION
Oxic	>1.0 ml/l
Dysoxic	1.0-0.2 ml/l
Suboxic	0-0.2 ml/l (Nitrates reduced)
Anoxic	0 ml/l
Euxinic	0 ml/l (free H ₂ S in water column)

Taken from Allison *et al.* (1995)

RESULTS AND DISCUSSION

Total Organic Carbon (TOC) values

Throughout the Upper Kimmeridgian the TOC values (Figure 3) are consistently high (2-4 wt%) but in the stone bands these values may be substantially higher. For instance, within the Black Stone Band organic carbon has been found to make up to 47 wt% of the rock. In the studied interval the wavelength of the organic carbon fluctuations decreases as the amount of carbon increases. This probably reflects a decrease in the rate of sedimentation, although that does not fully explain the exceptionally high quantities of organic matter found.

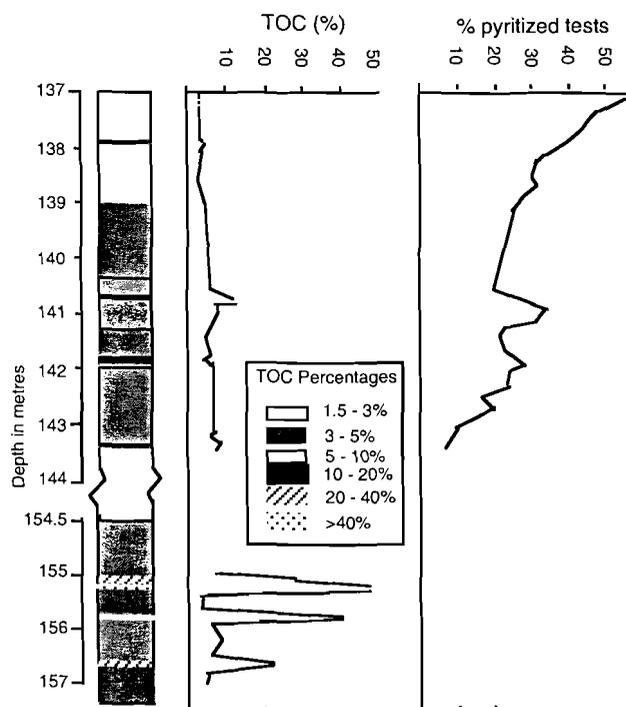


Figure 3. TOC values and smoothed percent pyrite observed plotted against a log of the section.

Thin-sections

The thin-sections of the Black Stone Band show five main features: 1) The laminae consist of alternating organic-rich layers and clay-rich horizons. 2) The organic-rich layers are continuous and uniform in structure and composition when observed in ultraviolet light. They have a wavy morphology and grade up into the clay laminae. 3) Trochamminid foraminiferal tests are present in large numbers with the largest, and by far the dominant concentrations found in the organic-rich laminae. Within the clay-rich horizons foraminiferal tests are rare. 4) Within the clay-rich layers the pyrite is fine grained and dispersed fairly evenly throughout the horizon. Within the organic-rich laminae the pyrite is far coarser, the individual crystals being larger (Table 3). The presence of wavy morphology is thought to be indicative of microbial mats (O'Brien, 1996, Tribovillard *et al.*, 1992), which are discussed in more detail below.

Pyrite

Within the Black Stone Band it is noticeable that the organic carbon-rich laminae have an uneven scatter of discrete pyrite crystals, larger in size than those found in the rest of the section (Table 3). Within the clay-rich laminae it is noticeable that the pyrite crystals are substantially smaller and disseminated more evenly. The crystal shape is, however, barely discernible due to their small size.

Table 3. Dimensions (μm) of dispersed pyrite within the clay-rich and organic carbon-rich laminae of the Black Stone Band.

	Clay-rich laminae (μm)	Organic carbon-rich laminae (μm)
Average length	4.02	6.05
Average width	3.86	5.23
Number of samples counted	250	253
Average number of grains per 100mm^2	68.8	35
R^2 correlation value for length against width	0.8355	0.7156

Pyrite is found throughout anoxic sediments that are rich in organic carbon. The slow sedimentation rate allows iron-rich minerals, such as clays, to react slowly under surface pressures and temperatures. Large quantities of H_2S produced by sulphate reduction are not consumed. As a consequence high levels of H_2S build up in the environment, especially where large amounts of organic carbon are present. If there is not significant current movement, this will lead to a build up of H_2S within the water column, contributing to an euxinic environment.

The largest number of pyritized tests are found within the upper part of the studied sedimentary column, in the interval between 137 and 140 m (Figure 3). This is where the depositional environment is thought to have contained higher amounts of oxygen, and the total amount of organic carbon is lower.

It is thought that the pyritization of the foraminiferal tests is associated with the availability of iron within the diagenetic environment. The sulphate necessary for sulphide production would have been easily available from the organic matter, which is abundant, but iron is only available in small quantities from the sea water, detrital grains from land masses, and from the siliciclastic minerals (Tyson, 1990). The land-derived siliciclastic minerals are dominated by clays with very low quantities of fine-grained quartz. The basin was sediment starved, as indicated by the low sedimentation rates (Miller, 1990). The liberation of iron from clay minerals is thought to take a long period of time in the

diagenetic environment (Berner, 1984) and therefore, it is supposed that this process was the main source of iron only during periods of low sedimentation. The sedimentation rate within the upper part of the core is higher, as suggested by the lower TOC values. This means that possibly more iron was available due to increased circulation of water and input from land. This study indicates that a greater quantity of pyritized tests represents a more energetic environment, meaning greater circulation within the water column.

Original foraminiferal assemblage or remnant assemblage?

The following observations have led to the conclusion that the foraminiferal assemblages have not been radically changed by diagenetic or syndepositional dissolution: 1) Calcareous foraminiferal tests were found in a large percentage of samples, though mainly in low numbers. 2) Ammonite shells occur within most horizons, frequently with the nacreous layer preserved. 3) In some layers nanofossils (frequently also coccospheres) are common, and are for the most part in good condition. 4) The calcareous foraminiferal tests show little corrosion or breakage, and in general are very well-preserved.

