

# The palaeoenvironment associated with a partial *Iguanodon* skeleton from the Upper Weald Clay (Barremian, Early Cretaceous) at Smokejacks Brickworks (Ockley, Surrey, UK), based on palynomorphs and ostracods

Eleanor Nye<sup>a</sup>, Susanne Feist-Burkhardt<sup>a,\*</sup>, David J. Horne<sup>b,c</sup>,  
Andrew J. Ross<sup>a</sup>, John E. Whittaker<sup>a</sup>

<sup>a</sup> Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

<sup>b</sup> Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

<sup>c</sup> Department of Geography, Queen Mary, University of London, Mile End Road, London E1 4NS, UK

Received 20 June 2007; accepted in revised form 8 January 2008

Available online 6 February 2008

## Abstract

In 2001 a partial skeleton of an *Iguanodon* was discovered in the Upper Weald Clay (Barremian, Early Cretaceous) at Smokejacks Brickworks near Ockley, Surrey, UK. When the dinosaur was excavated, a detailed stratigraphic section was logged and 25 samples taken for palynological and micropalaeontological (ostracod and megaspore) analysis, including a detailed sample set of the dinosaur bed itself. Qualitative and quantitative analysis of the palynoflora revealed rich and well-preserved non-marine assemblages of pollen and spores, including early angiosperms, and freshwater green algae. Four types of angiosperm pollen are described and assigned to the genus *Retimonocolpites* Pierce, 1961, but left in open nomenclature. Some marine elements such as dinoflagellate cysts are identified as the result of reworking of Middle and Upper Jurassic sediments. The pollen/spore assemblages depict a vegetational change from principally gymnosperm-dominated assemblages at the base to principally pteridophyte-dominated assemblages at the top of the section. The dinosaur bed shows a pteridophyte-dominated assemblage, with a significantly high amount of the freshwater green alga *Scenedesmus novilunaris* He Cheng-quan et al., 1992. Samples close to the dinosaur bed yielded the first useful ostracod finds from Smokejacks Brickworks: well-preserved assemblages containing *Cypridea clavata* (Anderson, 1939), *Damonella* cf. *pygmaea* (Anderson, 1941), *Stenestroemia* cf. *cressida* Anderson, 1971 and *Stenestroemia* sp. A, and fragments and damaged valves of a thin-shelled ostracod, possibly belonging to *Mantelliana* Anderson, 1966. Those identified as *Cypridea clavata* show a wide range of morphological variety and in opposition to Anderson's (1967, 1985) taxonomic scheme, which would assign them to up to five different taxa, they are considered to be intraspecific variants of a single species. The possibilities and limitations of age determination of the Wealden sediments using palynomorphs and ostracods are discussed; distinct forms of early angiosperm pollen, together with the ostracod fauna, are consistent with an early Barremian age. Pollen and spores are discussed in terms of their parent plants and the reconstruction of vegetation and palaeoclimate. Palynology and ostracods give evidence for temporary freshwater conditions at the time when the *Iguanodon* died and the carcase was buried.

© 2008 The Natural History Museum. Published by Elsevier Ltd. All rights reserved.

**Keywords:** Lower Cretaceous; Wealden; England; Palynology; Ostracods; Megaspores; *Iguanodon*; Palaeoenvironment; Palaeoclimate; Preservation

## 1. Introduction

The sediments exposed at Smokejacks Brickworks near Ockley, Surrey, UK (Fig. 1), have long been of interest due

to the occurrence of fossil vertebrate remains, most famously the 1983 discovery of the fish-eating theropod dinosaur *Baryonyx walkeri*, described by Charig and Milner (1997). On 22nd July 2001 a partial skeleton of the dinosaur *Iguanodon atherfieldensis* Hooley, 1925 was discovered by Mr Geoff Toye on a Geologists' Association field trip (Austen, 2001). That summer a team from the Natural History Museum, London,

\* Corresponding author.

E-mail address: s.feist-burkhardt@nhm.ac.uk (S. Feist-Burkhardt).

excavated the dinosaur, measured sections and collected samples for palynological and micropalaeontological studies. The dinosaur remains show exceptionally good preservation and the micropalaeontological samples have yielded a well-preserved ostracod assemblage previously unrecorded from the locality, along with rich microfloral assemblages. Associated with the *Iguanodon* were *Baryonyx* teeth, a turtle plate, crocodile scute, scales of the freshwater fish *Lepidotes* and bivalve molluscs. Palynomorphs were recovered from 24 samples including a detailed set from the dinosaur bed and a 10 m section encompassing the sediments above and below this bed. Ostracods and megaspores were recovered from samples of the dinosaur bed. We use the micropalaeontological evidence to reconstruct the local palaeoenvironment of the time during which the *Iguanodon* lived and died.

## 2. Geological setting

### 2.1. The Wealden Supergroup

The Wealden Supergroup (divided into the Hastings Group and the Weald Clay Group) consists of a sequence of alternating sand-dominated and clay-dominated formations deposited by rivers and fresh or brackish water lakes in two interconnected subsiding basins (the Weald and Wessex sub-basins) in an area that now forms southern England (Allen, 1981, 1990).

The climate was a seasonal, hot to warm (mean annual temperature around 25 °C), ‘Mediterranean’ type climate, alternating with cooler periods (mean annual temperature around 10 °C); rainfall was high during times dominated by sand deposition (Ashdown Beds, Lower and Upper Tunbridge Wells Sand formations, all of the Hastings Group), while clay-dominated times (Wadhurst Clay and Grinstead Clay formations of the Hastings group, Weald Clay Group) were drier (Sladen and Batten, 1984; Allen, 1998). Storms resulted in flash floods and wildfires ignited by lightning (Allen, 1998; Wright et al., 2000). Some (e.g., Allen, 1998) have regarded

the dry intervals as periods of drought, but Haywood et al. (2004) suggested that there may have had substantial precipitation as high as 4–8 mm/day, and that high surface temperatures (possibly reaching 36–40 °C) may have resulted in evaporation rates that exceeded rainfall, giving restricted soil moisture levels as opposed to prolonged drought.

### 2.2. Weald Clay Group stratigraphy

In the Weald Sub-basin the Weald Clay Group forms a low-lying C-shaped outcrop in the Weald and reaches a maximum thickness of 740 m (Fig. 1). It consists of non-marine fluvial/deltaic/lacustrine floodplain deposits and is dominated by argillaceous lithologies (typically silty mudstones), but includes numerous horizons of sandstone, shelly limestone and clay ironstone (Worssam, 1978; Batten, 1998; Rasnitsyn et al., 1998). Thurrell et al. (1968) introduced a scheme, modified from Topley (1875), in which every mapped sandstone and limestone bed in the Weald Clay was given a number; nowadays these are referred to as British Geological Survey (BGS) bed numbers. Allen (1976) gave names to many of these beds. Worssam (1978) recognised two major cyclic units in the Weald Clay which he termed the lower and upper divisions and which have been regarded as formations by subsequent authors (e.g., Gallois and Worssam, 1993; Rasnitsyn et al., 1998), although some (e.g., Batten, 1998) have referred to the whole Weald Clay Group as a single formation. The Lower Weald Clay Formation corresponds more or less to the Hauterivian Stage and overlies the Valanginian sandstones of the Upper Tunbridge Wells Sand Formation (Hastings Beds Group). The base of the Upper Weald Clay Formation is represented by BGS Bed 3a (the Okehurst Sand/Sandstone of Allen, 1976, equivalent to the top of Topley’s Bed 5) which also constitutes a good lithological marker of the Hauterivian/Barremian boundary, although biostratigraphical considerations place the boundary a little below the sandstone (see discussion in Horne, 1995 and Batten, 1998).

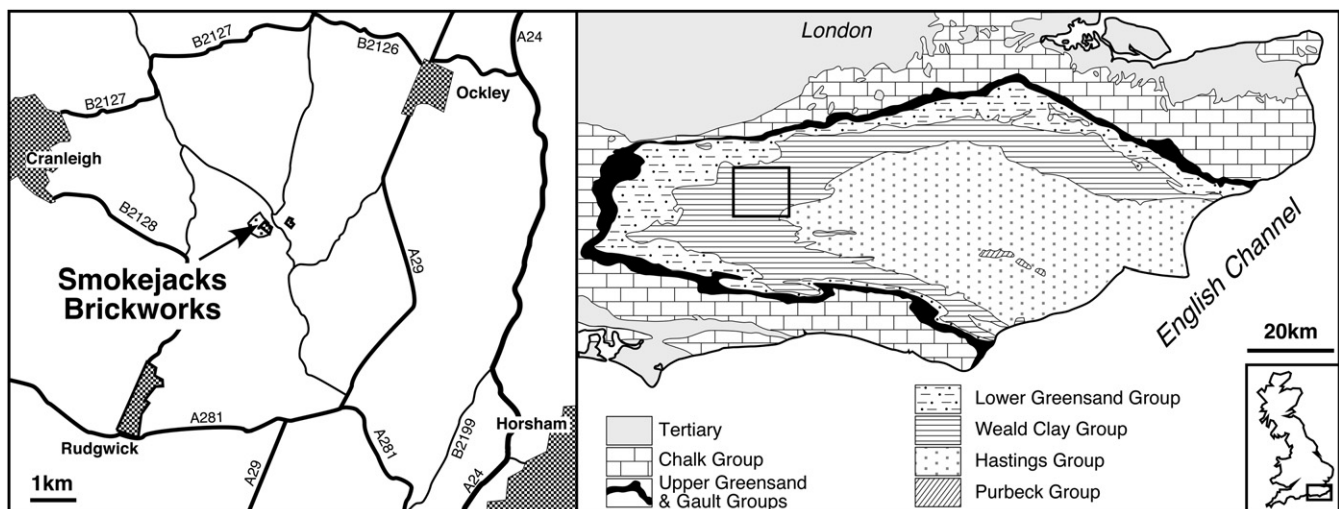


Fig. 1. Geological map of the Weald Sub-basin in SE England and location map of Smokejacks Brickworks.

### 3. The section at Smokejacks Brickworks

Smokejacks Brickworks is a claypit situated in Surrey, about 40 km southeast of London, roughly in the middle of a triangle formed by the villages Ockley, Cranleigh and Horsham (National Grid Reference TQ 113 373; Fig. 1). In 2001, at the time of the *Iguanodon* excavation, the pit was owned by the company Chelwood Brick; it now belongs to The Brick Business Ltd., Ockley.

