The palynology of the Kimmeridge Clay and Carstone Formations (Upper Jurassic–Lower Cretaceous) at Middlegate Quarry, North Lincolnshire, UK, and its biostratigraphical and palaeoenvironmental significance

Roderick D. Black¹ and Paul Dodsworth²*

Abstract: At Middlegate Quarry, the Carstone Formation is a c. 0.8 m thick unit of oolitic ferruginous sandstone. It rests unconformably on the lower Kimmeridge Clay Formation (KCF) and is overlain by the Hunstanton Formation (Red Chalk) with an apparently gradational junction. Marine dinoflagellate cysts (dinocysts) are present at a concentration of 9520 to 13 600 specimens per gram in the 0.15 m of KCF below the unconformity, and include taxa that confirm ammonite evidence for the intra-Lower Kimmeridgian Substage (Upper Jurassic, Cymodoce Ammonite Zone). A rich recovery of well-preserved Lower Cretaceous palynomorphs is reported for the first time from the overlying Carstone. Reworking of mudstone from the KCF into the formation appears to have provided a local argillaceous preservation matrix at Middlegate. The basal 0.15 m is dominated by palynomorphs derived from the KCF but the interval from 0.15 to 0.55 m above the unconformity mainly contains indigenous Lower Cretaceous palynomorphs. Dinoflagellate cysts are present in the Carstone at an average concentration of 454 specimens per gram, and include taxa that probably have stratigraphical range bases above the Aptian–Albian stage boundary: Cyclonephelium compactum, Cyclonephelium intonsum, Endoscrinium heikeae, Leptodinium coronatum (consistent), Stephodinium coronatum and Stephodinium spinulosum. The additional presence of taxa with range tops/event tops in the Lower Albian Tardefurcata Ammonite Zone (common Cauca parva, frequent Canningiporus monile and Kleithriasphaeridium einoeides, and rare Dingodinium albertii, Discorsia nannus and Kiokansium protakum) indicate probable assignment to this zone. The new palynological data support previous macrofossil (brachiopod) study of the Carstone at Middlegate and nearby Melton Bottom Quarry which tentatively assigns its highest part to the Tardefurcata Zone. The palynological and palynofacies assemblages are interpreted to confirm a relatively proximal to shore line site of deposition, possibly inner to middle neritic.

Supplementary material: Quarry photographs and a palynological distribution chart are available at https://doi.org/10.6084/m9.figshare.c.5538977

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The extensive (>1 km wide) section at Middlegate Quarry, near the village of South Ferriby in North Lincolnshire (Figs 1 and 2), comprises the Upper Jurassic Ancholme Clay Group (upper Amlphill Clay Formation, Oxfordian, and lower Kimmeridge Clay Formation (KCF), Kimmeridgian), the Lower Cretaceous Carstone Formation, Lower to Upper Cretaceous Hunstanton Formation (formerly known as the Red Chalk, Albion–Conomanian), and Upper Cretaceous Ferriby Chalk Formation type section (Conomanian) and Welton Chalk Formation (Conomanian–Turonian). Middlegate was designated a Site of Special Scientific Interest status for geology in 1987.

There has been a cement factory at South Ferriby since 1938 (Cox and Wright 2001); both chalk (limestone) and clay, the main raw materials used in cement manufacture, were supplied to it from the quarry via a 1.75 km long conveyer belt (Whitham 1992). The quarry was owned and operated by the Rugby Cement company (now Cemex) from 1993 to 1995 when our fieldwork was undertaken and samples collected. It was abandoned as a working quarry in 2020. The pumping of water from the quarry has ceased and it is estimated that an ingress of water will flood the lower part of the quarry, submerging all of the Ancholme Clay and Carstone (Hildreth 2020a).

The quarry has afforded the opportunity to examine the contact between deposits of Late Jurassic age with those of Early Cretaceous age. In 1993, c. 17.2 m of grey mudstones belonging to the Ancholme Clay Group were exposed in the quarry bottom. Wignall (1990) provided a summary of the stratigraphy, paleoentology and paleoecology of the Ancholme Clay succession at Middlegate. The contact with the overlying Carstone Formation is irregular, with the Carstone filling shallow hollows, troughs and burrows in the mudstones (Smart and Wood 1976).

The Carstone, as defined by Gaunt et al. (1992), is c. 0.8 m thick on average along the northern quarry face where we sampled it (Fig. 3). It is mainly composed of quartz sands, with limonite and calcite ooliths, and sand-sized grains of degraded glauconite. Pebbles of phosphate, polished quartz and calcareous siltstone (Gaunt et al. 1992; Whitham 1992), along with grey-coloured argillaceous matrix material, occur at the base and throughout the lower c. 0.45 m of the formation at Middlegate. The Carstone is friable and can be dug out by spade but is cemented in patches. It is highly...
porous and a significant aquifer (Gaunt et al. 1992). Above it, a 0.1 m unit of sandy marl with a burrowed-base (probably indicating a non-sequence; Hopson 2005), and overlying 0.15 m unit of banded red- and cream-coloured sandy marl, are interpreted to be Hunstanton Formation beds 1 and 2 of Gaunt et al. (1992). These layers are a lithological gradation between the sandstones of the Carstone and the more typical chalks and marls of the Hunstanton Formation (beds 3–11 of Gaunt et al. 1992). They have probably been included with the Carstone by earlier workers, such as Whitham (1992) who measured its thickness at Middlegate as about 1 m.

In this paper, Aptian and Albian chronostratigraphical substages and their corresponding ages are treated as formal units, using initial upper case letters, consistent with the usual practice, although only the Lower Albian Substage has to date been ratified by the International Union of Geological Sciences (IUGS; see below). The palaeontology of the Carstone was summarized by Gaunt et al. (1992). It contains derived Jurassic and Lower Cretaceous remaniéd macrofossil suites, predominantly ammonites and bivalve molluscs. According to Casey (1961), the Carstone has not yielded indigenous ammonites in Norfolk or Lincolnshire. Indigenous brachiopods were reported from the top 0.15 m of Carstone at Melton Bottom Quarry near the village of Melton (Fig. 1; Owen et al. 1968) and the top 0.2 m at Middlegate Quarry (Smart and Wood 1976; Whitham 1992). Brachiopod faunas including Burrirhynchia leightonensis (Lamplugh and Walker) are comparable to those of the