MAIN FEATURES

Calcareous foraminiferal abundances

The abundance of hyaline calcareous foraminifera is extremely low in most of the section studied (Figure 4). Hyaline forms increase as TOC values decrease.

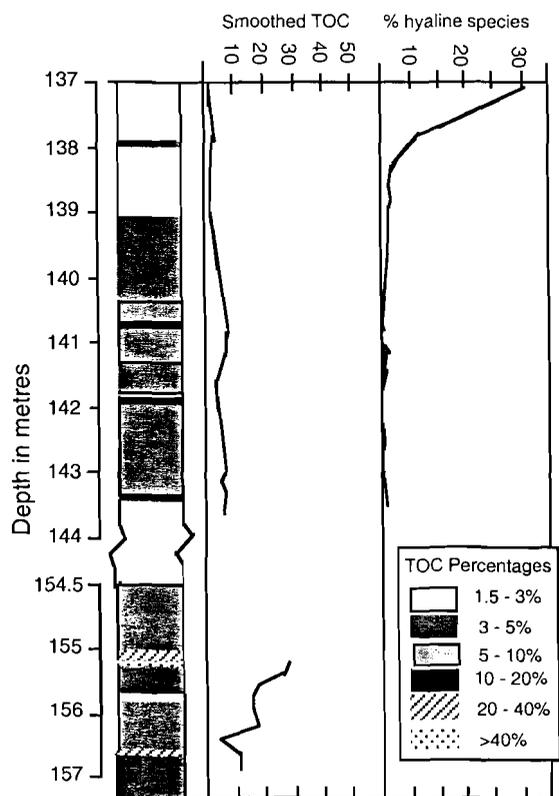


Figure 4. Smoothed percentages (3-point moving average) of hyaline tests and TOC values in the section studied.

Dominance

During periods of increasing deposition of organic matter the foraminiferal assemblages are dominated by a single genus (Figure 5). Within the Black Stone Band this genus is invariably *Kutsevelia*. Within the rest of the core studied, where the TOC values are lower, a variety of species belonging to different genera dominate.

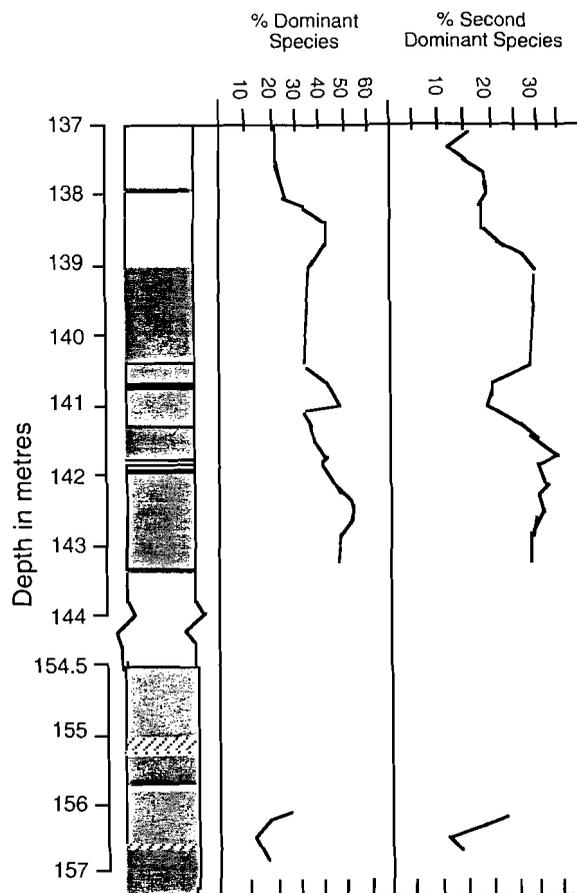


Figure 5. Smoothed percentage (3-point moving average) of the dominant genera within each sample and the second most dominant genera against the TOC values in the section studied.

It can be seen that when the environment becomes harsher, one species dominates to a larger degree.

Diversity indices

A general trend towards lower diversities is observed as the TOC content increases (Figure 6). This would be expected if the availability of dissolved oxygen content decreases, and there is more resident H₂S. Diversity values of foraminifera in the BSB are uniformly low, the values for both alpha and H(S) being between 1 and 2.

Epifaunal and Infaunal genera

The microhabitat of the foraminifera was interpreted using the morphogroups and subgroups defined by Jones & Charnock (1985), Nagy (1992) and Nagy *et al.* (1995). There is a general decrease in the numbers of infaunal species (Figure 7) found as the TOC values decrease upcore.

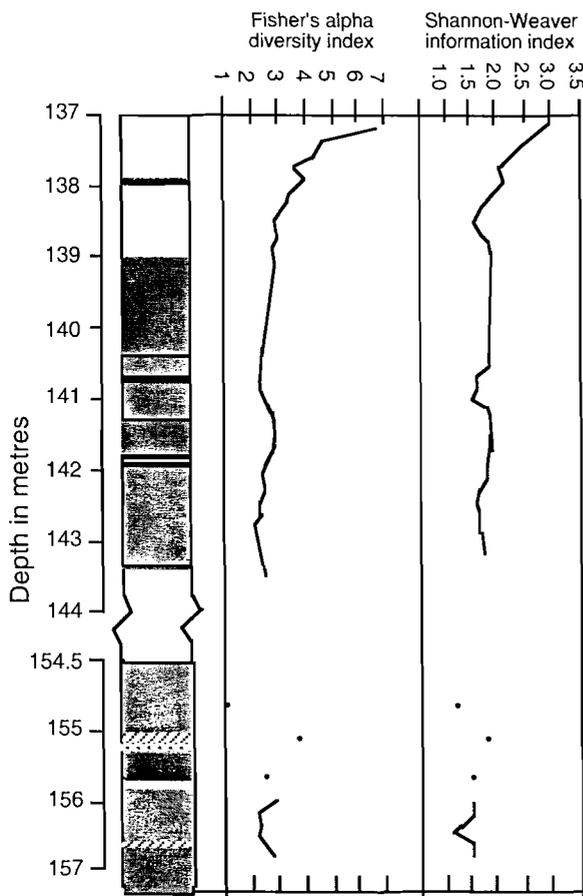


Figure 6. Diversity indices plotted against TOC in the section studied.