The sediments exposed at Smokejacks Brickworks belong to the Upper Weald Clay Formation and are Barremian in age. Ross and Cook (1995) provided a detailed stratigraphic study of the rocks exposed in the claypit, concluding that the sediments show a progressive shallowing from a lake/lagoon to a fluvial mudplain environment. Batten (1998) briefly described the succession with the aid of a composite log. Lithostratigraphical correlations between sections recorded at different times and places in the claypit are rendered difficult by lateral variation in lithologies and thicknesses, combined with changing locations and orientations of claypit faces. The new section was measured on 25/07/2001 on the sloping south-eastern face of the claypit (Fig. 2). A GPS reading at the base of the face gave a National Grid Reference of TQ 11239 37293 ( $\pm 6$  m), whereas the top was at 11257 37255 ( $\pm 6$  m). The *Iguanodon* lay at 11252 37263 ( $\pm 6$  m). This section is comparable to Section 1 of Ross and Cook (1995), however this face has been cut back since the earlier section was measured and does not show the lowest beds. Section 1 of Ross and Cook (1995) was measured in a gully when the face was heavily weathered whereas the new section was measured on a fresh face. The *Iguanodon* lay in the same horizon as the 1983 find of *Baronyx*, approximately 7 m below BGS Bed 5c (the Alfold Sand of Allen, 1976, sometimes misspelt as Alford), which is exposed near the tops of some faces of the claypit (Ross and Cook, 1995). From aerial photographs it was possible to work out that *Baryonyx* was found about 100 m due west of the *Iguanodon*. Batten's (1998, fig.3) identification of a sandstone sandwiched between two ironstones as BGS Bed 5c is probably incorrect; it most likely correlates with the sandstone immediately above the *Baryonyx/Iguanodon* horizon (near the top of Section 2 in fig. 3 of Ross and Cook, 1995) and at least 2 m below the base of the true Bed 5c.

Three beds are easily correlated between the two sections. In the order from the bottom to the top: (1) a bed of light-grey silt near the base of the current section (half way up in section 1 of Ross and Cook, 1995), (2) a bed of medium-brown clay with siderite nodules, and (3) a bed of fine-grained sandstone near the top. Both dinosaurs were collected below this sandstone. Most of the *Iguanodon* remains were collected within a bed of 20–30 cm thickness, immediately above a pair of distinct, thin, tabular ironstones, which were convoluted where the skeleton lay. The bases of these ironstones, which can be traced along the south-east face to the north face of the claypit (sometimes combining into a single bed), show trails, burrows and toolmarks; an arthropod trackway on one piece of ironstone is now at Maidstone Museum. The ironstones were not recorded by Ross and Cook (1995) due to the heavily

weathered nature of the exposed faces at the time. Large, irregular sideritic siltstone nodules, attributed to dinosaur trampling because of highly distorted laminations within them, were recorded in Section 1 of Ross and Cook (1995); they were not seen in the new section, but are considered to lie at a horizon just above that of the tabular ironstones.

### 4. Material and methods

A total of 25 samples was taken for palynological and micropalaeontological study. Sample set 1 comprises samples 1–12 taken from the different beds of the approximately 10 m thick section (Fig. 2). 10 additional samples (10/1 to 10/10) making up sample set 2 were taken from the dinosaur bed after excavation of the *Iguanodon*. These 10 samples each consisted of 3 cm thick blocks of sediment taken from immediately above the upper of two thin ironstone bands up to 30 cm above the upper ironstone (Fig. 2).

Three further samples were taken directly from the sediment surrounding the bones prior to preparation at the Natural History Museum. Sample 10b was taken from excavation block 1 containing the *Iguanodon* skull, and samples 10c and 10d were taken from block no. 78 which contained the right tibia and fibula. In order to sample the variations in the sediment surrounding the dinosaur, 10c was taken from silty sediment in direct contact with the tibia, whereas 10d sampled a small (cm-scale) pocket of finer clay from within the same block.

Samples were processed with standard palynological processing techniques using concentrated HCl and HF to dissolve carbonates and silicates, and concentrated HNO<sub>3</sub> for oxidation. No heavy liquid separation was necessary. The residue was filtered at a mesh size of 15  $\mu$ m and a set of oxidized and unoxidized slides were prepared for each sample, mounted in glycerine jelly and/or Elvacite. The oxidized samples were used for counts of at least 300 pollen grains and spores per slide. Green algae and reworked palynomorphs were counted in addition to the 300 pollen grains and spores. Further slides were scanned for rare taxa. Light microscope images were taken with a Zeiss Axioskop microscope using a 100 $\times$  oil immersion objective, and equipped with a Canon S45 digital camera. Confocal laser scanning microscopy (CLSM) was carried out on unstained conventional palynological slides at the NHM-Emma facilities using the Leica TCS SP confocal microscope and Leica TCSNTV software. CLSM images were obtained with FITCwide standard filter settings at an excitation wavelength of 488 nm, using a HCX PL APO CS 63.0  $\times$  1.40 oil immersion objective and an image resolution of 1024  $\times$  1024 pixels. Details on the application of CLSM to fossil palynomorphs can be found in Feist-Burkhardt and Pross (1999).

Approximately 200 g of each sample was processed for ostracod analysis. The samples had been allowed to dry naturally after collection. They were then placed in ceramic bowls and hydrogen peroxide, diluted in hot water, was poured over them. A little sodium carbonate was also added to aid breakdown. The reaction was not allowed to continue for more than an hour because of its known adverse effect on the microfauna (Hodgkinson, 1991). Each sample was then washed



# Smokejacks Brickworks, SE face section

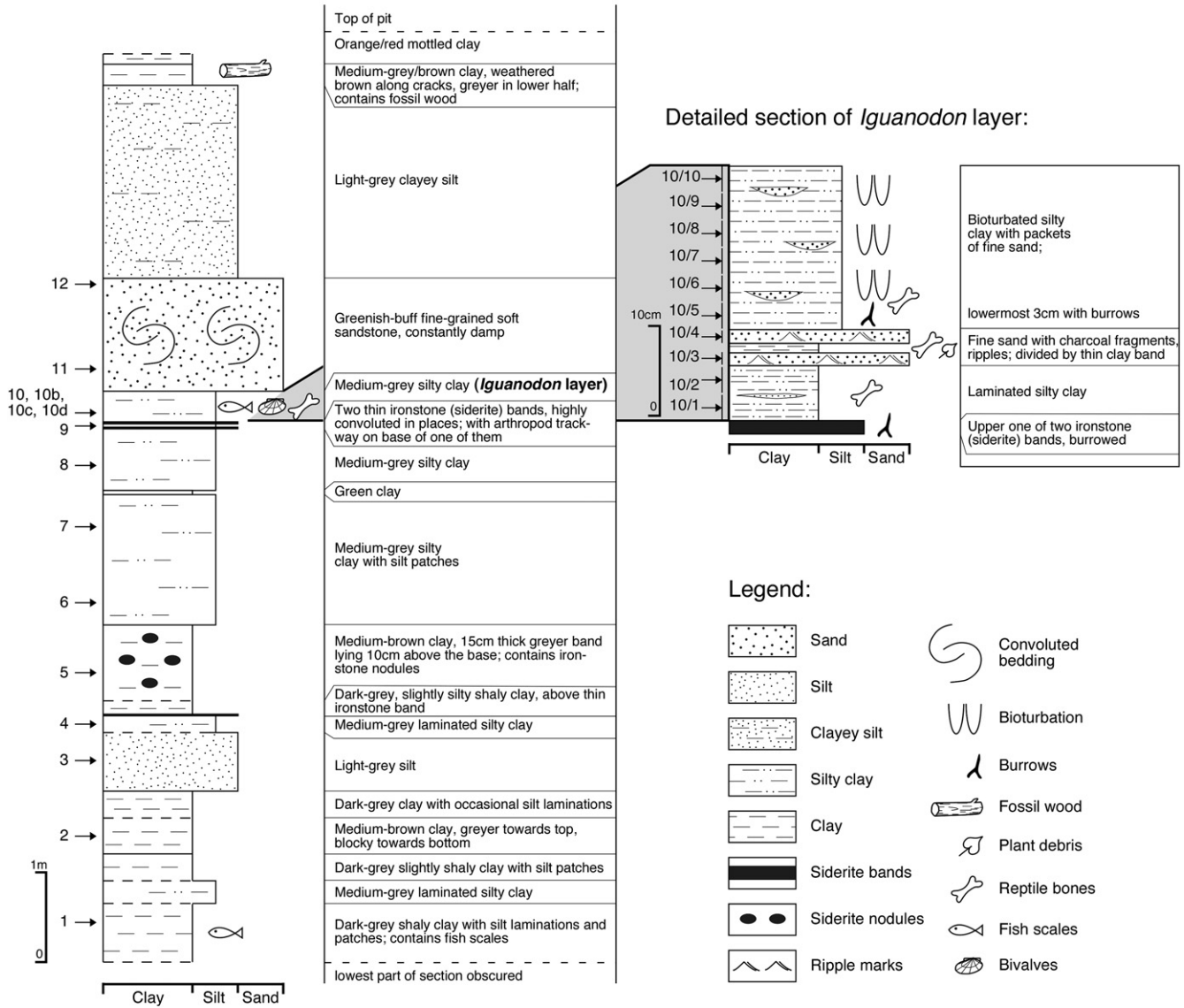


Fig. 2. Lithological logs and descriptions of the Upper Weald Clay section at the *Iguanodon* site, southeastern face of Smokejacks Brickworks [National Grid Reference: base TQ 11239 37293 ( $\pm 6$  m), top TQ 11257 37255 ( $\pm 6$  m)]. Palynological and micropalaeontological sample levels are indicated by arrows. The *Iguanodon* bed lies approximately 7 metres below BGS bed 5c (Alfold Sand), which crops out in the other faces of the claypit. The photograph shows the south-eastern slope of the claypit during the *Iguanodon* excavation in summer 2001. Note the tent and team at the excavation site (left of the image) for scale.

through a 63 µm sieve and the residue returned to the bowl to be dried in an oven. This procedure was repeated, where necessary, to complete the breakdown. The residues were then examined for ostracods and organic fossil remains, under a binocular microscope. All the ostracods were either picked out or counted, so the results are fully quantitative. At the same time a selection of megaspores was also picked for identification and photography. The ostracod and megaspore specimens were photographed using a Hitachi S2500 scanning electron microscope. The images were scanned in and digitized from 120-size negatives, and the resulting figures assembled using Photoshop.

All figured specimens are housed in the micropalaeontological collections at the Natural History Museum, London.

## 5. Results: palynology

This contribution is based in part on the unpublished work by Nye (2004) and gives the first comprehensive published account of the palynology of the Upper Weald Clay from Smokejacks Brickworks. A few palynological data from this locality were previously provided by Batten (1998), when he described the organic-walled mesofossils (size fraction over 100 µm) from Smokejacks Brickworks.