![Fig. 1. The Cretaceous outcrop in eastern England and Carstone Formation localities and boreholes mentioned in the text (modified from Hart 2019; Dodsworth et al. 2020).]
Shenley Limestone in Bedfordshire, SE England, which is assigned to the Lower Albian Tardefurcata Ammonite Zone, named for *Leymeriella* tardefurcata (Leymerie). Dilley (1969) reported indigenous foraminifera from the top 0.15 m at Melton Bottom, including *Osangularia schloenbachi* (Reuss) which has an Upper Aptian to Middle Albian stratigraphical range in the North Sea region (Crittenden 1983; Crittenden and Price 1991). Gaunt et al. (1992) reported foraminifera and long-ranging Albian ostracods from the top part of the Carstone in a motorway excavation at Melton Gallows. The lower half of the Carstone has remained undated at these localities due to a lack of indigenous fossils. However, Kent and Dilley (1968) recorded Upper Aptian to possibly Lower Albian foraminiferal assemblages from a locally developed 3 m thick mudstone underlying the (0.6 m thick) Carstone at Elsham (Fig. 1).

The only previous palynological investigation of the Carstone in eastern England (localities undisclosed; Gaunt et al. 1992) reported that ‘dinoflagellate cysts are sparse, poorly preserved and dominated by the long-ranging *Odontochitina operculata*, many specimens of which are corroded’. Similarly, Hesselbo et al. (1990) reported ‘trace’ concentrations of dinoflagellate cysts in the Carstone of the Calne area, Wiltshire, southern England, but these offered no control for its age. Although shown on lithological logs, the Carstone has not been sampled in some Cretaceous palynological studies, e.g. the Trunch borehole of Norfolk (Fig. 1; Pearce et al. 2020) and a Lower Greensand investigation of the Isle of Wight, southern England (Duxbury 1983), presumably due to its lithology appearing to be unsuitable, i.e. too coarse-grained, for palynological preservation.

During sampling of the Ancholme Clay at Middlegate in 1993 for a Master of Science palynology research dissertation (Black 1994), the grey colouration of the lower half of the Carstone was noted, potentially indicating reworking of Upper Jurassic mudstone into its matrix. Six samples were collected (RB10B to RB5B; Fig. 3) to check for reworked palynomorphs. After laboratory processing revealed rich palynological recovery of *in situ* and reworked taxa from the lower four samples, a further four infill samples were collected in 1995 from around the KCF–Carstone boundary (PD9503-1 to -4). While reworked Upper Jurassic taxa are prominent in samples from the lowest 0.15 m of the Carstone, they are only a minor component of assemblages from 0.15 to 0.55 m above the unconformity, in which indigenous Lower Cretaceous palynomorphs dominate.

This paper documents our Carstone samples, providing the first detailed palynological study of the formation and the
first account of well-preserved indigenous fossils from its lower half on the East Midlands Shelf. We discuss dinoflagellate cyst evidence for its age at Middlegate, and broader palynological and palynofacies implications for Carstone palaeoenvironments. Five samples from the uppermost 2.75 m of the KCF (Bed 12 of Birkelund and Callomon 1985) are also documented for comparison with reworked specimens in the Carstone.

Geological setting

The term Carstone was first formally applied by Strahan (1886), who described it as a coarse reddish-brown ferruginous grit with small phosphatic pebbles and flakes of iron ore. It was deposited during a phase of unconformable transgression (Versey and Carter 1926; Whitham 1992) and combined brachiopods, bivalve molluscs and belemnites in distributions in the Hunstanton Formation (c. 18.03 m and above; Gaunt et al. 1992, fig. 29); 2. Lower Cretaceous dinoflagellate cyst zonation of Duxbury (2001, 2002) and Jurassic zonation of Riding and Thomas (1992). Lithostratigraphy: Kimmeridge Clay Formation bed 12 of Birkelund and Callomon (1985); interpreted Hunstanton Formation beds 1–4 of Gaunt et al. (1992). Note that beds 1–2 are gradational lithologies between Carstone and Hunstanton Formations.

Differences in Carstone colouration are denoted (this paper) by (i) coarse sands, pebbles and clasts with a relatively dark grey colour when fresh, weathering to a greenish colour, probably reflecting the mineral chamosite (Versey and Carter 1926; Owen et al. 1968) and a reworked Kimmeridge Clay Formation argillaceous component; sandstone with fewer pebbles, mainly coloured orange (ii) and red (iii). Metres are height above the base of the quarry, as measured in 1993. Jac. (u.) = upper Jacobi Ammonite Zone. Dinoflagellate cyst range/event tops of taxa coloured in green are calibrated in NW Europe to the Tardefurcata Ammonite Zone. Range bases of taxa coloured in red are calibrated to the Tardefurcata Zone or upper Jacobi Zone; the latter is included in the lowermost part of the Albanian Stage at its Global Stratotype Section and Point (Kennedy et al. 2017). Taxa in black range through the interval; the count for the total number of reworked Upper Jurassic specimens is also indicated in black. See the text for a discussion.

Fig. 3. Lithological log of part of the Middlegate Quarry section, and ranges of selected dinoflagellate cysts in the Carstone Formation. Biostratigraphy: 1, ammonite zones, based on in situ ammonites faunas (Cymodoce Zone) or zones inferred from dinoflagellate cyst assemblages (17.2–17.7 m; this paper), brachiopods (c. 17.7–17.9 m; Smart and Wood 1976; Whitham 1992) and combined brachiopods, bivalve molluscs and belemnite distributions in the Hunstanton Formation (c. 18.03 m and above; Gaunt et al. 1992, fig. 29); 2. Lower Cretaceous dinoflagellate cyst zonation of Duxbury (2001, 2002) and Jurassic zonation of Riding and Thomas (1992). Lithostratigraphy: Kimmeridge Clay Formation bed 12 of Birkelund and Callomon (1985); interpreted Hunstanton Formation beds 1–4 of Gaunt et al. (1992). Note that beds 1–2 are gradational lithologies between Carstone and Hunstanton Formations.

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Across the East Midlands Shelf, a pattern of thinning and attenuation has long been recognized within the Jurassic deposits when traced northwards toward the southern margin of the Market Weighton Structure (Swinnerton and Kent 1976). Within the overlying sequence of Lower Cretaceous deposits a number of stratigraphical breaks are recognized, the extent of these breaks becoming more pronounced northwards. In Lincolnshire, the Carstone oversteps progressively older formations, i.e. the Sutterby Marl, Fulletby, Roach, Tealby, Claxby Ironstone and Spilsby Sandstone Formations, to rest directly upon the KCF in the South Ferriby area (Gaunt et al. 1992; BGS Lexicon of Named Rock Units 2021). Most of the KCF is eroded by the sub-Carstone unconformity at Middlegate Quarry; the lower KCF preserved there is 9–10 m thick (Wignall 1990; see below).