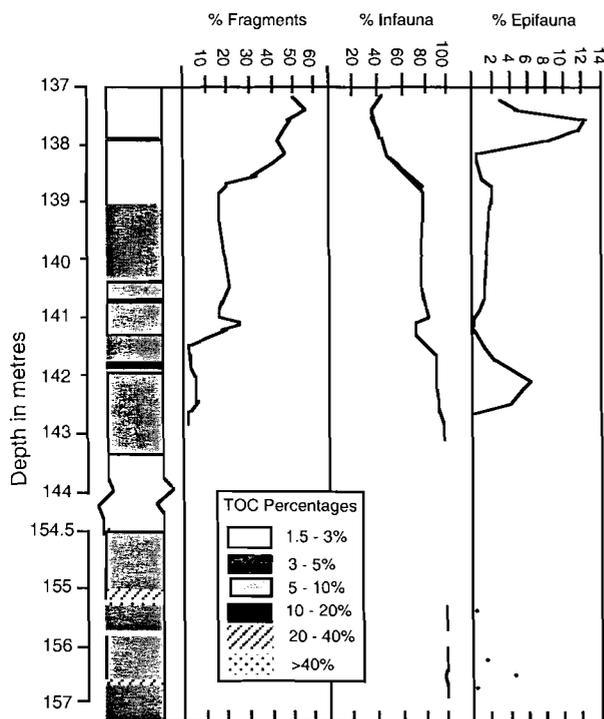


Figure 7. Percentage of test fragments and infaunal and epifaunal taxa (unidentifiable test fragments not included) against TOC in the section studied.

Test fragments and their implications

There is a decrease in the number of broken unidentifiable tests as the TOC increases (Figure 7). The abundance distribution is the opposite of that expected as the samples low in organic carbon required less processing, and therefore less damage to the test was expected. This result suggests that the number of broken tests found are a mixture of those broken before, or as a result of, burial and those broken by processing. The breakage is not thought to be due to transport, as all other evidence indicates that the energy of the environment was low. The breakage observed between 137 and 140 m is thought, for the most part, to be a function of the original environment, probably due to the greater oxygenation. This would allow microbes to act upon the test effectively and thus the organic cement would be more susceptible to microbial attack. The cement would have also been vulnerable to oxidation that would either destroy it or leave the test brittle.

MORPHOLOGICAL UNITS

Jones & Charnock (1985) established a series of morphological groups and subgroups for applications to palaeontological studies. Nagy (1992) and Nagy *et al.* (1995) further adapted the model for use with Jurassic foraminifera. It is proposed by the present author that morphological units can be correlated to genera, as these can be regarded as the building blocks of morphological classification. The morphogroups below are taken from Nagy *et al.* (1995).

Morphogroup 2: This group comprises species that live on the sediment surface, or at the sediment-water transition; an area termed the flocculent layer by Sanders (1960). This layer contains a mixture of organic and mineralic particles being deposited, plus bacteria and other organisms living there.

Subgroup 2b: This group consists of species that are: 1. Plano-convex to concavo-convex, 2. Streptospiral. Tests with these morphologies are supposed to be surface dwellers, and for the most part, active deposit feeders. The evidence for this assumption is the presence of the downward facing aperture which is assumed to be in contact with the surface of the sediment, and is thought to be indicative of surface dwellers. They also have a rounded periphery that is found in mobile epifaunal species. The *Trochammina* and *Recurvoides* found in the samples fit into this group.

Morphogroup 3: This group consists of those species with an infaunal lifestyle. The group includes two subgroups with widely varying test shapes.

Subgroup 3a: This group consists of planispiral taxa with a rounded periphery. Some members of the subgroup may also have a later uncoiled uniserial portion. In this study, the group includes the genera *Ammobaculites* and *Kutsevella*. Nagy (1992) specu-

lated that the formation of an uncoiled stage is an indicator of a less active period in the animal's life, when mobility is less likely to be necessary for survival.

Subgroup 3b: This group consists of multilocular, elongate taxa. This is supposed to be the best morphology for active infaunal scavenging. The genera found exhibiting these features are *Bulbobaculites*, *Spiroplectammina*, *Reophax*, and *Textularia*. The group is represented by the largest number of individuals in this study.

Morphogroup 4: This group consists of genera with a flattened test and planispiral, trochospiral or irregular coiling. These are thought to be epifaunal vagrants. In this study only *Ammodiscus* was found to belong to this group.

Environmental Significance of Agglutinated Genera

The agglutinated genera found in this study are:

<i>Textularia</i>	<i>Ammobaculites</i>
<i>Spiroplectammina</i>	<i>Kutsevella</i>
<i>Recurvoides</i>	<i>Ammodiscus</i>
<i>Haplophagmoides</i>	<i>Trochammina</i>
<i>Reophax</i>	<i>Bulbobaculites</i>

Genus *Reophax*

In the studied core, this genus displays an increase in numbers during the build-up of the TOC content. However, variations between 138.2 and 140 m show no clear relationship to the organic carbon content of the sediment (Figure 8), suggesting that there are more environmental factors involved in the distribution of this genus than organic carbon content alone.

Reophax is an infaunal genus, and modern representatives are found burrowing down to 15 cm into the sediment (Kaminski *et al.*, 1988). Under normal marine conditions, the genus is able to live in lowered oxygen levels (~0.5 ml/l) off southern California (Kaminski *et al.*, 1995).

Genus *Ammobaculites*

Work by Nagy (1992) indicates that the straight portion in *Ammobaculites* may point to a more sessile mode of life. This negative correlation with TOC values (Figure 8) supports an infaunal interpretation. Increases in the TOC correlate well with peaks of *Ammobaculites* specimens that are without an uncoiled portion.