Here we deal mainly with the results of “standard palynological” samples, in other words the organic residue of the fraction under about 100 µm in size. Megaspores were recovered from the samples washed for ostracods, but are not treated comprehensively. The full count data for each palynological sample are given in Tables 1 and 2. Authors of all species noted are provided in the Appendix. Some typical palynomorphs for the Weald Clay Formation are illustrated in Figs. 5–9. A more comprehensive illustration of the palynomorph assemblages from Smokejacks Brickworks can be found in Nye (2004).

All samples processed for palynology, except sample 12, yielded well-preserved and quite rich palynomorph assemblages. A total of 38 genera and 52 species of spores and pollen, including probable early angiosperm pollen, as well as 6 genera and 7 species of green algae, have been recorded. The palynological residues are further characterized by high amounts of palynoclasts. In all slide preparations small opaque phytoclasts are present, which are interpreted as fragments of fossil charcoal. Small sooty patches of fossil charcoal are particularly abundant in sample 1. Samples 10b and 11 contain abundant fragments of (unburnt) plant cuticles. The sandstone of sample 12 contained larger fragments of burnt plant debris and very few preserved palynomorphs. Only 51 spores and pollen grains were counted from two oxidised slides from sample 12; since the statistically viable 300 grains could not be counted these data cannot be compared directly with those of the other samples. The sandstone sample contains disproportionately high amounts of large pollen grains and spores. Because of their greater specific gravity these are likely to have been favoured for preservation in this sandstone, whereas small pollen grains and spores were washed out. Relative abundance data under these circumstances must be taken with caution.

Palynological assemblages associated with Early Cretaceous dinosaur sites have been reported from Inner Mongolia (P. R. China) in the Dashuiguo Formation (Van Itterbeek et al., 2004) and in the Mazongshan area (Tang et al., 2001), and also from Bernissart in Belgium (Yans et al., 2004, 2005; Dejax et al., 2007). At the Chinese sites, most palynological samples were found to be barren, and palynomorphs were only recovered from one sample (Van Itterbeek et al., 2004) and three samples (Tang et al., 2001) respectively. The assemblages from Bernissart were rich and well preserved. Yans et al. (2004, 2005) used angiosperm pollen for the age determination of the dinosaur-containing sediments. Most of the emphasis of these studies was on stratigraphic correlation and little detailed information was provided on the local palaeoenvironment. Dejax et al. (2007), however, used palynology to reconstruct the mid-Barremian to earliest Aptian palaeoenvironment around Bernissart, describing a flora of ferns, Taxodiaceae, freshwater algae and angiosperms associated with the lake environs, with gymnosperms flourishing in the nearby hills.

### 5.1. Systematic palynology

In the following section we give descriptions of the four angiosperm pollen grain types that were found in the palynology assemblages. All four types are placed in the genus *Retimonocolpites* as they have a tectum made up of baculate columellae distally connected to form a regular reticulum with lumina sizes even over the entire grain, relative to other contemporaneous angiosperm pollen (see, e.g., Couper, 1958). Many of the published records of early angiosperm pollen have been illustrated using poor transmitted light images, making it difficult to assign our distinct types to published species; consequently our four species are here left in open nomenclature.

The original description of *Retimonocolpites* from the Cenomanian of Minnesota by Pierce (1961) is brief and the type species *R. dividuus* is illustrated with only a single, very small image. Kemp (1968) re-examined Couper's (1958) original type material of Barremian angiosperm pollen *Clavatipollenites hughesii* from the Wealden of Southern England and distinguished two species within *Clavatipollenites*. However, several of our distinct forms could easily be included in either of these species. Kemp's figured specimens of *C. rotundus* have the baculate columellae and visible reticulum which characterise the genus *Retimonocolpites*; on the other hand, *C. rotundus* does not have the clavate columellae characteristic of the genus *Clavatipollenites*. Most of our comparisons here are with the ‘biorecords’ of Hughes and others, who, although suggesting some doubtful biostratigraphical applications, provided well-defined descriptions of the various forms of angiosperm pollen which emerged during this time.

#### Genus *Retimonocolpites* Pierce, 1961

*Type species. Retimonocolpites dividuus* Pierce, 1961, p. 47, pl. 3, fig. 87

*Remarks.* The few angiosperm pollen types found in Smokejacks clay pit are here all attributed to the genus *Retimonocolpites*. Hill (1996) described a marsh-dwelling plant *Bevhalstia pebja* Hill, 1996 from Smokejacks Brickworks that he suggested to be an early angiosperm, which could possibly be the parent plant of this pollen. No other fossil plant with angiosperm organs has been reported from the Wealden in SE England or other Barremian localities. The monosulcate, reticulate structure of *Retimonocolpites* is similar to that produced by species within the Liliaceae (lily) family, and is of similar size. The parent plant of *Retimonocolpites* may have been a monocot closely related to this family.

*Retimonocolpites* sp. 1  
Figs. 6G, 7 A–D, P

*Description.* Elongate-spherical monosulcate pollen grain with a maximum diameter of 25 µm. Sulcus is oval/subcircular in shape and has a ragged appearance. Muri form a coarse reticulum with an average lumina width of 1.5–2 µm. This species has a distinctive single row of blunt, rounded supratectal processes on the reticulum. This is the most common form of angiosperm pollen found in the Smokejacks palynological assemblages.

*Comparison.* This species closely resembles *Retisulcudentat*, figured by Hughes et al. (1979, pl. 57, figs. 1–12).

*Retimonocolpites* sp. 2  
Figs. 6 H, 7 E–L

*Description.* Elongate-spherical monosulcate pollen grain with a maximum diameter of 25 µm. The sulcus in this species characteristically extends around the grain, almost splitting the endexine into two hemispheres. The reticulum sometimes shows indentations/ridges perpendicular to the muri and it appears to be loose fitting, often starting to break away from the endexine. Thickenings in the reticulum can be seen where the muri intersect.

*Comparison.* The sulcus encircling the grain is characteristic of *Clavatipollenites rotundus* (Kemp, 1968) and this sulcus morphology was described in the original description of the type species *Retimonocolpites dividiuus* Pierce, 1961, although this species differs significantly from both *R. dividiuus* and *C. rotundus* in having a much coarser reticulum. The indentations/ridges on the reticulum are similar to the tectum morphology of *Retisulc-muribeaded* (Hughes, 1994, fig. 9.17). The very large lumina size and the maximum diameter of this type also make *Retisulc-muribeaded* the most favourable comparison.

*Retimonocolpites* sp. 3  
Figs. 6 I, 7 O

*Description.* Elongate, monosulcate pollen grain, relatively large, with a maximum diameter of 35 µm. When viewed under transmitted light, the reticulum appears dense and closely fitting to the endexine, but CLSM study of these grains shows

distinct triangular supratectal elements on the reticulum. The single occurrence *Retimonocolpites* sp. 3 is of two grains together in a remnant tetrad.

*Comparison.* The triangular supratectal elements which appear to be present on these grains are comparable to those of biorecord *Superret-triang* (Hughes et al., 1979, pl. 63, figs. 1–9).

*Retimonocolpites* sp. 4  
Figs. 6J, 7 M–N

*Description.* Elongate, monosulcate pollen grain. Small, with a maximum diameter of 20 µm. Sulcus extends almost the length of the grain, gaping in what may be the fold parallel to the sulcus in the emended diagnosis of *Clavatipollenites hughesii* by Kemp (1968). This species has a finer reticulum than the other species recorded in the present study and the lumina are not so easily distinguished in transmitted light. Both occurrences of *Retimonocolpites* sp. 4 are of two or more grains together in a remnant tetrad.

*Comparison.* This type does not compare well to any published records, although many characteristics of these grains are similar to *Clavatipollenites hughesii* (Couper, 1958, in the emended diagnosis of Kemp, 1968).

## 5.2. Trends in the pollen and spore assemblages

The pollen/spore assemblages of samples 1 to 12 depict a vegetational change from a principally gymnosperm-dominated assemblage at the base to a principally pteridophyte-dominated assemblage at the top of the section (Fig. 3). Gymnosperm pollen grains mainly composed of the small, spherical, thin-walled *Inaperturopollenites dubius* and *Taxodiaceapollenites hiatus*, both of conifer affinity, along with Cheirolepidiaceae pollen *Classopollis torosus* and bisaccate pollen attributed to the Pinaceae (*Alisporites bilateralis*) and the Podocarpaceae (*Podocarpidites* sp.), characterize the darker, more laminated clays and silts towards the base of the section (Fig. 3). Conifer pollen makes up over 90% of the pollen/spore assemblage in sample 1, and remains dominant at 80–90% up-section through to sample 4 where it constitutes 66% of the pollen/spore assemblage. Pteridophyte spores begin to become important in sample 5 but conifer pollen remains at 39%, significantly higher than in the pteridophyte-dominated deposits further up the section. Samples 6 and 7 are both conifer pollen-dominated by 87% and 63% respectively. The increasing relative abundance of pteridophyte spores up-section is concomitant with a progressive diversification of heavily-sculptured trilete fern spores. Pteridophyte spores typically make up 80–90% of the pollen/spore assemblage in samples 8 to 11. Representatives of the Schizaeaceae fern family (*Cicatricosisporites* spp., *Plicatella* spp.) are dominant alongside an indeterminate fern which produced the spores *Leptolepidites*. The Mesozoic tree fern family Cyatheaaceae is also represented by *Cyathidites australis* and *C. minor*.