The Carstone has petrographic and mineralogical uniformity across Norfolk, Lincolnshire and Yorkshire, in contrast to the underlying Lower Cretaceous sandstones of
more local character (Versey and Carter 1926). However, there is some thickness and lithological variation across the region. Two distinct facies are recognized in the Carstone of southern Lincolnshire (Swinnerton 1935): the Carstone sands and clays, and overlying Carstone grits. Only the upper ‘grit’ facies is developed between Clixby and Melton, where it is up to 1 m thick (Fig. 1; Kelly and Rawson 1983). To the north of Melton, over the Market Weighton Structure in Yorkshire (e.g. Kent 1955; Mitchell 1996, 2000), the Carstone is patchily developed (Versey 1931; Jeans 1973; Gaunt et al. 1992; Whitham 1994; Mitchell 1996), often only a few centimetres thick, but is 3.7 to 6.7 m in Painthorpe Dale, where it may be an infilling of a channel or local fault trough in the eroded Jurassic surface (Jeans 1973). As at Middlegate Quarry (see above), Jeans (1973) noted considerable amounts of argillaceous material within the Carstone at some localities on the Market Weighton Structure, where it rests unconformably on Jurassic mudstones; the Carstone overlies the Upper Jurassic (Oxfordian) Amphilay Clay Formation at Melton Bottom (e.g. Sarjeant 1962), and the Lower Jurassic Lias Group at Goodmanham (De Boer et al. 1958).

The KCF is preserved to the north of the Market Weighton Structure in Yorkshire at thicknesses of up to 155 m (Gallois 2021). It is unconformably overlain by an expanded Lower Cretaceous Series (Berriasian to Albian), represented by the Speeton Clay Formation (100 m thick; Rawson et al. 1978) and overlying Hunstanton Formation (2021). It is unconformably overlain by a relatively expanded 

sands and clays, and overlying Carstone grits. Only the finer fraction which settled out above the coarser grains was sieved for palynology, as this was presumed to contain most palynomorphs present. All preparations were sieved with a 10 µm mesh. Carstone preparations were swirled in a dish to separate any remaining silicate grains and strewn on microscope coverslips after this stage. Post-HF kerogen slides were made for two of the KCF samples (PD9503-1 and -2). To improve the ratio of palynomorphs to amorphous organic matter (AOM; Table 1) for palynological study, KCF residues were oxidised with Schulze’s solution (70% nitric acid, HNO3, supersaturated with potassium chloride, KClO3) for between five minutes and one hour, followed by one subsequent rinse with a 2% potassium hydroxide (KOH) solution. Some oxidized preparations were stained with Safanin O solution (red stain).

Where palynological recovery permitted, approximately equal portions of quantified organic residues from each sample were strewn over three to six 22 × 22 mm coverslips, dried, and mounted onto microscope slides using Petropoxy 154. Palynomorph counts were conducted with an initial 100 specimen count, to establish the ratio between terrestrial and marine palynomorphs (T/M ratio), as a proxy of terrigenous nutrient input (see the discussion below). Counting was continued until 250 terrestrial palynomorphs and 250 marine palynomorphs were reached. From the dinoflagellate cyst counts, the ratio of mainly heterotrophic peridinioids (‘P-cysts’) to phototrophic gonyaulacoids (‘G-cysts’) was calculated, as a proxy of palaeo-productivity (see McLachlan et al. 2018 for a recent review of the P/G ratio). The remaining strewn material was examined for rare taxa outside of the count. Selected dinoflagellate cysts are illustrated in Figures 4–6.

Semi-quantitative abundances are recorded as rare (1 specimen or outside the count), frequent (2–4 specimens), common (5–14 specimens), abundant (15–49 specimens) or super-abundant (50+ specimens). The volumetric method described in Dodsworth et al. (2020) was used to estimate ‘absolute abundance’, i.e. the concentration of palynomorphs in each sample (counts per gram, cpg; Table 1). Given the errors inherent in calculating absolute abundances, numbers are expressed to three significant figures (as recommended by Pearce et al. 2020). Separate counts of 100 kerogen particles (AOM, brown and black phytoclasts, palynomorphs and cuticle) were made from the un-oxidized KCF and Carstone kerogen slides.

The Middlegate Quarry palynological microscope slides are curated at the Centre for Palynology, University of Sheffield. A full range chart of palynological data is available in the Supplementary Material. Full author names and synonyms of dinoflagellate cysts, algae and acritarchs can be found in Fensome et al. (2019a). Corrections to the nomenclature of Fensome et al. (2019a) proposed by Dodsworth et al. (2020), with respect to Peredoniunum crassimuratum (Davey and Williams) being a senior synonym, and Pearce et al. (2020) and Jarvis et al. (2021), with respect to Sepispina ambigua (Deflandre) being a senior synonym and a confident generic assignment, are used in this paper. In addition, we informally retain Cyclonephelium longispinatum (Davey), as C. ‘longispinatum’ in the text below and in Figures 3 and 4. Fensome et al. (2019a, b) considered C. longispinatum, a species initially reported from Upper Cretaceous deposits of offshore southwestern Africa (Davey 1978), to be a heterotypic junior synonym of Tenua anaphrissa (Sarjeant), a Barremian (Lower Cretaceous) marker taxon in NW Europe (Costa and Davey 1992). The synonymy is based on the holotype photograph of

Material and methods

KCF samples (5 g) and up to 180 g of Carstone samples were prepared for palynology, using hydrochloric acid (35% HCl) and hydrofluoric acid (40% HF) to dissolve carbonate and silicate minerals, respectively. After daily stirring of the Carstone samples in HF for at least two weeks, however, the coarser-grained silicates were disaggregated but mostly undissolved. Only the fine fraction which settled out above the coarser grains was sieved for palynology, as this was presumed to contain most palynomorphs present. All preparations were sieved with a 10 µm mesh. Carstone preparations were swirled in a dish to separate any remaining silicate grains and strewn on microscope coverslips after this stage. Post-HF kerogen slides were made for two of the KCF samples (PD9503-1 and -2). To improve the ratio of palynomorphs to amorphous organic matter (AOM; Table 1) for palynological study, KCF residues were oxidised with Schulze’s solution (70% nitric acid, HNO3, supersaturated with potassium chloride, KClO3) for between five minutes and one hour, followed by one subsequent rinse with a 2% potassium hydroxide (KOH) solution. Some oxidized preparations were stained with Safanin O solution (red stain).