These findings suggest that it was advantageous during these organic-rich periods to be more mobile. The loss of the uncoiled portion also means that the morphogroup designation for this genus moves from 3b to 3a following Nagy (1992) and from C1 to B3 in the Jones & Charnock (1985) scheme. This would indicate that *Ammobaculites* changed its preferred habitat from infaunal to surficial.

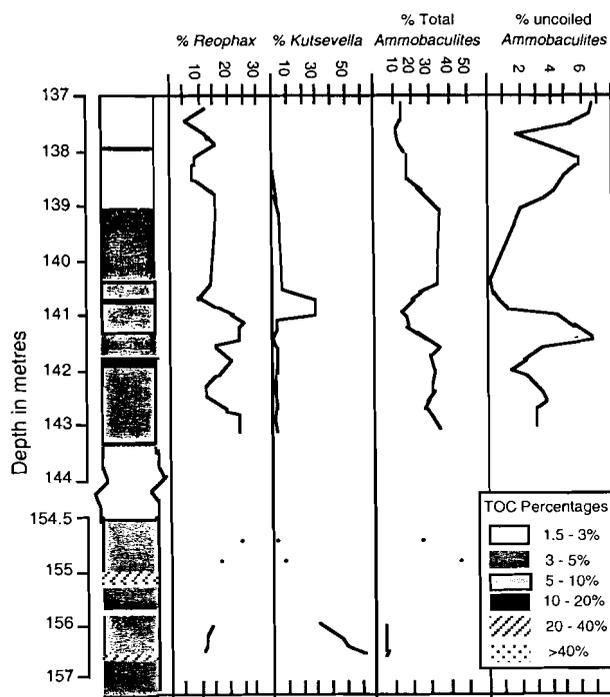


Figure 8. Smoothed percentages of *Reophax*, *Kutsevella* and *Ammobaculites* against TOC values in the studied core. Also shown are the percentages of *Ammobaculites* that possess a straight (uncoiled) portion.

Genus *Kutsevella*

There is a negative correlation between organic carbon build-up into the BSB and the numbers of *Kutsevella* found (Figure 8). The morphology of *Kutsevella* suggests that this genus was an active detritivore or herbivore.

The assumption that the wall of *Kutsevella* was impermeable to oxygen is open to question as the test was held together by an organic cement which may have been permeable to oxygen. The morphology also suggests that *Kutsevella* would not have been able to withstand very low oxygen concentrations, as they had comparatively thick walls and a high volume to surface area ratio. These factors combine to indicate that the taxon lived in a region of the environment that was better oxygenated than is indicated by the amount of organic carbon. This contrasts sharply with the geochemistry conducted by Wignall (1994) which indicates an anoxic environment of deposition.

Wignall (1990) suggested that the Kimmeridgian sediment was soupy, and this is true for modern environments where the water column has undergone stagnation. This suggestion is refuted, however, by the size and shape of the *Kutsevella* test, which is comparatively large and robust, and therefore required a fairly firm substrate to live on or within. Its morphology suggests it was an active shallow infaunal to surficial vagrant herbivore. These observations suggest that a microbial mat may have been present, as this would increase the stability of the substrate. The presence of microbial mats could

allow the environment to be relatively oxygenated, while the sediment beneath could be anoxic.

Genus *Textularia*

Every sample examined in this study contains *Textularia*, and in a large number of samples this genus is found to be dominant. Figure 9 indicates that there is a general increase in its abundance as TOC increases, although there are indications that there is a retardation of the population when the TOC value exceeds 7%. Even so, *Textularia* are abundant within the BSB. The largest numbers are found when TOC values are between 5 and 7%. Between samples 138.1 and 138.9 m large numbers of tests are found. These findings indicate that there are other factors affecting the abundance of *Textularia* in the environment of deposition than those which dictate the amount of organic carbon being deposited, although all these factors are probably linked.

A number of interesting features of the *Textularia* assemblage are worth noting: Firstly, there is a general decrease in the number of whole *Textularia* tests as TOC increases (Figure 9). This ignores the amount of crushing the tests have undergone, as this is found to be primarily a function of the amount of pyritization affecting the individual, and is therefore a diagenetic product.

The amount of breakage could be due to a number of factors: 1) Physiological changes in the chemical makeup of the test during processing, leaving it more brittle and more susceptible to being broken; 2) The original test secreted by the foraminifer was weakened by environmental parameters affecting it while living; 3) Breakage due to processing. This is a difficult factor to assess. The same processing technique was used for all samples, thereby minimising the part this factor plays, but it must be noted that some of the carbon-rich samples needed longer processing. The position of the peaks suggests that the cause of the breakage is not primarily due to processing.

The following measurements were taken of all whole *Textularia* tests: length, width at the widest part of the test, width at the narrowest part of the test. Based on these data, two calculations were made: Width/length (an indication of size), (widest width/narrowest width)/length (an indication of tapering).

As can be seen from Figure 12 there is a general decrease in the size of the test as the environment became more organic carbon-rich. The average decrease in size is about 9%. Figure 9 also indicates that there is greater tapering in this genus when the environment is better oxygenated, as it is in the higher part of the section. The increase in tapering will increase the volume of the test, thereby decreasing the volume to surface area ratio. The elongate tapered morphology indicates that this genus is an infaunal vagrant, and it may have had the ability to withstand lower oxygen levels, and

therefore may have migrated over short distances to the sediment surface. Kaminski *et al.* (1995) found modern examples of small, organically-cemented *Textularia* to dominate in stations from the San Pedro Basin off California, where oxygen values are 0.2 ml/l or lower.

In recent studies conducted by Hess & Kuhnt (1996) on the recovery of the foraminiferal populations after the 1991 Mount Pinatubo eruption, *Textularia* and *Reophax* have been observed to be the first to colonise the ash, indicating that these are opportunistic genera. This opens up the possibility that this was also true of Kimmeridgian representatives of these genera.