Lycopod (club moss) spores increase steadily in relative abundance up-section in line with the fern spores (Fig. 3)

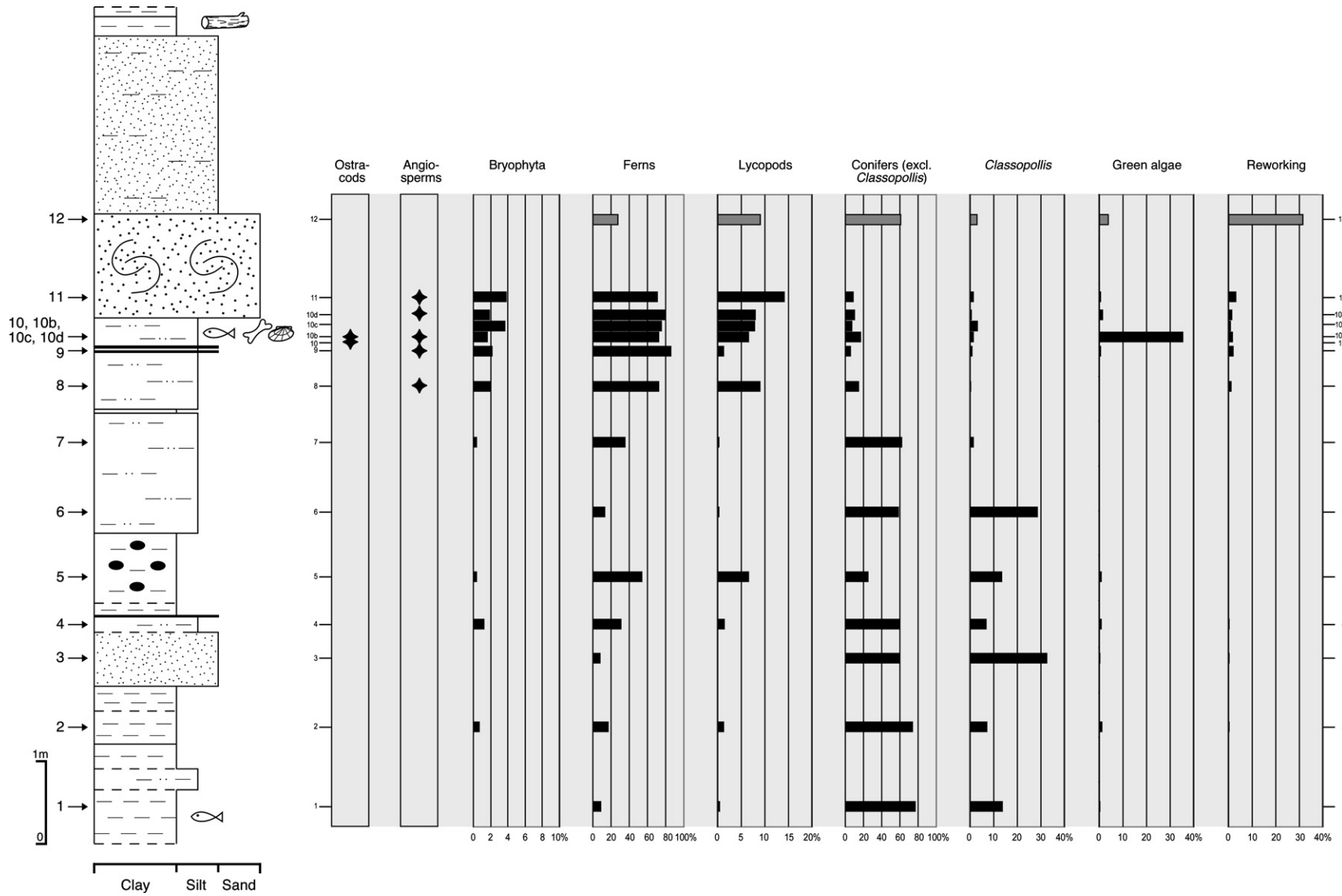


Fig. 3. Relative abundances of palynomorph groups in the Upper Weald Clay section at Smokejacks Brickworks: parent plant groups represented by the miospore assemblages, green algae, and extent of reworking. Presence of angiosperm pollen and ostracods are indicated by a star. Note different scales of the bar charts. In sample 12, palynomorphs were too rare to achieve a readily comparable and statistically reliable number of overall counts; bars are therefore greyed.



and are largely represented by *Echinatisporis varispinosus*, thought by Pocock (1962, as *Acanthotriletes varispinosus*) to be the spores of a Cretaceous species of the modern club moss *Selaginella*. A fossil *Selaginella* species, *S. dawsonii* is mentioned from the Wealden (Watson and Alvin, 1996) and may have been the dominant lycopod if it was the parent plant of these spores. The sharp increase in lycopod spore abundance, to over 14% of the pollen/spore assemblage in sample 11, is shown in Table 1 to represent a diversification in lycopod spores, with a sharp increase in importance of *Kraeuselisporites hastilobatus*. The parent plant of *K. hastilobatus* may have found its preferred niche in the sandy overbank deposit of sample 11 and the preservation of its spores may indicate that the miospore assemblage is representative of the immediately adjacent vegetation, picking up small scale vegetation changes due to a local change in substrate.

Hepatic (liverwort) spores show a small-scale increase in relative abundance up-section but remain minor constituents of the pollen/spore assemblage (Fig. 3). They are largely represented by *Triporoletes reticulatus* which has morphological similarity to modern hepatic spores of the Ricciaceae family (Dettmann, 1963). Also present is *Coptospora striata*, comparable to spores produced by modern *Geothallus tuberosus* (see Dettmann, 1963).

The four *Retimonocolpites* species of probable early angiosperm affinity occur associated with the pteridophyte rich samples surrounding the *Iguanodon* towards the top of the section (samples 8 to 11; Fig. 3). In these samples, angiosperm pollen is rare with one or two, to a maximum of 7 grains counted, which represents a maximum of 1 to 2% of the pollen/spore assemblage.

Samples 10/1 to 10/10 within sample set 2 show very similar spore and pollen assemblage to samples 10b, 10c and 10d, dominated by pteridophyte spores with no significant shifts in relative abundance of the main groups (Fig. 4).

### 5.3. Green algae

The green algae taxa *Pediastrum* sp., *Scenedesmus bifidus*, *S. novilunaris* and *Tetraedron paraincus* are present in association with the pteridophyte-dominated deposits. They generally occur at <1% of the total palynomorph assemblage, but show a distinct peak in sample 10b (taken from sediment surrounding the *Iguanodon* skull) where *Scenedesmus novilunaris* constitutes 34% of the total palynomorph assemblage. No anomalous increased abundance of green algae was seen in samples 10c and 10d, the other samples taken from close to the right tibia of the *Iguanodon*. Two minor peaks in *S. novilunaris* are evident in samples 10/4 and 10/6 where green algae constitute 5% and 3% respectively. The coenobia of *S. novilunaris* are formed most commonly of 16 cells, occasionally 8 cells and very rarely 4-cell coenobia occur (Fig. 8 A, B, D). The probable zygnetacean cyst (zygospore) *Tetranguladinium conspicuum* was present associated with other algae taxa.

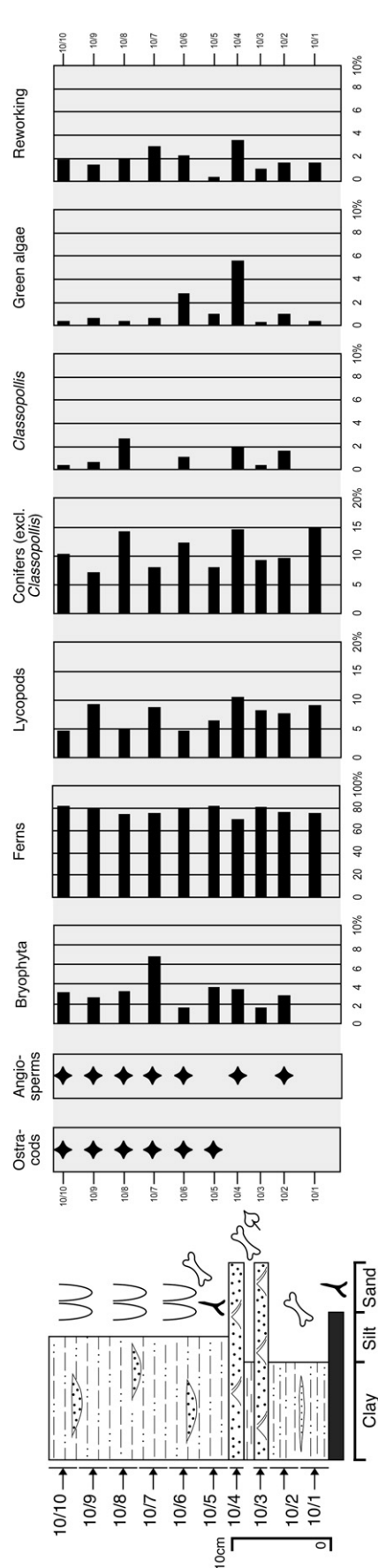


Fig. 4. Relative abundances of palynomorph groups in the dinosaur bed (bed 10) at Smokejacks Brickworks: parent plant groups represented by the miospore assemblages, green algae, and extent of reworking. Presence of angiosperm pollen and ostracods are indicated by a star. Note different scales of the bar charts.



#### 5.4. Reworked palynomorphs

Reworked palynomorphs are evident in the Smokejacks palynological assemblages but make up only a small percentage of the total counted palynomorphs, generally occurring at <1% of the total count, rising to 3% in sample 11, and jumping to 31% in sample 12 (Table 2; Figs. 3, 4). The most obvious reworked palynomorphs are cysts of exclusively marine dinoflagellates that belong to typically Jurassic genera such as *Ctenidodinium* and *Rhynchodiniopsis*. Some well-preserved specimens could be identified to species level, and the stratigraphic ranges of the following species span the Middle to Late Jurassic: *Ctenidodinium combazii* (latest Bajocian–earliest Callovian); *Gonyaulacysta jurassica* (Bajocian–Kimmeridgian) and *Subtilisphaera inaffecta* (Kimmeridgian). Other palynomorphs are foraminiferal test linings and several species of the acritarch genus *Micrhystridium*, which are known only from marine sediments, and also are evidence of reworking of a marine deposit. Therefore, erosion of Middle to Late Jurassic sediments was occurring during deposition of the Upper Weald Clay Formation. Many of the Lower Cretaceous pollen and spore taxa present at Smokejacks are long ranging and common in Jurassic assemblages. Some may be reworked, as the reworked material is quite well preserved with no visible difference in maturity (colour) compared to Lower Cretaceous pollen and spores known to be *in situ*.

#### 5.5. Megaspores

Megaspores were very abundant in the samples sieved for ostracods (63 µm sieve) and some examples are shown in Fig. 9. Batten (1969) built on work by Dijkstra (1949, 1951) on Wealden megaspores. Some specimens from Smokejacks have been identified as *Erlansonisporites* sp., *Minerisporites* sp., *Ricinospora* sp., *Striatriletes sulcatus* (Dijkstra, 1951) Potonié, 1956, aff. *Flabellisporites* sp. of Lupia (2004, his fig. 4) and “*Clockhousea*” of Batten, 1998 (pers. comm. D. Batten, 2007). These were probably produced by lycopods and early heterosporous ferns which first appeared in the earliest Cretaceous. *Flabellisporites* megaspores were attributed to the Isoetales (quillworts), the most advanced lycopods, by Lupia (2004). Many modern *Isoetes* inhabit freshwater, living submerged in lakes (Dijkstra, 1949). Wealden representatives of the more primitive lycopod order Selaginellales probably produced most of the other megaspores from Smokejacks.

### 6. Results: ostracods

Well-preserved ostracod assemblages were obtained from the upper five (10/6–10/10) of the ten samples collected through the dinosaur bed (Table 3); sample 10/5 yielded only a few fragments of valves and the lower four samples (10/1–10/4) were barren of ostracods. Two washings of subsamples of sample 10b (from the excavated *Iguanodon* skull) yielded essentially similar assemblages (combined on Table 3), mostly closely matching that of 10/7. These represent the first useful ostracods to be found anywhere in the Smokejacks

Brickworks Upper Weald Clay Formation exposures, previous finds being limited to poorly-preserved specimens identified only as “non-cyprid” (Ross and Cook, 1995). The assemblages from the ostracod-bearing samples are essentially similar (Table 3), comprising four species: *Cypridea clavata* (Anderson, 1939), *Damonella* cf. *pygmaea* (Anderson, 1941) and two species of *Stenestroemia* (one of which is referred to *S. cressida* Anderson, 1971, the other left in open nomenclature). Fragments and damaged valves of a thin-shelled ostracod may indicate the presence of a fifth species, possibly belonging to the genus *Mantelliana*.