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Table 1. Summary of palynomorph concentration (counts per gram, to three significant figures, >10 μm counts of 100 kerogen particles (AOM = amorphous organic matter; black and brown phytoclasts; cuticle; palynomorphs), gymnosperm pollen and pteridophyte/bryophyte spores as percentages of total terrigenous palynomorphs, and dinoflagellate cyst species richness (‘diversity’) of Cretaceous taxa in the Carstone and Jurassic taxa in the Kimmeridge Clay (obvious reworked specimens not included)

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<th>Lithostrat.</th>
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<th>Marine palynomorphs</th>
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<td>Gymnosp. (%)</td>
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<td>Phytoclasts (black)</td>
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T/M ratio, terrestrial/marine ratio. P/G ratio, the ratio between peridiniod (P) and gonyaulacoid (G) dinoflagellate cysts. rw., reworked.
C. longispinatum (Davey 1978, pl. 3, fig. 7) not displaying dorsoventral areas clearly devoid of ornament, and comparable thin processes on both taxa. However, *C. longispinatum* has a more symmetrical shape and less densely distributed processes than *T. anaphrissa*; its processes are longer, relative to central body diameter (c. one-eighth to one-fifth), than those on the holotype of *T. anaphrissa* (less than one-tenth; Sarjeant 1966, pl. 22, fig. 8). Dorsoventral areas devoid of processes were reported by Davey (1978) for *C. longispinatum* and are clearly visible on an illustrated specimen (Davey 1978, pl. 3, fig. 4) that he considered to be possibly transitional with *Cyclonephelium compactum* Deflandre and Cookson.

**Results**

In the upper part of KCF Bed 12, high concentrations of palynomorphs were recovered (119 000 cpg in sample PD9503-1; 59 700 cpg in sample PD9503-2). The Carstone samples yielded much lower concentrations (273–1330; average 755 cpg, from samples PD9503-3, RB10B, RB9B, RB8B and RB7B). An
Fig. 5. Cretaceous dinoflagellate cysts from the Carstone Formation in Middlegate Quarry. All specimens were photographed at x400. Sample slide numbers and England Finder co-ordinates are given. 1. Cauca parva, RB10B(1), H44/4; 2. Carpodinium granulatum, RB10B(5), E31/1; 3. Codoniella psygma, RB8B(5), X47/3; 4. Kiokansium prolatum, RB10B(1), Q30/2; 5. Leptodinium? hyalodermopses sensu Davey (1982), RB9(B), Q46/2; 6. Dingodinium alberti, RB7B(2), B42/0. (a) Focus on apical region, including periphragm horn. (b) Focus on antapical region and caviation; 7. Litosphaeridium? sp., RB7B(2), M46/4. Broken specimen with c. 16 processes which are dome-shaped, typical of the genus (Stover and Evitt 1978; Lucas-Clark 1984); 8. Kiokansium uniberculatum, RB8B(3), Q42/3; 9. Leptodinium cancellatum, RB10B(1), H43/1; 10. Microdinium setosum, RB10B(2), C42/0; 11. Microdinium? cristatum, RB8B(6), X42/2; 12. Cometophidium? comatum, RB7B(3), H33/4; 13. Ellipsidictyum imperfectum subsp. imperfectum, RB8B(3), X37/4; 14. Protoellipsoidium spinosum, RB9B(2), U43/1; 15. Protoellipsoidium clavulus subsp. clavulus, RB10B(2), U29/2; 16. Protoellipsoidium spinocristatum, RB8B(3), M32/4; 17. Spiniferites cf. jarvisii, RB7B(2), H33/2. Note the thickened intra-plate areas. This morphotype is possibly transitional between Pterodinium crassimuratum and Spiniferites jarvisi; 18. Discorsia nannus, RB10B(5), T34/4.
exception is the sample PD9503-4 which is almost entirely composed of reworked Upper Jurassic taxa and has a corresponding high concentration of palynomorphs (67,200 cpg). Samples from the upper part of the Carstone are impoverished of palynomorphs (sample RB6B, 11 specimens only, <1 cpg) or barren (sample RB5B). Two additional samples were collected from the Hunstanton Formation (detailed positions not recorded) but these are also barren of palynomorphs.

The dinoflagellate cyst assemblages from the KCF contain between 34 and 49 (average 39) taxa. The Carstone

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assemblages contain between 61 and 96 (average 81) in situ taxa from samples PD9503-3 and RB10B to RB7B. The KCF samples are dominated by G-cysts, occurring at a stratigraphically deeper level within the Lower Kimmeridgian than the widespread inception of P-cysts, including that of Corculodinium inaffectum in the Mutabilis Ammonite Zone (see below). In the Carstone, G-cysts are also prominent, with the Spiniferites ramosus ‘group’ and Oligosphaeridium complex being consistently abundant (Fig. 3). P-cysts are mainly represented by Palaeoperidinium cinctum (Fig. 6.6), with subordinate Oovodinium spp. and Subtilisphaera spp., but comprise not more than 5.3% of dinoflagellate cyst assemblages.

The prasinophyte algae Pterospermella and Tasmanites are frequent in most samples from the KCF and Carstone, while Leiosphaeridia is abundant in the KCF and rare in the Carstone. Acritarchs, mainly Micrhystridium (Acanthomorphitae), with subordinate Veryhachium (Polygonomorphitae), are common to abundant in the KCF and frequent to common in the Carstone. Fresh/brackish-water algae, mainly Botryococcus braunii Kützing and Lecaniella foveata Singh, are sporadically present but rare in both the KCF and Carstone.