Genus *Trochammina*

Trochammina test linings have been found in all the palynological preparations, but preserved tests were recovered from only a small number of samples prepared for foraminiferal analysis (Figure 10). The genus is present in large numbers in thin sections from the BSB, which is thought to have been deposited under anoxic conditions. These findings are interesting for a number of reasons:

Because of their abundance in palynological preparations, it was found that the choice of sieve size affects the assemblage composition. This agrees with studies by Schröder (1987), and implies that *Trochammina* is possibly the dominant genus, not *Textularia*, as suggested by the foraminiferal preparations.

Trochamminids have not been found in Recent anoxic environments. This implies that either the Kimmeridgian environment was not totally oxygen deficient, or that the trochamminids lived in a part of the environment that was supplied with oxygen. The genus may, of course, changed its preference since the Jurassic.

Trochamminids found in this study may have been able to withstand very low oxygen levels and occasional anoxia, but this is thought unlikely as this is not corroborated by other studies. The genus is not considered to be morphologically best suited to this environment, as it has a moderate surface area to volume ratio, although their size and shape would enable them to have more stability on soft sediment.

It is likely that the environment was dysaerobic as there were massive amounts of organic carbon preserved, a large percentage of which being of the amorphous type. If the sediment had been oxygenated then it is likely that the organic carbon would have been oxidised to a large extent. A second possibility is that algal or bacterial mats may have been present. If this were so, this would have enabled the foraminifera to live above the anoxia. It has been found that in modern microbial mats, anoxia may develop below the mat, but need not extend above into the water column.

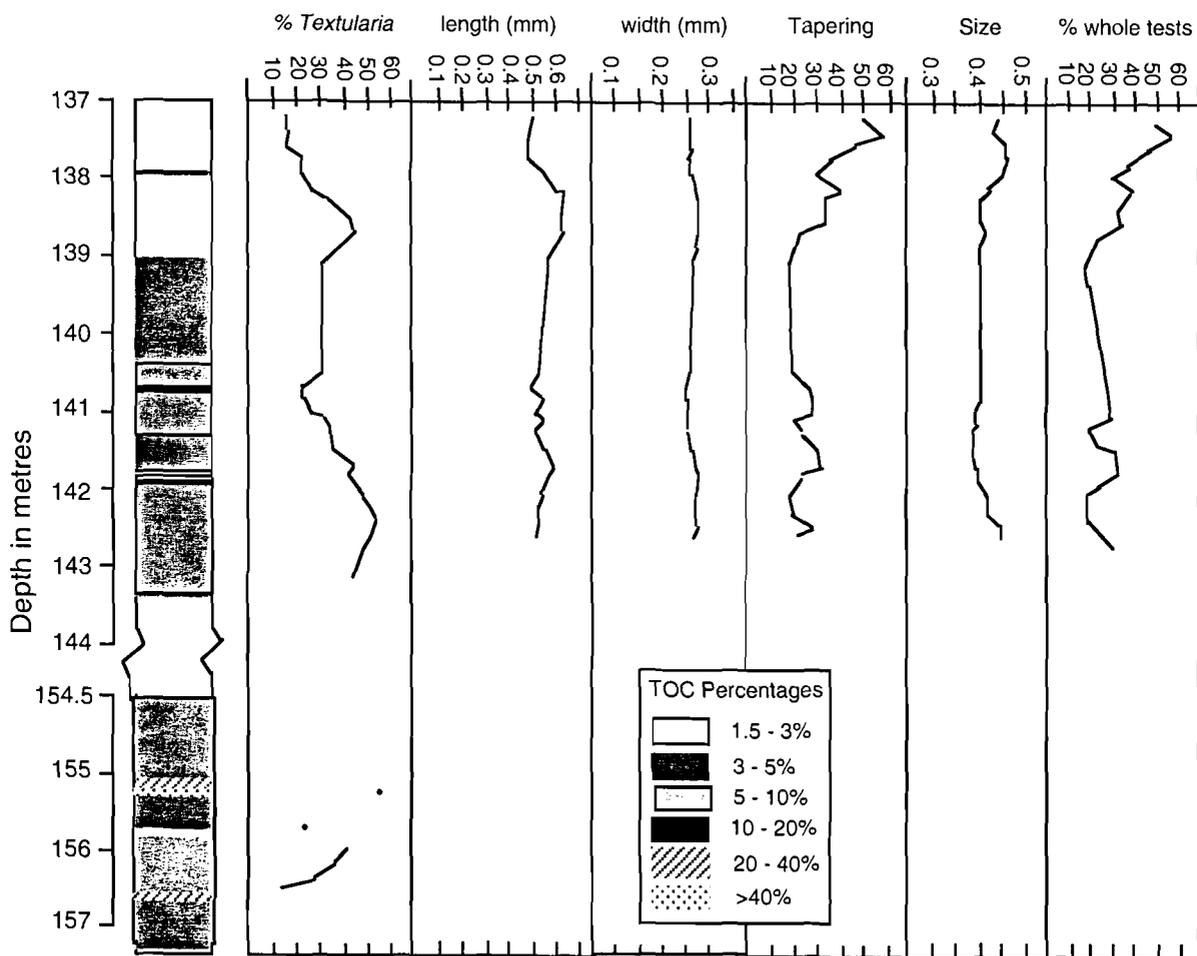


Figure 9. Smoothed percentages of *Textularia* against a log of the studied core. Also given are measured test parameters.

Studies by Nagy (1995) and Jones & Charnock (1985) indicate that this morphotype was an active epifaunal detritivore, consuming bacteria, algae and various other organic detritus. For the present study it is thought that this morphogroup had the ability to migrate to more hospitable parts of the environment when the oxygen content of the water at the sediment water interface decreased. Similar behaviour has been observed in Recent calcareous foraminifera under experimental conditions by Alve & Bernhard (1995).