#### 6.1. Systematic micropalaeontology

Order: Podocopida G. W. Müller, 1894  
 Suborder: Cypridocopina Jones, 1901  
 Superfamily: Cypridoidea Baird, 1845  
 Family: Cyprideidae Martin, 1940  
 Genus *Cypridea* Bosquet, 1852

*Cypridea clavata* (Anderson, 1939)  
 Fig. 10 A–P

- 1939 *Ullwellia clavata* sp. nov. Anderson, 300, pl. 13, figs 1, 9a–b.  
 1967 *Cypridea clavata clavata* (Anderson); Anderson, 240–241, pl. 16, fig. 26.  
 1967 *Cypridea clavata beltana* subsp. nov., 240–241, pl. 16, fig. 33.  
 1967 *Cypridea clavata maleta* subsp. nov., Anderson, 240–241, pl. 16, fig. 34.  
 ?1967 *Cypridea insulae* sp. nov., Anderson, 246, pl. 16, figs 10–14.  
 1967 *Cypridea bogdenensis* sp. nov. Anderson, 238, pl. 16, figs 25, 25, 29, 30; Fig. 1b.  
 1985 *Cypridea clavata clavata* (Anderson); Anderson, pl. 9, fig. 15.  
 1985 *Cypridea clavata beltana* Anderson; Anderson, pl. 9, fig. 18.  
 1985 *Cypridea clavata maleta* Anderson; Anderson, pl. 10, fig. 1.  
 1985 *Cypridea bogdenensis* Anderson; Anderson, pl. 10, fig. 10.  
 ?1985 *Cypridea insulae* Anderson, 1967; Anderson, 29, pl. 10, fig. 14.

*Remarks.* *Cypridea clavata* is an “inverse” *Cypridea* (that is, the right valve overlaps the left) ornamented with fine pitting and variously developed tubercles. Adherence to Anderson’s (1967, 1985) taxonomic scheme could result in the assignment of most of our *Cypridea* specimens to up to five taxa: *Cypridea clavata clavata*, *C. clavata beltana*, *C. clavata maleta*, *C. insulae* and *C. bogdenensis* (all noted as “variants” in Fig. 10). In some cases the decision to place a specimen in one or other subspecies of *C. clavata* would be arbitrary, however, since the differences between them (and four other subspecies of *C. clavata* also described by Anderson, 1967) are

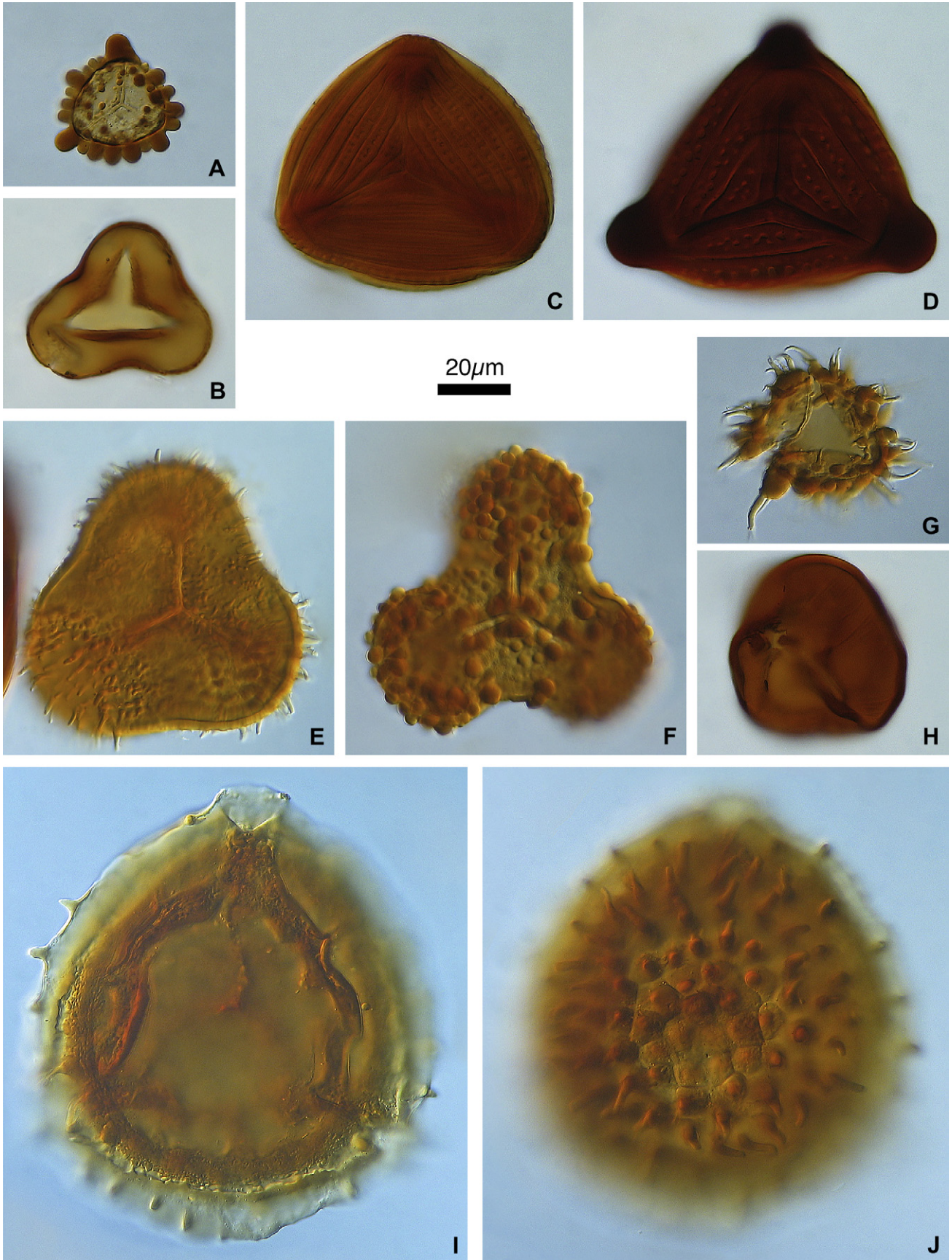






Fig. 6. Pollen grains from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. All images were taken using transmitted light and Nomarski interference contrast. A, *Ephedripites* sp., sample 10b, slide 4, E.F. reference: W34. B, *Podocarpidites* sp., sample 10/5, slide 3, E.F. reference: L54/4. C, *Alisporites bilateralis* Rouse, 1959, sample 10/1, slide 3, E.F. reference: J37/3. D, *Classopollis torosus* (Reissinger, 1950) Couper, 1958, tetrad, sample 10/5, slide 3, E.F. reference: O52. E, *Classopollis torosus* (Reissinger, 1950) Couper, 1958, sample 10/1, slide 3, E.F. reference: K55. F, *Taxodiaceapollenites hiatus* (Potonié, 1931) Kremp, 1949, sample 10b, slide 2, E.F. reference: T56/3. G, *Retimonocolpites* sp. 1, sample 10b, slide 3, E.F. reference: V63/4. H, *Retimonocolpites* sp. 2, sample 10/4, slide 2, E.F. reference: R49. I, *Retimonocolpites* sp. 3, sample 10/2, slide 2, E.F. reference: G33. J, *Retimonocolpites* sp. 4, sample 8, slide 3, E.F. reference: G47/3.

concerned with the degree of development of the tubercles and there appear to be many intermediate forms. As Anderson himself admitted (1967, p. 241): “These subspecies are linked by intermediate forms which it is not always possible to place, for individual tubercles may be reduced in size until they are barely detectable or may be represented by only slightly raised areas of the surface which can be interpreted as relict tubercles

or not. Moreover, several subspecies may be present in one assemblage, but the steady increase with time in the percentage of reduced forms shows an evident trend.” We consider these forms to represent intrapopulational variants of a single species and as such, separate formal taxonomic status is unwarranted. Adult forms show variation in ornament from those mostly or completely devoid of tubercles (=“*maleta*” form;

Fig. 5. Spores from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. All images were taken using transmitted light and Nomarski interference contrast. A, *Leptolepidites verrucatus* Couper, 1953, sample 8, slide 3, England Finder (E.F.) reference: R41. B, *Cyathidites australis* Couper, 1953 sample 10/1, slide 3, E.F. reference: P51/3. C, *Cicatricosisporites angicanalis* Döring, 1965, sample 10b, slide 4, E.F. reference: G48/1. D, *Plicatella robusta* (Kemp, 1970) Davies, 1985, sample 10b, slide 4, E.F. reference: G58. E, *Pilososporites trichopapillosus* (Thiergart, 1949) Delcourt & Sprumont, 1955, sample 10b, slide 4, E.F. reference: E43. F, *Impardecispora apiverrucata* (Couper, 1958) Venkatachala, Kar & Raza, 1968, sample 10b, slide 3, E.F. reference: Y56. G, *Echinatisporis varispinosus* (Pocock, 1962) Srivastava, 1977, sample 10b, slide 3, E.F. reference: J37/2. H, *Coptospora striata* Dettmann, 1963, sample 10/3, slide 3, E.F. reference: L57/2. I–J, *Couperisporites complexus* (Couper, 1958) Pocock, 1962: I, proximal face, J, distal face, sample 10b, slide 3, E.F. reference: M41/1.