In the KCF, terrigenous pollen and spores dominate over marine palynomorphs, with a T/M ratio of 0.71 to 0.86 (average 0.78; Table 1). Gymnosperm pollen are prominent, mainly represented by bisaccate pollen, associated with common Araucariacites australis Cookson, Callialasporites (including C. dampieri (Balme) and C. turbatus (Balme)), Cerebropollenites macroverrucosus (Fig. 4.4), E. tumulus (Balme) and Cribroperidinium globatum (Acanthomorphitae), with subordinate Microsphaeridium Schulz and Exesipollenites (mainly E. tumulus Balme). A marked influx of the last occurs immediately below the Jurassic–Cretaceous boundary, comprising over one-half of the terrigenous assemblage in samples PD9503-1 and -2. Reworked Exesipollenites is also recorded in abundance immediately above the boundary, in samples PD9503-3 and -4. The remainder of the palynologically productive Carstone, overlying samples RB10B to RB7B, contain a T/M ratio of 0.22 to 0.49 (average 0.36) and relatively uniform terrigenous assemblages dominated by bisaccate pollen (average 72%) associated with smooth-walled trilette pteridophyte/bryophyte spores, mainly Deltoideospora and Gleichenidites (average 18%).

In the >10 μm fraction of the kerogen, the KCF samples are dominated by AOM, a typical feature of the formation. In Carstone samples, phytočlasts and palynomorphs are prominent. The ratio of the former to the latter appears to increase up-section between samples RB10B and RB7B (Table 1) although, with just four samples considered, it is unclear whether this apparent trend is significant. The swirling stage of preparation of Carstone samples (see above) may have biased the Carstone residues, in terms of removal of larger relatively dense phytočlasts from the kerogen.

**Biostратigraphy of Kimmeridge Clay Formation Bed 12**

The Global Stratotype Section and Point (GSSP) for the base of the Kimmeridgian Stage and, by default, that of the Lower Kimmeridgian Substage, have recently (February 2021) been ratified by the IUGS. The boundary is dated as 157.3 ± 1.0 Ma (International Commission on Stratigraphy, ICS 2021) and placed in the upper part of Bed 35 of the Staffin Shale Formation at Flodigarry, Staffin Bay, Isle of Skye, Scotland (https://jurassic.stratigraphy.org).

At Middlegate, the lowermost Kimmeridgian Baylei Ammonite Zone is present in beds 9–10 of Birkelund and Callomon (1985), 8.2–14.2 m above the base of the section in 1993. The overlying intra-Lower Kimmeridgian Cymodoce Ammonite Zone is present in Bed 11, 14.2–14.4 m, and Bed 12, 14.4–17.2 m, immediately below the Jurassic–Cretaceous unconformity (Wignall 1990). The remaining ammonite zones of the Kimmeridgian are eroded by the unconformity.

Research on the dinoflagellate cyst floras of the UK Kimmeridgian is extensive and well-established (e.g. Gitmez 1970; Gitmez and Sarjeant 1972; Riley 1974; Birkelund et al. 1983; Riding 1984, 1987, 2005; Nohr-Hansen 1986; Riding and Thomas 1988, 1992, 1997; Thomas and Cox 1988; Bailey 1993; Bailey et al. 1997). Typical Lower Kimmeridgian dinoflagellate cyst assemblages are recovered from Bed 12 at Middlegate, including common to abundant occurrences of longer ranging taxa such as Chytroeisphaeridia ctyroideaes (Figs 4.9 and 4.10), Cribroperidinium globatum ‘group’, Dichadogonyaulax chondra (Fig. 4.4), Gonyaulacysta jurassica subsp. jurassica (Fig. 4.6), Mendicodinium groenlandicum, Pareodina ceratophora, Rhynchodiiniopsis cladophora, Scriniodinium dictyotum subsp. pyrum (Fig. 4.1), Tubotuberella apatela (Fig. 4.8) and Valensiella ovatum. The presence of Senoniaasphaera jurassica (sample RB1C, 15.4–15.5 m) confirms an age no older than Early Kimmeridgian, while Endocrinitum luridum (Fig. 4.5), S. dictyotum subsp. pyrum and Stephanelectron calytones (all present in the top 0.15 m of Bed 12) confirm an age no younger than Early Kimmeridgian. In addition, the presence of Dingodinium tuberosum (sample RB4, 14.4–14.5 m) is consistent with a broad latest Oxfordian to Early Kimmeridgian age (cf. Woollam and Riding 1983; Riding and Thomas 1992; Poulsen and Riding 2003).

The UK dinoflagellate cyst Zone Elu(a) of Riding and Thomas (1992), and corresponding NW Europe Zone DSJ28 of Poulsen and Riding (2003), have been calibrated to the Cymodoce Ammonite Zone by these authors. An absence of taxa with range bases in Zone Elu(b) (upper DSJ28–29), calibrated to the overlying Mutabilis Ammonite Zone of the Lower Kimmeridgian, namely Corculodinium inaffectum and Perissieisphaeridium pannosum, confirms a stratigraphical position for Bed 12 below this level. Taxa with range tops in Zone Scr(d) (DSJ27), namely Gongayaulacysta eisenackii, Nannoceratopsis pellucida and Scriniodinium crystallinum, calibrated to the underlying Baylei Ammonite Zone are also absent, apart from isolated, possibly reworked specimens in sample RB11B (N. pellicida) and PD9503-2 (17.1–17.15 m; S. crystallinum). Scriniodinium crystallinum is a consistent component of assemblages in the (Oxfordian) Amphitill Clay Formation at Middlegate (0–8.2 m above the base of the section in 1993; cf. Stancliffe 1984). Bed 12 is assigned on the basis of the above discussion to Zone Elu(a).

**Biostratigraphy of the Carstone Formation**

There is no direct ammonite evidence for the age of the Carstone on the East Midlands Shelf or Market Weighton Structure. The presence of indigenous Lower Cretaceous
Dinoflagellate cysts allow deductions to be made about its age at Middlegate.

The base of the Albian Stage and Lower Albian Substage, dated as c. 113.0 Ma (ICS 2021), has a ratified GSSP at 37.4 m above the topmost limestone of the Faiseau Fromaget (the section’s zero datum) at Col de Pré-Guitard in the Vocontian Trough, SE France (Kennedy et al. 2017). The boundary is denoted by the First Appearance Datum there of the planktonic foraminifer Microhedbergella renilaevis Huber and Leckie. This stratigraphical level is lower than previous placement of the Aptian–Albian stage boundary as determined by ammonites, at the base of the Tardefurcata Zone (see Kennedy et al. 2000 for a historical review) and assigned from 68.0 m at Col de Pré-Guitard. The GSSP at 37.4 m correlates with mid-levels of the underlying Jacobi Zone which is assigned between the zero datum and 68.0 m. The zone is named for the ammonite Hysacanthophytes jacobi (Collet). Although H. plesiopcytos (Fritzel) is now considered to be its senior synonym, the Jacobi zonal name is retained (Kennedy et al. 2000). The distributions of some of the Aptian–Albian dinoflagellate cyst marker taxa discussed below were documented by Davey, in Kennedy et al. (2000) at Col de Pré-Guitard and the nearby Tartonne section.