Genera *Haplophagmoides*, *Recurvoides*, *Bulbobaculites*, *Spiroplectammina* and *Ammodiscus*
 These genera are found in very low numbers (typically less than one percent of the assemblage) in those parts of the succession with low TOC values (Figure 10). The implications of this are that these genera are less tolerant of oxygen depletion than the other genera recorded. Therefore, their occurrence may be attributed to the higher oxygen levels that are assumed to be associated with lower levels of organic carbon deposition.

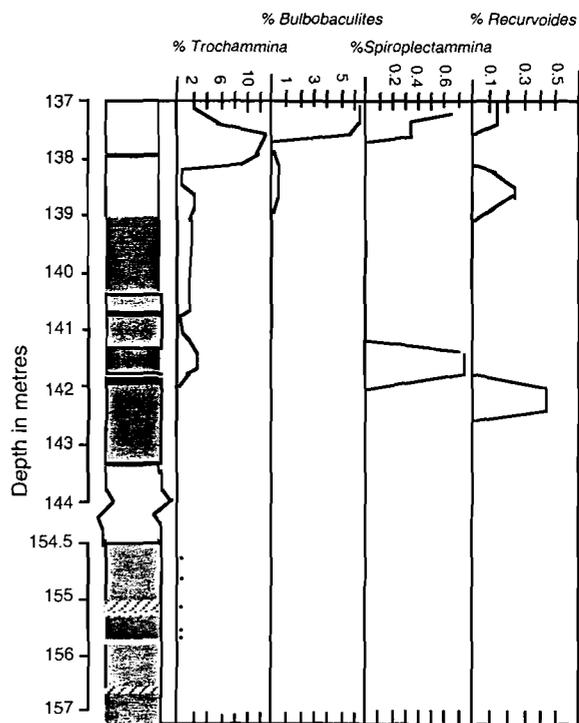


Figure 10. Smoothed percentages of *Trochammina*, *Bulbobaculites*, *Spiroplectammina* and *Recurvoides* in the core.

Microbial mats

This study has brought to light the possibility that microbial mats may have occupied the sediment water interface during periods of deposition within the Kimmeridgian seas of Southern England. The evidence for this assumption is: 1) The presence of wavy laminae, seen in thin section. 2) The homogenous nature of the organic matter within the laminae, having very similar composition and structure over laterally extensive regions of the Wessex basin, as shown by ultraviolet microscopy. 3) It has been stated by Wignall (1994) that because of the widespread presence of microbial mats in oxygen depleted regions of modern oceans, it is unlikely they were not present within the Kimmeridgian seas. 4) The presence of mats might provide a solution to the long-standing problem of the presence of agglutinated foraminifera in the Kimmeridgian seas, while the geochemistry gives an unequivocal anoxic signal (Wignall, 1994). The mats would have enabled the foraminifera to live above the toxic sediment, rather than an anoxic environment. Recent studies by Alve & Bernhard (1995) indicate that foraminifera are unable to live in anoxic environments for long periods of time.

The implications of this are that the foraminiferal assemblages recovered are, perhaps, those typical of microbial mats rather than open marine muddy substrates. The presence of microbial mats means that the water column was probably not as oxygen depleted as generally assumed, although it was probably dysoxic. This would inhibit the presence of benthic grazers.

Studies by Canfield & Des Marais (1994) on microbial mats indicated that the effects of low oxygen are enhanced within the mat and sediment by the respiration of the microbes that make up the mat. It means that oxygen depletion can rapidly lead to complete anoxia. These factors will have led to additional stresses on the foraminiferal population, helping to explain the low diversity assemblages found

CONCLUSIONS

1. The depositional environment represented by the *wheatleyensis* - *hudlestoni* Zones is rich in organic carbon. Values of between 3 and 47% are recorded, and although the water column was not anoxic, the infaunal environment was oxygen deficient.
2. The presence of microbial mats is strongly suggested. The presence of mats could have caused anoxic sediments, while the water column could have been oxygenated, although it is likely that the environment of deposition was still low in dissolved oxygen. The assemblages of foraminifera would have been strongly influenced by the ecology of the mats. Furthermore, the mats would have restricted the flow of water through the sediment and therefore enhanced the anoxia, as suggested by modern studies.

3. The foraminifera are interpreted as possessing four main features that allowed them to survive within this environment: a) tolerance of low oxygen levels; b) mobility; as the study has found that many of the foraminiferal present can be defined as vagrant under morphological analysis; c) tolerance of higher than normal marine levels of H₂S; d) the ability to live in conjunction with microbial mats.
4. The decrease in wavelength in the TOC signature indicates a decrease in the sedimentation rate, although the condensation associated with this is not thought to be the only factor responsible for the large quantities of organic carbon found.
5. It is thought that both preservation and production play a part in the generation of large quantities of organic carbon recorded in the sediments. The stratified water column, while causing stagnation, would not account for the pulses in TOC observed. Though a stratified water column is envisaged it does not need to be strongly stratified, as it is thought that the presence of a microbial mat would magnify the effect of low oxygen levels.

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REFERENCES

- Allison, P.A., Wignall, P.B. & Brett, C.E. 1995. Palaeo-oxygenation: effects and recognition. In: Bosence, D.W.J. & Allison, P.A. (eds), *Marine Palaeoenvironmental analysis from fossils. Geological Society Special Publication*, **83**, 97-112.
- Alve, E. 1990. Variations in estuarine foraminiferal biofacies with diminishing oxygen conditions in Drammensfjord, SE Norway. In: Hembleben, C., Kaminski, M.A., Kunht, W. & Scott, D.B. (eds), *Palaeoecology, Biostratigraphy, Palaeoceanography and Taxonomy of Agglutinated Foraminifera*. NATO ASI Series C-327, 661-694. Kluwer.
- Alve, E. 1994. Opportunistic features of the foraminifera *Stainforthia fusiformis* (Williamson): evidence from Frierfjord Norway. *Journal of Micropalaeontology*, **13**, 24.
- Alve, E. & Bernhard, J.M. 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. *Marine Ecology Progress Series*, **116**, 137-151.
- Arkell, W. J. 1933. *The Jurassic system in Great Britain*. Clarendon Press, Oxford, 681 pp.
- Bernhard, J.M. 1986. Characteristic assemblages and morphologies of benthic foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene. *Journal of Foraminiferal Research*, **16**, 207-215.
- Bernhard, J.M. 1996. Microaerophilic and facultative anaerobic benthic foraminifera: A review of experimental and ultrastructural evidence. *Revue de Paléobiologie*, **15**, 261-275.
- Bernhard, J.M. & Alve, E. 1996. Survival, ATP pool, and ultrastructural characterization of benthic foraminifera from Drammensfjord (Norway): response to anoxia. *Marine Micropalaeontology* **28**, 5-17.
- Bernhard, J.M. & Reimers, C.E. 1991. Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin. *Biogeochemistry*, **15**, 127-149.
- Barnard, T. 1952. Foraminifera from the Upper Oxford Clay (Jurassic) of Warboys Huntingdonshire. *Proceedings of the Geologists' Association*. **63**, 336-350.