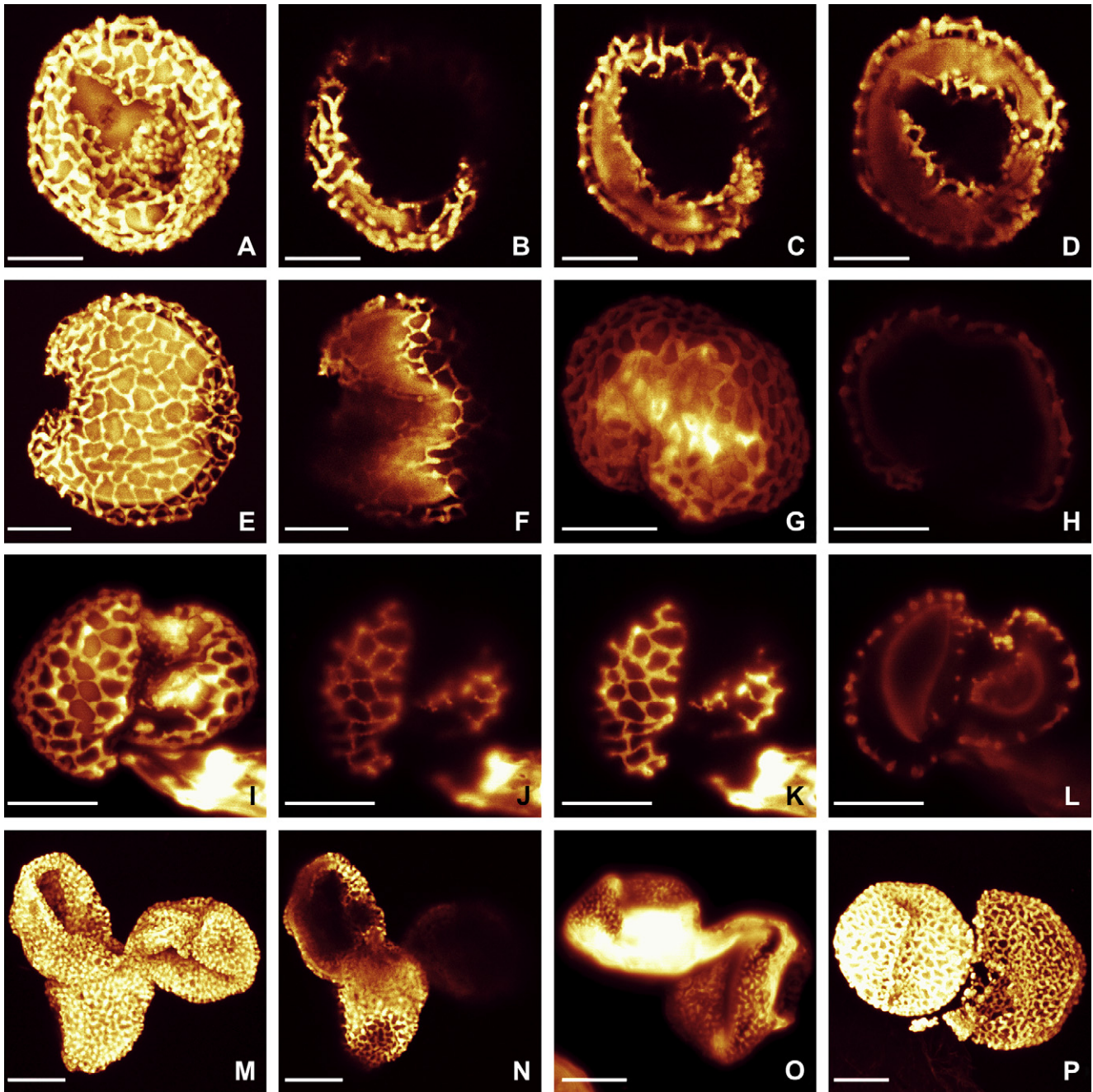


Fig. 7. Angiosperm pollen grains from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. All images taken using confocal laser scanning microscopy (CLSM). A–D, *Retimonocolpites* sp. 1, sample 10b, slide 3, E.F. reference: V63/4. A, Maximum projection, extended focus image of 60 optical sections. B–D, single optical sections, section thickness (voxel height) 448 nm. E, F, *Retimonocolpites* sp. 2, sample 11, slide 3, E.F. reference: B60. E, Maximum projection, extended focus image of 31 optical sections. F, single optical section, section thickness (voxel height) 529 nm. G, H, *Retimonocolpites* sp. 2, sample 10/6, slide 2, E.F. reference: M52. G, Maximum projection, extended focus image of 33 optical sections. H, single optical section, section thickness (voxel height) 420 nm. I–L, *Retimonocolpites* sp. 2, sample 10/4, slide 2, E.F. reference: R49. I, Maximum projection, extended focus image of 39 optical sections. J–L, single optical sections, section thickness (voxel height) 387 nm. M, N, *Retimonocolpites* sp. 4, sample 8, slide 3, E.F. reference: G47/3. M, Maximum projection, extended focus image of 31 optical sections. N, single optical section, section thickness (voxel height) 642 nm. O, *Retimonocolpites* sp. 3, sample 10/2, slide 2, E.F. reference: G33. Maximum projection, extended focus image of 25 optical sections, section thickness (voxel height) 465 nm. P, *Retimonocolpites* sp. 1, sample 10b, slide 4, E.F. reference: K45/2. Maximum projection, extended focus image of 54 optical sections, section thickness (voxel height) 529 nm.

e.g., Fig. 10 I–L) through those with moderately-developed posterior tubercles (“*beltana*” and “*bogdenensis*” forms; Fig. 10 E, F, H) to specimens with maximum development of large tubercles (“*clavata*” form; Fig. 10 A–D, G). The “*insulæ*” form represents tuberculate juveniles (Fig. 10 N). All

of our specimens show the same valve overlap relationship, general outline in lateral and dorsal view, and development of the rostrum and alveolus (the *Cypridea* “beak”) and the shallow, convex cyathus; minor variations in adult carapace outline and size are easily within the range of variation



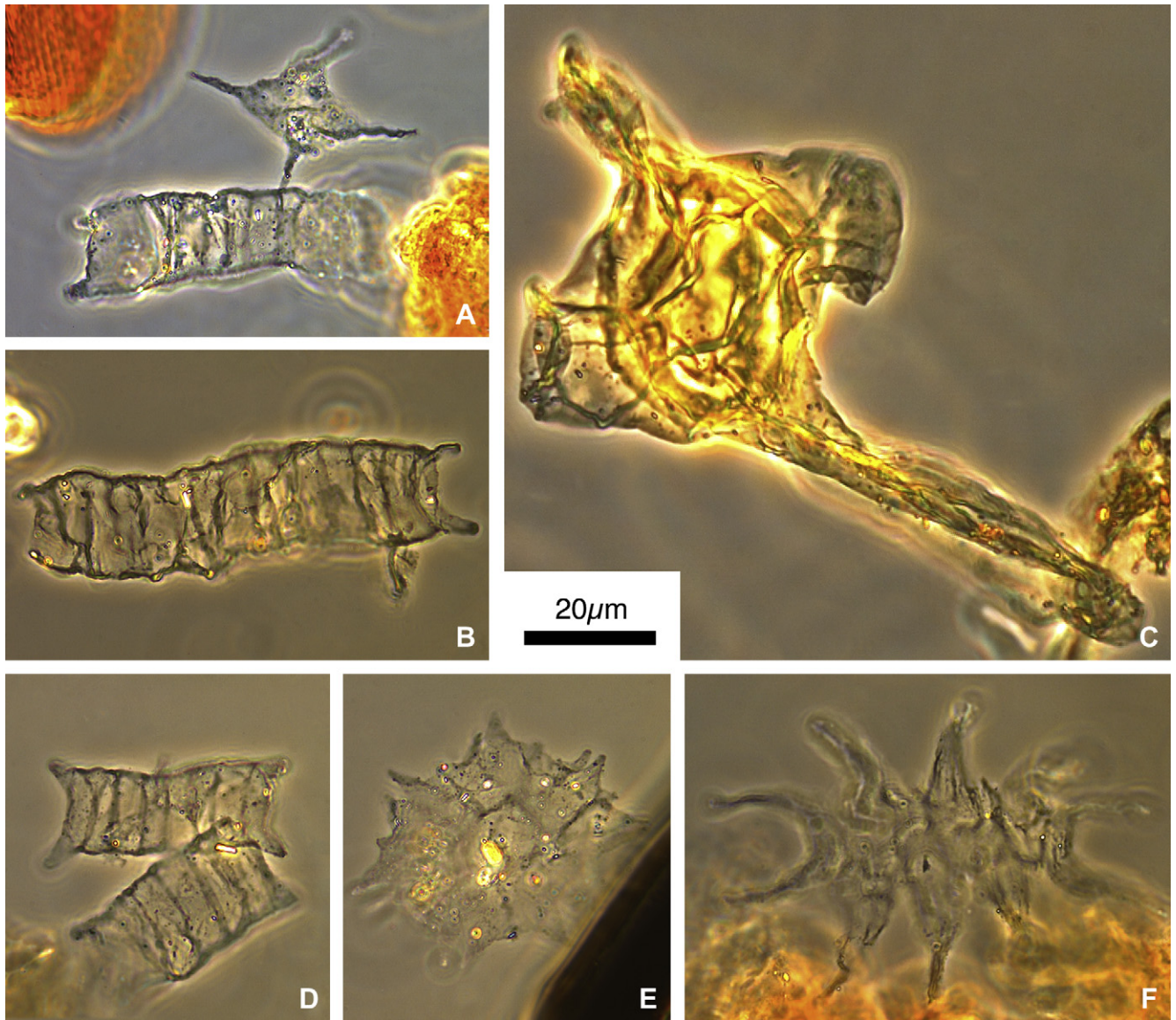


Fig. 8. Green algae from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. All images taken using transmitted light and phase contrast. A, *Tetraedron paraincus* (top specimen) Batten & Lister, 1988b, and *Scenedesmus novilunaris* He Cheng-quan et al., 1992 (bottom specimen), sample 10b, slide 3, E.F. reference: L48/1. B, *Scenedesmus novilunaris* He Cheng-quan et al., 1992, 16-cell coenobium, sample 8, slide 3, E.F. reference: R54/3. C, *Tetranguladinium conspicuum* Yu Jingxian, Guo Zhengying & Mao Shaozhi, 1983 ex Chen et al. 1988, sample 10b, slide 4, E.F. reference: P39/1. D, *Scenedesmus novilunaris* He Cheng-quan et al., 1992, sample 10b, slide 4, E.F. reference: C64. The top specimen is an 8-cell coenobium, the bottom one is incomplete. E, *Pediastrum* sp. sample 10b, slide 4, E.F. reference: P49. F, *Scenedesmus bifidus* Batten & Lister, 1988b, sample 5, slide 3, E.F. reference: J46/2.

recorded in populations of living cypridoidean species (see, e.g., Baltanás et al., 2002).

*Cypridea bogdenensis* was described by Anderson (1967) from Bogden in Kent, from a Weald Clay horizon near the base of his *Cypridea clavata* Zone at the time; he subsequently extended the zone downwards (Anderson, 1985) so that the short-ranging *C. bogdenensis* occurred near its top. This puts it close to or within the interval exposed at Smokejacks Brickworks (Ross and Cook, 1995; Horne, 1995); its limited vertical range led Horne (1995) to note its potential as a biostratigraphical marker at the base of his *Cypridea fasciata* Subzone. According to Anderson (1967, p. 238) *C. bogdenensis* is an inverse species that “differs from the smaller inverse *C. clavata*

(Anderson) in lacking tubercles in the area behind the adductor muscle scars and in the antero-dorsal area”. However, his length measurement of 0.91 mm for *C. bogdenensis* is well within the range of 0.805–1.04 mm for his subspecies of *C. clavata* given in the same publication; as with those subspecies, we consider the differences in tuberculation to fall within the range of variation of a single species, *C. clavata*. We therefore consider *C. bogdenensis* to be a junior synonym of *C. clavata*.