**Dinoflagellate cyst range bases**

Intra-Tardefurcata Zone range bases have been calibrated for the Albian-restricted marker taxa Endoscrinium heikeae (Fig. 6.12; Prössl 1990; Duxbury 2001), Litosphaeridium arundum (Davey and Verdier 1971; Costa and Davey 1992; Duxbury 2001) and Odontochitina singhii (Kennedy et al. 2000; Duxbury 2001). Only the first of these is recorded at Middlegate, in the RB10B to RB7B samples (Fig. 3). An isolated questionable specimen of Litosphaeridium (Fig. 5.7) in sample RB7B probably has too few processes (approximately one per paraplate area) to be assigned to L. arundum (cf. Lucas-Clark 1984).

At Middlegate, Cyclonephelium intonsum (Fig. 6.4) is rare but present in most Carstone samples. Its only previously published UK record may be from a relatively short stratigraphical interval, upper-Jacobi Zone to intra-Tardefurcata Zone on the Isle of Wight (Duxbury 1983). More widely distributed (NW Europe) taxa with known lowest occurrences either at the base of the Tardefurcata Zone or in the upper Jacobi Zone are Cyclonephelium compactum (Fig. 6.2), Stephodinium coronatum (Fig. 6.10) and Stephodinium spinulosum (Fig. 6.11; Davey 1982; Duxbury 1983, 2001; Costa and Davey 1992). Significantly, Kennedy et al. (2000) only recorded C. (cf.) compactum and S. coronatum from the Albian at Col de Pré-Guitard and Tartonne (C. intonsum and S. spinulosum were not recorded there). The presence of all four taxa in the lowermost Carstone sample at Middlegate (PD9503-3), a clast or lens of sandstone that is lighter-coloured than the encasing deposits, suggests an age probably not older than Albian.

**Leptodinium cancellatum** (Fig. 5.9) has a basal consistent occurrence around the Tardefurcata–Jacobi zonal boundary (Duxbury 2001) but can also occur sporadically throughout the Upper Aptian (Costa and Davey 1992). Canninginopsis monile (Fig. 6.1) has a range base in the Jacobi Zone (Duxbury 2002). Ellipsoidictyum imperfectum subsp. imperfectum (Fig. 5.13) has a range base in intra-Upper Aptian deposits (pre-Jacobi Zone), as does Kiokiansium prolatum (Fig. 5.4; Costa and Davey 1992; Duxbury 2001) and possibly Microdinium setosum (Fig. 5.10; Davey 1982). All five taxa are present in most Carstone samples, including consistent L. cancellatum in samples RB10B to RB7B, though only E. imperfectum subsp. imperfectum is recorded in the lowermost sample PD9503-3.

**Dinoflagellate cyst range tops**

The following taxa occur consistently in the Carstone at Middlegate and have range tops reported from the Tardefurcata Zone (Duxbury 1983, 2001, 2002; Costa and Davey 1992; Kennedy et al. 2000): frequent Canninginopsis monile and frequent Kleithriasphaeridium coenoides (Fig. 6.7), rare Discorsia nannus (Fig. 5.18) and rare Kiokiansium prolatum. Occasional specimens of Dingodinium albertii (Fig. 5.6) and Occiscycla tentorium (Fig. 6.8), along with common Kiokiansium unituberculatum (Fig. 5.8) also indicate a stratigraphical position probably no higher than the Tardefurcata Zone (Costa and Davey 1992; Duxbury 2001). Common Ellipsoidictyum imperfectum subsp. imperfectum supports an age not younger than Early Albian (cf. Duxbury 2001). Protoellipsoidinium clavus subsp. clavus (Fig. 5.15) is present in most of the Carstone samples. It has a range top in the Tardefurcata Zone on the Isle of Wight (Duxbury 1983) but has a deeper (Jacobi Zone) range top farther north in the Central North Sea (Duxbury 2001).

At Middlegate, Cauca parva (Fig. 5.1) is common to abundant in the lower part of the Carstone (samples PD9503-3, RB10B). It occurs throughout the Aptian and Albian stages in NW Europe (e.g. Costa and Davey 1992) and is abundant at some levels within the Aptian (e.g. Davey 1982; Duxbury 1983). It has a top common occurrence in the Tardefurcata Zone of the North Sea region (Duxbury 2001). At Col de Pré-Guitard and Tartonne, Kennedy et al. (2000) reported it to be relatively rare, apart from an isolated common occurrence in the Tardefurcata Zone at the former locality (their sample 15a, at c. 69 m above the zero datum).

**Reworking in the Carstone**

Isolated occurrences of dinoflagellate cysts that are typical of Aptian deposits (i.e. those with intra- or pre-Jacobi Zone range tops) are interpreted as reworked: Aptea polymorpha (sample RB10B) and questionable Cerbia tabulata (samples RB8B and RB9B). Other widely occurring Aptian forms (e.g. Davey and Verdier 1974; Duxbury 1983, 2001, 2019; Costa and Davey 1992) such as Chlamydophorella trabeoculosa, Circulodinium vectense, Spiculodinium neptuni and (with the exception of a questionable specimen in sample RB10B) Systematophora silyba, were not recorded at Middlegate. Isolated specimens of Callaoiasphaeridium trycherium, Desmocysta plekta and Druggidium augustum in sample RB10B, along with Nexosispinum vetusculum and questionable Heslertonia heslertonensis in sample RB7B, are probably reworked from pre-Upper Aptian, Lower Cretaceous deposits (cf. Duxbury 1977, 1980, 2001, 2018, 2019; Costa and Davey 1992).

Evidence from reworked macrofossils and mineralogy suggests that the Carstone in eastern England is mainly

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Kimmeridge Clay and Carstone palynology

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derived from older Lower Cretaceous sandstones (Strahan 1886; Versey and Carter 1926; Swinnerton 1935; Casey 1961; Gaunt et al. 1992). The paucity of corresponding reworked Lower Cretaceous dinoflagellate cysts at Middlegate might be explained by oxidative destruction of palynomorphs in original coarse-grained host rocks or during subsequent transport.