- Barnard, T. 1953. Foraminifera from the Upper Oxford Clay of Redcliff Point, near Weymouth, England. *Proceedings of the Geologists' Association*, **64**, 183-97.
- Barnard, T., Cordey, W.G. & Shipp, D.J. 1981. Foraminifera from the Oxford Clay (Callovian - Oxfordian of England). *Revista Española de Micropaleontología*, **13**, 386-462.
- Barnard, T. & Shipp, D.J. 1981. Kimmeridgian foraminifera from the Boulonnais. *Revue de Micropaleontologie*, **24**, 3-26.
- Canfield, D.E. & Des Marais, D.J. 1993. Biogeochemical cycles of carbon, sulphur and free oxygen in a microbial mat. *Geochimica et Cosmochimica Acta*, **57**, 3971-3984.
- Chadwick, R.A. 1986. Extension tectonics in the Wessex Basin, Southern England. *Journal of the Geological Society, London*, **143**, 465-488.
- Chadwick, R.A., Livermore, R.A. & Penn, I.E. 1989. Continental extension in Southern Britain and the surrounding areas and its relationship to the opening of the North Atlantic Ocean. In: Tankard, A.J. & Balkwill, H.R. (eds), *Extensional tectonics and stratigraphy of the North Atlantic margins*, AAPG Memoir, **46**, 411-424.
- Cordey, W.G. 1962. Foraminifera from the Oxford Clay of Staffin Bay, Isle of Skye, Scotland. *Senckenbergiana Lethaeae*, **B**, **43**, 653 - 657.
- 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. *Institute of Geological Sciences, Report 80/4*.
- Dain, L.G. 1972. Foraminifera of upper Jurassic deposits of Western Siberia. *Trudy Vsesoyuznogo Neftyanogo Nauchno-issledovatel'skogo Geologo-razvedochinogo Instituta (VNIGRI)*, **317**, 1-272.
- Gallois, R.W. 1976. Coccolith blooms in the Kimmeridge Clay and the origin of North Sea oil. *Nature*, **259**, 473-475.
- Gallois, R.W. & Cox, B.M. 1974. Stratigraphy of the Upper Kimmeridge Clay of the Wash area. *Bulletin Geological Survey, Great Britain*, **47**, 1-16.
- Gregory, F.J. 1989. Palaeoenvironmental interpretation and deposition of Lower Kimmeridgian foraminifera from Brora- Helmsdale outlier, Northwest Scotland. In: Batten, D.J. & Keen, M.C. (eds) *North Western European Micropalaeontology and Palynology*. pp. 173-192. Ellis Horwood Limited, Chichester.
- Hallam, A. 1975. *Jurassic Environments*. Cambridge University Press. 269 pp.
- Haq, B.U., Hardenbol, J. & Vail, P.R. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sea level change. In: *Sea-level changes-An integrated approach*, SEPM Special publication No. 42.
- Herbin, J.P., Fernandez-Martinez, J.L., Geysant, J.R., El-Albani, A., Deconinck, J.F., Proust, J.N., Colbeaux, J.P., & Vidier, J.P. 1995. Sequence stratigraphy of source rocks applied to the study of the Kimmeridgian/Tithonian in the north-west European shelf (Dorset/UK, Yorkshire/UK and Boulonnais/France). *Marine and Petroleum Geology*, **12**, 177-194.
- House, M.R. 1995. Orbital forcing timescales: an introduction. In: House, M.R. & Gale, A.S. (eds) *Orbital forcing timescales and cyclostratigraphy*, Geological Society Special Publication No. 85.
- Jones, R.W. & Charnock, M.A. 1985. "Morphogroups" of agglutinating foraminifera. Their life positions and feeding habits and potential applicability in (paleo)ecological studies. *Revue de Paléobiologie* **4**, 311-320.
- Kaminski, M.A., Gradstein, F.M., Berggren, W.A. Geroch, S. & Beckmann, J.P. 1988. Agglutinated foraminiferal assemblages from Trinidad: taxonomy, stratigraphy and palaeobathymetry. *Abhandlungen des Geologischen Bundesanstalt*, **41**, 155-228.
- Kaminski, M.A., Boersma, A., Tyszka, J., & Holbourn, A.E.L. 1995. Response of deep-water agglutinated foraminifera to dysoxic conditions in the California Borderland Basins. In: Kaminski, M.A., Geroch, S. & Gasinski, M.A. (eds). *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Grzybowski Foundation Special Publication, **3**, 131-140.
- Lloyd, A.J. 1958. *The foraminiferal faunas of the type Kimmeridgian*. Unpublished Ph.D Thesis, University of London.
- Lloyd, A.J. 1959. Arenaceous foraminifera from the type Kimmeridgian (Upper Jurassic). *Palaeontology*, **1**, 298-320.
- Lloyd, A.J. 1962. Polymorphinid, miliolid and rotaliform foraminifera from the type Kimmeridgian. *Micropaleontology*, **8**, 369-383.
- Løfaldli, M. & Nagy, J. 1980. Foraminiferal stratigraphy of Jurassic deposits on Kongsøya, Svalbard. *Norsk Polarinstittutt, Skrifter*, **172**, 63-95.
- Løfaldli, M. & Nagy, J. 1983. Agglutinated foraminifera in Jurassic and Cretaceous dark shales in southern Spitsbergen. In: Verdenius, J.G., Van Hinte, J.E. & Fortuin, A.R. (eds) *Proceedings of the First Workshop on Arenaceous Foraminifera*. Continental Shelf Institute Special Publication, **108**, 91-107.
- Miller, R.G. 1990. A paleoceanographic approach to the Kimmeridge Clay Formation. In: Huc, A.Y. (ed.), *Deposition of Organic Facies. APPG Studies in Geology*, **30**, 13-26.
- Mozeelaar, R. & Stal, L.J. 1994. Fermentation in the unicellular cyanobacterium microcystis PCC7806. *Archives of Microbiology*, **162**, 63-69.
- Nagy, J. 1985. Jurassic foraminiferal facies in Statfjord Area, Northern North sea, I. *Journal of Petroleum Geology*, **8**, 273-295.
- Nagy, J. 1985. Jurassic foraminiferal facies in Statfjord Area, Northern North Sea, II. *Journal of Petroleum Geology*, **8**, 389-403.
- Nagy, J. 1992. Environmental significance of foraminiferal morphogroups in Jurassic North Sea deltas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **95**, 111-134.
- Nagy, J., Dypvik, H. & Bjaerke, T. 1984. Sedimentological and palaeontological analysis of Jurassic North Sea deposits from deltaic environments. *Journal of Petroleum Geology*, **7**, 169-188.
- Nagy, J., Gradstein, F.M., Kaminski, M.A. & Holbourn, A.E. 1995. Foraminiferal morphogroups, palaeoenvironments and new taxa from the Jurassic to Cretaceous strata of Thakkhola, Nepal. In: Kaminski, M.A., Geroch, S. & Gasinski, M.A. (eds), *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Grzybowski Foundation Special Publication, **3**, 181-209.
- Nagy, J. & Johansen, H.O. 1989. Preservation and distribution pattern of *Reophax metensis* (Foraminifera) in the Jurassic of the North Sea. *Journal of Foraminiferal Research*, **19**, 337-348.
- Nagy, J. & Løfaldli, M. 1981. Agglutinating foraminifera in Jurassic dark shale facies in Svalbard. In: Neale, J.W., & Brasier, M.D. (eds), *Microfossils from recent and fossil shelf seas*. Ellis Horwood Limited, Chichester, 113-121.
- Nagy, J., Pilskog, B. & Wilhelmson, R. 1990. facies controlled distribution of foraminifera in the Jurassic North Sea Basin. In: Hemleben, C., Kaminski, M.A., Kuhnt, W. & Scott D.B. (eds), *Palaeoecology, biostratigraphy, palaeoceanography and taxonomy of agglutinated foraminifera*. NATO ASI Series C-327, 621-657. Kluwer Academic Publishers.
- Nagy, J., Løfaldli, M. & Bäckström, S.A. 1988. Aspects of foraminiferal distribution and depositional conditions in Middle Jurassic to Early Cretaceous Shales in Eastern Spitsbergen. *Abhandlungen des Geologischen Bundesanstalt*, **41**, 287-300.
- Nagy, J., Løfaldli, M., Bäckström, S.A. & Johansen, H. 1990. Agglutinated foraminiferal stratigraphy of Middle Jurassic to basal Cretaceous shales, central Spitsbergen. In: Hemleben, C., Kaminski M.A., Kuhnt W. & Scott D.B. (eds), *Palaeoecology, biostratigraphy, palaeoceanography and taxonomy of agglutinated foraminifera*. NATO ASI Series C-327, 969 - 1015, Kluwer Academic Publishers.
- Neagu, T. & Neagu, M. 1995. Smaller Agglutinated foraminifera from the *acanthicum* limestone (Upper Jurassic), eastern Carpathians, Romania. In: Kaminski, M.A., Geroch, S. & Gasinski, M.A. (eds) *Proceedings of the Fourth International Workshop on Agglutinated*