*Cypridea insulae* was described by Anderson (1967) on the basis of a few specimens from the lower (Barremian) part of the Vectis Formation on the Isle of Wight (Barremian—earliest Aptian) in the Wessex Sub-basin. It is notable for its small

Table 1  
Quantitative data of palynomorphs (except megaspores) recorded from Smokejacks Brickworks

	Sample set 1 (Whole section)												Sample set 2 (Detail of dinosaur bed, bed 10)											
	1	2	3	4	5	6	7	8	9	10b	10c	10d	11	12	10/1	10/2	10/3	10/4	10/5	10/6	10/7	10/8	10/9	10/10
Bryophyta																								
Hepaticophyta																								
<i>Aequitriradites verrucosus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Coptospora striata</i>	0	0	0	1	0	0	0	0	1	0	2	1	1	0	1	1	0	0	0	0	3	0	1	2
<i>Couperisporites complexus</i>	0	0	0	0	0	0	0	0	0	1	0	1	4	0	2	0	0	0	1	3	2	2	3	
<i>Triporoletes reticulatus</i>	0	2	0	3	1	0	1	6	5	4	10	4	8	0	4	5	11	11	4	16	8	6	5	
Pteridophyta																								
Ferns																								
<i>Baculatisporites comaumensis</i>	2	1	1	1	7	0	0	5	0	7	0	7	14	0	4	2	11	3	8	2	13	9	17	8
<i>Cicatricosisporites</i> spp.	11	8	8	30	51	13	43	41	45	43	51	42	79	3	35	48	48	42	33	58	47	55	65	56
<i>Cicatricosisporites angicanalis</i>	0	3	1	4	14	0	2	15	5	20	8	12	29	0	19	11	25	5	27	9	23	7	18	10
<i>Cicatricosisporites australiensis</i>	0	1	0	9	1	0	0	4	2	3	4	5	1	0	1	6	2	4	0	4	3	0	3	1
<i>Cicatricosisporites brevilaesuratus</i>	0	0	0	0	0	0	0	2	0	1	1	2	0	0	0	0	1	0	1	0	1	0	0	0
<i>Cicatricosisporites hallei</i>	1	4	1	9	6	3	3	4	9	6	6	7	14	0	9	3	11	10	12	12	9	10	10	7
<i>Cicatricosisporites hughesi</i>	2	1	1	1	2	4	5	1	1	2	6	5	2	0	11	4	12	1	4	2	8	5	5	2
<i>Cicatricosisporites mohriodes</i>	0	0	2	3	6	2	2	5	8	5	2	0	4	0	5	2	0	1	7	2	9	3	5	7
<i>Cicatricosisporites myrtellii</i>	1	1	1	2	2	0	0	2	3	4	2	3	6	1	5	3	6	4	1	1	3	7	7	3
<i>Concavissimisporites</i> sp.	0	0	0	0	2	0	2	1	0	0	1	0	5	0	1	1	4	0	3	1	2	0	4	1
<i>Contignisporites dorsostriatum</i>	0	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0
<i>Coronatipora valdensis</i>	3	3	0	3	1	0	1	1	3	0	0	0	0	0	0	1	0	3	1	0	1	3	0	1
<i>Cyathidites australis</i>	6	1	0	1	5	0	11	4	2	4	2	5	4	0	4	3	7	4	4	3	1	3	1	1
<i>Cyathidites minor</i>	0	7	2	5	1	4	2	1	5	1	5	8	2	0	6	5	4	11	0	11	4	9	3	9
<i>Dictyophyllidites equixinus</i>	1	2	0	0	2	1	0	0	2	2	1	3	0	0	0	0	1	0	1	0	1	0	0	0
<i>Distaltriangulisporites perplexus</i>	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	1	1	2	1	0	0	2	0
<i>Gleicheniidites circinidites</i>	2	6	3	1	0	4	1	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0
<i>Impardecispora apiverrucata</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1
<i>Klukisporites foveolatus</i>	0	0	0	2	3	1	2	1	0	0	0	0	0	0	3	2	2	0	4	0	0	3	3	2
<i>Leptolepidites verrucatus</i>	0	3	0	21	46	4	5	121	170	104	145	137	54	3	120	139	149	121	101	129	96	103	102	127
<i>Microreticulatisporites crassiexinoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	1	0	2	0	0	0	3	0
<i>Pilososporites trichopapillosum</i>	1	4	0	6	7	0	8	1	6	7	1	7	5	1	2	5	6	4	13	5	13	6	9	11
<i>Pilososporites verus</i>	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plicatella concentrica</i>	0	0	0	0	1	0	2	1	1	1	0	3	5	0	0	0	0	0	2	1	2	0	0	0
<i>Plicatella robusta</i>	1	0	0	0	0	0	0	0	0	0	3	1	1	0	0	0	1	0	6	0	1	0	0	0
<i>Plicatella tricornitata</i>	1	5	4	1	0	2	3	0	3	3	3	3	6	0	1	0	4	0	9	2	3	3	3	6
<i>Taurocusporites reduncus</i>	0	0	0	0	1	0	0	1	1	0	1	2	1	0	0	2	0	0	0	0	0	0	0	0
<i>Taurocusporites segmentatus</i>	0	0	0	0	0	0	0	2	5	3	3	1	1	0	11	4	7	3	1	5	3	2	1	3
<i>Undulatisporites undulapolus</i>	0	0	0	1	1	0	0	0	0	0	0	3	0	0	3	0	3	0	0	0	1	0	3	0
<i>Verrucosisporites obscurilaesuratus</i>	0	0	0	3	0	0	0	1	0	0	0	0	1	0	1	1	3	0	3	0	1	0	3	0
Lycopods																								
<i>Echinatisporis varispinosus</i>	0	3	0	5	18	0	1	26	4	14	16	25	21	0	22	17	17	28	12	8	13	3	20	9
<i>Foveotriletes subtriangularis</i>	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	1	0	0	0	1	3	0
<i>Kraeuselisporites hastilobatus</i>	0	0	0	0	1	0	0	1	0	3	6	1	22	2	2	2	11	3	7	5	10	8	2	2
<i>Retitriletes austroclavaitidites</i>	1	1	0	0	1	1	0	0	0	3	4	0	3	1	5	4	3	1	0	1	5	3	6	3

## Coniferophyta

## Conifers

<i>Abietinaepollenites microreticulatus</i>	0	1	0	2	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	
<i>Alisporites bilateralis</i>	3	10	2	8	5	8	0	1	1	0	4	0	3	0	3	3	0	1	2	0	1	1	2	1
Other bisaccates	71	108	53	32	29	25	29	14	11	14	12	24	17	12	11	12	15	22	12	30	12	20	10	14
<i>Callialasporites dampieri</i>	1	3	3	0	2	0	2	3	0	4	2	3	4	1	10	1	3	5	6	1	1	3	4	5
<i>Cerebropollenites mesozoicus</i>	6	9	0	2	5	1	3	2	2	12	4	0	0	2	5	1	1	3	0	0	2	2	2	1
<i>Classopollis torosus</i>	50	22	98	23	40	87	4	1	3	5	11	2	5	1	0	5	1	6	0	3	0	8	2	1
<i>Eucommiidites troedssonii</i>	4	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Inaperturopollenites dubius</i>	57	60	33	92	15	97	69	6	3	11	1	3	3	4	10	5	2	6	1	6	9	10	4	9
<i>Perinopollenites elatoides</i>	11	1	6	3	3	0	3	7	0	3	0	0	0	1	4	0	2	1	1	0	1	1	2	0
<i>Podocarpidites</i> spp.	14	6	18	3	8	2	3	0	0	7	0	1	2	0	3	3	3	0	0	1	0	2	1	0
<i>Taxodiaceapollenites hiatus</i>	112	29	63	54	8	43	55	9	1	0	2	1	1	0	2	5	8	6	2	0	0	4	1	1

## Gnetales

## Ephedra

<i>Ephedripites patapscoensis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>Ephedripites</i> spp.	1	0	0	1	2	0	1	2	6	0	7	1	2	0	2	0	0	2	0	2	1	0	0	0

## Angiosperms

<i>Retimonocolpites</i> sp. 1	0	0	0	0	0	0	0	6	1	0	1	0	0	0	0	0	1	0	2	1	1	1	1	1
<i>Retimonocolpites</i> sp. 2	0	0	0	0	0	0	0	3	1	0	0	0	0	0	6	0	0	0	0	0	0	4	0	0
<i>Retimonocolpites</i> sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Retimonocolpites</i> sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

## Green algae

<i>Foveinaperturites forameniferus</i>	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Leioaletes calvatus</i>	0	1	1	2	2	0	0	1	2	0	1	2	0	1	0	1	0	3	1	1	0	2	0	0
<i>Scenedesmus bifidus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scenedesmus novilunaris</i>	0	3	0	1	1	0	0	0	0	159	0	2	0	2	0	2	0	18	0	8	0	1	0	1
<i>Schizosporis parvus</i>	1	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tetraedron paraincus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tetraguladinium conspicuum</i>	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0

## Reworked Jurassic aquatic palynomorphs

Reworked dinoflagellate cysts	0	0	0	1	0	0	0	1	5	5	2	5	9	13	4	4	3	10	0	6	7	5	3	5
Acritarchs	0	1	1	0	0	0	0	1	2	2	1	0	2	3	0	1	1	2	1	1	3	1	2	1
Foraminiferal test linings	0	0	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Tasmanites	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

## Total counts

<b>Total counts</b>	<b>365</b>	<b>311</b>	<b>302</b>	<b>338</b>	<b>303</b>	<b>303</b>	<b>268</b>	<b>301</b>	<b>327</b>	<b>481</b>	<b>330</b>	<b>335</b>	<b>353</b>	<b>51</b>	<b>328</b>	<b>326</b>	<b>390</b>	<b>344</b>	<b>305</b>	<b>328</b>	<b>336</b>	<b>314</b>	<b>349</b>	<b>321</b>
Total spores + pollen	364	306	300	334	300	303	268	297	318	301	327	325	340	33	322	318	385	313	301	312	324	307	342	314
Total Bryophyta	0	2	0	4	1	0	1	6	7	5	12	6	13	0	0	9	6	11	11	5	22	10	9	10
Total Ferns	32	51	24	105	161	39	95	215	272	218	246	257	240	9	243	242	312	217	245	250	245	228	268	256
Total Lycopods	2	4	0	5	20	1	1	27	4	20	26	26	48	3	29	24	31	33	19	14	28	15	31	14
Total Conifers (excl. <i>Classopollis</i> )	279	227	178	196	76	176	166	43	18	52	25	32	30	20	48	30	35	45	24	38	26	43	27	32
Total <i>Classopollis</i>	50	22	98	23	40	87	4	1	3	5	11	2	5	1	0	5	1	6	0	3	0	8	2	1
Total <i>Ephedra</i>	1	0	0	1	2	0	1	2	7	0	7	1	2	0	2	1	0	0	2	0	2	2	0	0
Total Angiosperms	0	0	0	0	0	0	0	3	7	1	0	1	2	0	0	7	0	1	0	2	1	1	5	1
Total Green algae	1	4	1	3	3	0	0	0	2	171	0	5	2	2	1	3	1	19	3	9	2	1	2	1
Total reworking	0	1	1	1	0	0	0	4	7	9	3	5	11	16	5	5	4	12	1	7	10	6	5	6

Sample set 1: whole measured section; sample set 2: detailed sample set from the dinosaur bed, bed 10.