The majority of reworked dinoflagellate cysts in the Carstone are derived from Upper Jurassic deposits. The same taxa that are recorded in situ in KCF Bed 12 comprise the bulk of the reworked specimens (see the supplementary palynological range chart). They are abundant in the basal Carstone clast or lens sample PD9503-3 (possibly as encasing reworked mudstone contaminants) and dominate in the overlying sample PD9503-4. Although mainly represented outside of the 250 microplankton count, 10–20 reworked Upper Jurassic taxa are also present in each of the overlying RB10B to RB7B Carstone samples. Single specimens of Perissesaephaeridium pannosum in samples RB8B and RB7B indicate an additional reworking component from stratigraphically higher levels of the KCF than those preserved at Middlegate (cf. Riding and Thomas 1992; Poulsen and Riding 2003). Amongst the terrigenous palynomorphs, prominent Exesipollenites, occurring in situ in the 0.15 m section below the Jurassic–Cretaceous unconformity, and reworked in the 0.15 m section above it, confirm mainly local derivation of mudstone matrix into the Carstone.

**Dinoflagellate cyst zonation of the Carstone**

The presence of dinoflagellate cysts with NW Europe range/ event tops in the Tardefurcata Zone, and range bases in the Tardefurcata Zone or upper part of the underlying Jacobi Zone, suggest an Early Albian age for the Carstone at Middlegate (Fig. 3). The section from 0.15 m (sample RB10B) to 0.55 m (sample RB7B) above the basal unconformity is assigned to dinoflagellate cyst Zone LKP32 of Duxbury (2001, 2002). The prominence of reworked Upper Jurassic taxa between the unconformity and 0.15 m above it renders precise dating of that part of the section less well-constrained. The presence of comparable Lower Cretaceous dinoflagellate cyst assemblages immediately above the unconformity, including rare C. intonsum, S. coronatum and S. spinulosum, and common C. compac-tum, suggests assignment to Zone LKP32 or LKP31.2, respectively corresponding to the Tardefurcata and upper Jacobi ammonite zones. The base of the Carstone may correlate with the Central North Sea LK32.1 maximum flooding event proposed by Duxbury (2001).

**Palaeoenvironments**

**Kimmeridge Clay Formation**

The species composition of dinoflagellate cyst assemblages from Bed 12 at Middlegate is comparable to those from Early Kimmeridgian open marine settings elsewhere in the UK (e.g. Riding 1987, 2005; Riding and Thomas 1988, 1992). Their diversity, along with an abundance of ammonites in Bed 12 (Wignall 1990) suggests an open marine palaeo-environment. The fine-grained organic-rich nature of the rocks indicates sedimentation under low-energy, generally quiescent conditions, a setting likely to produce poor oxygenation of the water column. Work by Wignall (1990) on the benthic fauna of the Ancholme Clay at Middlegate (Bivalvia, Gastropoda, Scaphopoda, Brachiopoda, Crustacea, Echinodermata, Annelida and Bryozoa) indicates variations in the diversity of the macro-benthos that were attributed to corresponding variations in oxygen depletion of bottom waters. This may have been compounded by the absence of an effective oxygen-replenishment mechanism and the development of a temporary temperature/density barrier within the water column (Wignall 1990). The upper part of Bed 12 records a decline in ostracods (Ahmed 1987) and a rapid disappearance of previously diverse macro-benthos (Wignall 1990), possibly indicating relatively early onset of regional anoxic benthic conditions associated with the KCF (Wignall 1990). This is consistent with the preservation of high concentrations of AOM and palynomorphs, 59 700–119 000 cpg in the 0.15 m interval below the Jurassic–Cretaceous unconformity (Table 1). In the Mesozoic of eastern England, concentrations as high as this have only previously been reported from organic-rich deposits of the Cenomanian–Turonian boundary interval, which correlate with the global Cretaceous Oceanic Anoxic Event 2 (Dodsworth et al. 2020). Frequent prasinophyte algal genera Pterospermella and Tasmanites and abundant Leiosphaeridia in Bed 12 possibly indicate oxygen-deficient waters periodically encroaching the photic zone during its deposition (cf. Prauss 2007).

The large terrigenous component of palynological assemblages from Bed 12 (average T/M ratio of 0.78) would have been sourced by wind and run-off from adjacent landmasses such as a ‘Pennine Massif’ and ‘London-Brabant Massif’ (e.g. Brookfield 1973). Abbink et al. (2004) outlined a model using pollen and spore eco-groups as indicators for terrestrial palaeoenvironments during the Jurassic. The dominance of the ‘upland’ group in Bed 12, i.e. relatively buoyant bisaccate conifer pollen (Travis and Ginsburg 1966), is consistent with a low-energy, possibly distal to palaeo-coastline depositional setting (cf. Batten 1996). The secondmost numerically important group in Bed 12 are the gymnosperm genera Araucariacites, Callialasporites, Cerebropollenites, Classopollis and Exesipollenites. Their parent plants may have mainly grown along the coast (Abbink et al. 2004). The marked increase in the ratio of coastal to upland pollen in the 0.15 m interval below the Jurassic–Cretaceous unconformity at Middlegate (i.e. an influx of Exesipollenites) possibly reflects a local or regional fall in relative sea level.

**Carstone Formation**

Most of the indigenous dinoflagellate cysts in the Carstone are G-cysts (average P/G ratio of 0.026). Modern gonyla-coid dinoflagellates are photosynthetic with high relative abundances occurring in areas of seas with lower productivity of heterotrophic phytoplankton, such as (proto-) peridinioid dinoflagellates (Harland 1988). Dinoflagellate cyst diversity is partly a function of environmental stress, with lower stress resulting in higher diversity (Wall et al. 1977). Generally, environmental stress decreases and species richness increases from near-shore to distal-shore areas (e.g.
Olde et al. 2015). The high diversity and low dominance (no taxa exceed 15% of assemblages) of G-cysts in the Carstone at Middlegate suggest a low-stress, open marine palaeoenvironment, with relatively low nutrient input and associated palaeo-productivity of peridinoid dinoflagellates. Open marine conditions are also indicated by the nature of indigenous brachiopod assemblages in the upper part of the Carstone (Gaunt et al. 1992).