- Foraminifera, Kraków, Poland, *Grzybowski Foundation Special Publication*, 3, 211-225
- Nørting, E. 1972. Jurassic stratigraphy and Foraminifera of Western Scania, Southern Sweden. *Sveriges Geologiska undersökning Avhandlingar och uppsatser*, 47, 1-120.
- 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 Northern European epic basin: interaction with atmospheric and hydrospheric circulations. *Sedimentary Geology*, 69, 313-332.
- Parrish, J.T., Ziegler, A.M. & Scotese, C.R. 1982. Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 40, 67-101.
- Partington, M.A. 1983. *The stratigraphy and distribution of circumpollen in Southern England*. Unpublished PhD thesis, University of Aberdeen.
- Sanders, H.L. 1960. Benthic studies in Buzzards Bay; III, the structure of the soft bottom community. *Limnology and Oceanography*, 5, 138-153.
- Schröder, C.J., Scott, D.B., & Machain-Castillo, M.L. 1987. Can smaller benthic foraminifera be ignored in palaeo-environmental analysis? *Journal of Foraminiferal Research*, 17, 101-105.
- Tyson, R.V., Wilson, R.C.L., & Downie, C. 1979. A stratified water column model for the type Kimmeridge Clay. *Nature*, 277, 377-380.
- Tyson, R.V. 1990. *Sedimentary organic matter, organic facies and palynofacies*. Chapman and Hall, London.
- Wignall, P.B. 1994. *Black Shales*, Clarendon Press, Oxford, 127 pp.
- Wignall, P.B. & Hallam, A. 1991. Biofacies, stratigraphic distribution and depositional models of British onshore Jurassic black shales. In: Tyson, R.V. & Pearson, T.H (eds) *Modern and ancient continental shelf anoxia* Geological Society Special Publication, 58, 291-309.
- Wilkinson, J.J. 1991. Volatile production during contact metamorphism: the role of organic matter in pelites. *Journal of the Geological Society, London*, 148, 731-736.