Apart from thick-bedding, sedimentary structures may not have been preserved in the Carstone of the East Midlands Shelf (e.g. Versey and Carter 1926; BGS Lexicon of Named Rock Units 2021). Gaunt et al. (1992) considered its lithologies to suggest an upper shore-face site of deposition. The prominence of phytoflagellates in samples RB10B to RB7B, along with common pteridophyte/bryophyte trilette spores, support a relatively proximal to shoreline depositional setting and/or fluvial–deltaic influence (cf. Prauss 1993; Stead and Batten 2018). In addition, Prauss (2000) suggested that associations of increased numbers of Cauca parva and the P-cyst Palaeoperidinium cretaceum in Aptian–Lower Albian deposits of NW Europe, as seen to a limited extent in Carstone samples PD9503-3 and RB10B, may indicate an estuarine influence (see also Harding 1990). At Middlegate, however, the low T/M ratio (average 0.36), high diversity of G-cysts with low numbers of P-cysts, and sparsity of fresh/brackish-water algae, conversely indicate limited nutrient supply from land-derived run-off. The palynological data could be interpreted to indicate an ultimate site of deposition at Middlegate farther offshore than upper shore-face but still above storm wave base, such as inner to middle neritic.

Gaunt et al. (1992) reported that the genus Odontochitina, a relatively thick-walled dinoflagellate cyst, is the main palynomorph preserved in their eastern England Carstone samples. It is possible that local ‘sheltered’ conditions, such as a topographic trough in the seafloor of the Middlegate area, may have led to enhanced preservation due to reduced winnowing of clay- and silt-grade particles (including palynomorphs). Possible establishment of dysoxia within sediments could also have locally impeded oxidation of palynomorphs, particularly of the more delicate dinoflagellate cyst forms.

Frequent to common occurrences of the prasinophyte algae Pierospermella and Tasmantites in Carstone samples RB10B to RB7B may be reworked from the KCF. Alternatively, they may be contemporary with the Carstone, derived from lower salinity, possibly lagoonal areas (e.g. Tappan 1980; Vieira and Jolley 2020) or, unlikely given there is no other evidence for oceanic anoxia during deposition of the Carstone, reflect oxygen-deficient conditions in the water column (cf. the KCF discussion above).

The extinct areoligeracean group of G-cysts are mainly represented by the species Circulodinium distinctum (Fig. 6.3), Cyclonephelium compactum and Cyclonephelium ‘longispinatum’ (Fig. 6.5) at Middlegate. They occur consistently in the Carstone samples, with the latter two showing an increase in relative abundance in samples RB9B and RB8B (Fig. 3). They are fairly ubiquitous in Lower Albian marine assemblages of NW Europe (Davey 1982; Duxbury 1983; Prössl 1990; Kennedy et al. 2000; Prauss 2000) but the increase may be significant in terms of a greater coastal/near-shore influence (cf. Brinkhuis and Zachariasse 1988; Harker et al. 1990, p. 202–204; Li and Habib 1996; Olde et al. 2015). The areoligeracean species Canninginopsis monile has not previously been reported in NW Europe outcrops. It is documented from the Central North Sea, offshore of northern Scotland (Duxbury 2002), and its presence at Middlegate (Fig. 3) may therefore indicate sea palaeo-currents from the north. The non-areoligeracean, related genera Palaeoetraedinium and Rhombodella, are frequent to common in the Carstone samples (see the supplementary palynological chart). Prauss (2000) noted that their presence in Aptian–Albian assemblages of NW Germany potentially indicates boreal to subboreal water masses, given that they are the dominant dinoflagellate cysts at some levels within the Albian of NE Greenland (Nøhr-Hansen 1993). Cauca parva may also occur in higher numbers in the more northerly areas of Europe (Prauss 2000).

Conclusions

Well-preserved palynomorph assemblages were retrieved from the grey mudstones of KCF Bed 12 at Middlegate. Dinoflagellate cyst species composition and diversity supports ammonite evidence for an open marine palaeoenvironment. High concentrations of AOM and palynomorphs in upper Bed 12 are consistent with oxygen-deficient bottom waters, as indicated by lithology and the decline of benthic macrofauna. Zonal dinoflagellate cyst marker taxa present are in agreement with regional calibration of Zone Elu(a) to the Cymodoce Ammonite Zone.

Palynological assemblages from the lowermost 0.15 m above the sub-Carstone unconformity are dominated by reworked, mainly locally derived KCF palynofloras. This is reflected by the grey colouration of the basal Carstone matrix at Middlegate which is caused by an admixture of KCF mudstone. A clast or lens of relatively light-coloured sandstone, sampled immediately above the unconformity, is interpreted to be of earliest Albian age, based on the presence and absence of stratigraphically important Lower Cretaceous dinoflagellate cysts (Zone LKP31.2–LKP32; upper Jacobi or Tardefurcata Ammonite Zone). On the Isle of Wight, Duxbury (1983) recorded comparable assemblages from Lower Albian mudstones underlying the Carstone, but pre-Carstone deposits of this age are not widely preserved on the East Midlands Shelf.

Relatively grey colouration of the Carstone matrix is also observed in the interval from 0.15 to 0.45 m above the unconformity, where reworked KCF palynofloras are a relatively minor component of assemblages. Indigenous Lower Cretaceous dinoflagellate cysts are interpreted to indicate an Early Albian age (Zone LKP32; Tardefurcata Ammonite Zone) for the interval. This is also the case for a sample from 0.45 to 0.55 m above the unconformity which has relatively orange colouration. The uppermost Carstone samples analysed (0.55–0.75 m) have orange to red colouration and are impoverished or barren of palynomorphs.

The palynological and palynofacies assemblages from the Carstone are interpreted to indicate a relatively proximal to shoreline site of deposition, possibly inner to middle neritic, with an open marine palaeoenvironment and limited supply of terrigenous nutrients washed-in from fluvial–deltaic and estuarine/lagoonal sources. Northerly palaeo-currents or
water masses may have contributed to subtle phytoplankton provincialism relative to coeval deposits in southern England, France and, to a lesser extent, NW Germany.

Future palynological study of the Carstone is recommended at other localities, to further assess palaeoenvironments and the timing of onset of preservation of sediments above the sub-Carstone unconformity. While coarse-grained gritty sandstones are not generally conducive to palynological preservation, as seen at Middleedge, an argillaceous component to the matrix can support preservation. Successful palynological investigations have previously been carried out on Aptian–Albian sandstone-dominated formations in southern England (e.g. Cookson and Hughes 1964; Duxbury 1983; Hesselbo et al. 1990).

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Author contributions

RDB: conceptualization (equal), formal analysis (equal), investigation (equal), writing – original draft (supporting); PD: conceptualization (equal), formal analysis (equal), investigation (equal), writing – original draft (lead).

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Data availability

All data generated or analysed during this study are included in this published article (and its supplementary information files).

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References