Table 2  
Quantitative data and relative abundances of miospores parental groups, green algae, and reworked palynomorphs from Smokejacks Brickworks, as used for Figs. 3 and 4

	Sample set 1 (Whole section)													
	1	2	3	4	5	6	7	8	9	10b	10c	10d	11	12
Palynomorph group														
Total spores + pollen	364	306	300	334	300	303	268	297	318	301	327	325	340	33
Total Bryophyta	0	2	0	4	1	0	1	6	7	5	12	6	13	0
% Bryophyta	0.0%	0.7%	0.0%	1.2%	0.3%	0.0%	0.4%	2.0%	2.2%	1.7%	3.7%	1.8%	3.8%	0.0%
Total Ferns	32	51	24	105	161	39	95	215	272	218	246	257	240	9
% Ferns	8.8%	16.7%	8.0%	31.4%	53.7%	12.9%	35.4%	72.4%	85.5%	72.4%	75.2%	79.1%	70.6%	27.3%
Total Lycopods	2	4	0	5	20	1	1	27	4	20	26	26	48	3
% Lycopods	0.5%	1.3%	0.0%	1.5%	6.7%	0.3%	0.4%	9.1%	1.3%	6.6%	8.0%	8.0%	14.1%	9.1%
Total Conifers (excl. <i>Classopollis</i> )	279	227	178	196	76	176	166	43	18	52	25	32	30	20
% Conifers (excl. <i>Classopollis</i> )	76.6%	74.2%	59.3%	58.7%	25.3%	58.1%	61.9%	14.5%	5.7%	17.3%	7.6%	9.8%	8.8%	60.6%
Total <i>Classopollis</i>	50	22	98	23	40	87	4	1	3	5	11	2	5	1
% <i>Classopollis</i>	13.7%	7.2%	32.7%	6.9%	13.3%	28.7%	1.5%	0.3%	0.9%	1.7%	3.4%	0.6%	1.5%	3.0%
Total counts	365	311	302	338	303	303	268	301	327	481	330	335	353	51
Total green algae	1	4	1	3	3	0	0	0	2	171	0	5	2	2
% green algae	0.3%	1.3%	0.3%	0.9%	1.0%	0.0%	0.0%	0.0%	0.6%	35.6%	0.0%	1.5%	0.6%	3.9%
Total reworking	0	1	1	1	0	0	0	4	7	9	3	5	11	16
% reworking		0.3%	0.3%	0.3%	0.0%	0.0%	0.0%	1.3%	2.1%	1.9%	0.9%	1.5%	3.1%	31.4%
	Sample set 2 (Detail of dinosaur bed, bed 10)													
	10/1	10/2	10/3	10/4	10/5	10/6	10/7	10/8	10/9	10/10				
Palynomorph group														
Total spores + pollen	322	318	385	313	301	312	324	307	342	314				
Total Bryophyta	0	9	6	11	11	5	22	10	9	10				
% Bryophyta	0.0%	2.8%	1.6%	3.5%	3.7%	1.6%	6.8%	3.3%	2.6%	3.2%				
Total Ferns	243	242	312	217	245	250	245	228	268	256				
% Ferns	75.5%	76.3%	81.0%	69.3%	81.4%	80.1%	75.6%	74.3%	78.4%	81.5%				
Total Lycopods	29	24	31	33	19	14	28	15	31	14				
% Lycopods	9.0%	7.6%	8.1%	10.5%	6.3%	4.5%	8.6%	4.9%	9.1%	4.5%				
Total Conifers (excl. <i>Classopollis</i> )	48	30	35	45	24	38	26	43	27	32				
% Conifers (excl. <i>Classopollis</i> )	14.9%	9.5%	9.1%	14.4%	7.9%	12.2%	8.0%	14.1%	7.1%	10.2%				
Total <i>Classopollis</i>	0	5	1	6	0	3	0	8	2	1				
% <i>Classopollis</i>	0.0%	1.6%	0.3%	1.9%	0.0%	1.0%	0.0%	2.6%	0.6%	0.3%				
Total counts	328	326	390	344	305	328	336	314	349	321				
Total green algae	1	3	1	19	3	9	2	1	2	1				
% green algae	0.3%	0.9%	0.3%	5.5%	1.0%	2.7%	0.6%	0.3%	0.6%	0.3%				
Total reworking	5	5	4	12	1	7	10	6	5	6				
% reworking	1.5%	1.5%	1.0%	3.5%	0.3%	2.1%	3.0%	1.9%	1.4%	1.9%				

Percentages of miospores plant groups are relative to total spores + pollen; percentages of green algae and reworking are relative to total counts. Sample set 1: whole measured section; sample set 2: detailed sample set from the dinosaur bed, bed 10.



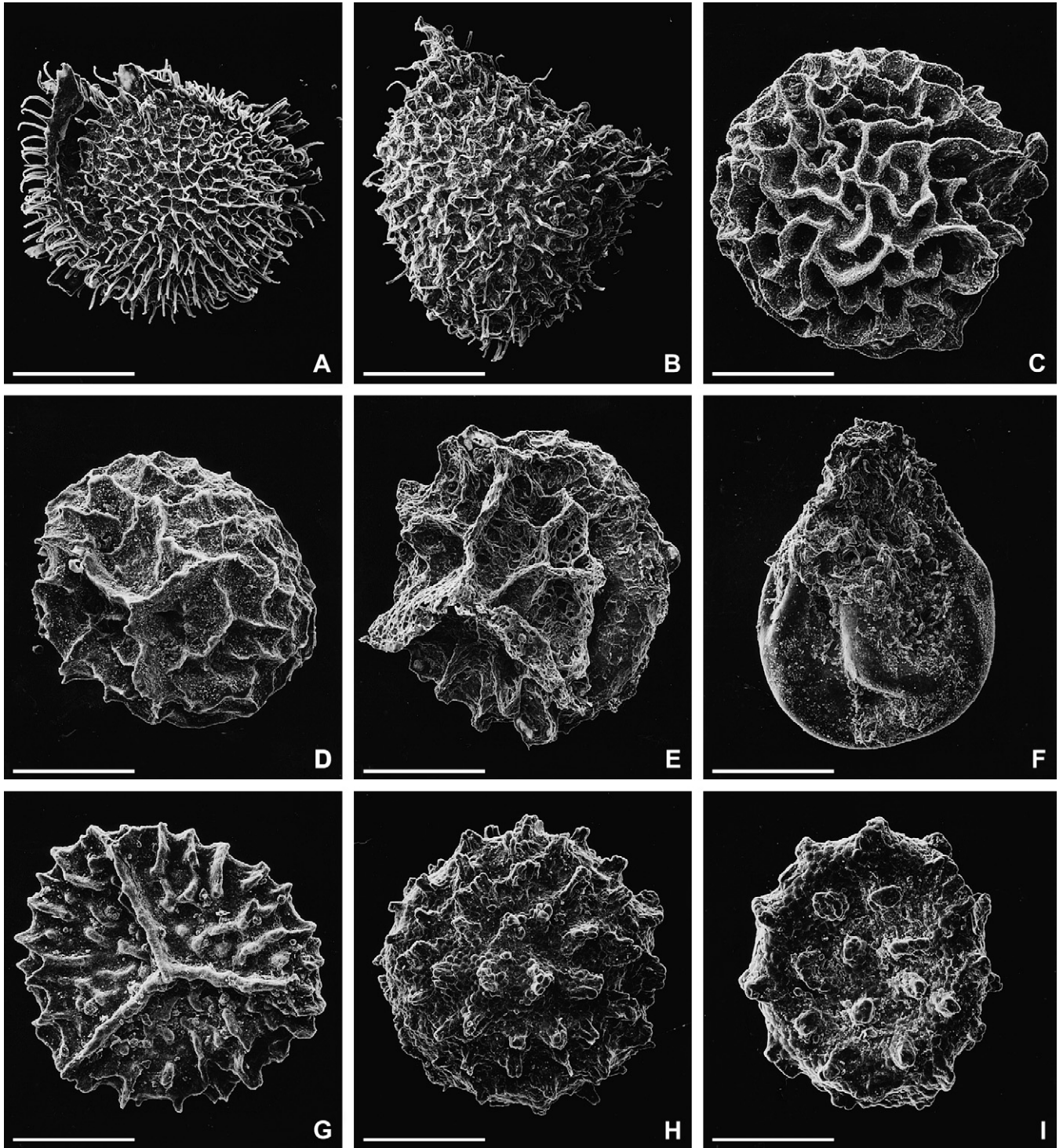


Fig. 9. Megaspores from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. SEM images. A, aff. *Flabellisporites* sp. of Lupia, 2004, megaspore specimen 08, sample 10/10, scale bar: 231  $\mu$ m. B, megaspore specimen 22, sample 10/6, scale bar: 231  $\mu$ m. C, *Erlansonisporites* sp., megaspore specimen 02, sample 10/7, scale bar: 270  $\mu$ m. D, *Erlansonisporites* sp., megaspore specimen 01, sample 10/7, scale bar: 176  $\mu$ m. E, *Minerisporites* sp., megaspore specimen 12, sample SJ1104/5, scale bar: 270  $\mu$ m. F, *Ricinospora* sp. megaspore specimen 21, sample 10/7, scale bar: 231  $\mu$ m. G, *Striatriletes sulcatus* (Dijkstra, 1951) Potonié, 1956, megaspore specimen 11, sample SJ1104/5, scale bar: 136  $\mu$ m. H, “*Clockhousea*” of Batten, 1998, megaspore specimen 3, sample 10/7, scale bar: 231  $\mu$ m. I, “*Clockhousea*” of Batten, 1998, megaspore specimen 18, sample 10B, scale bar: 176  $\mu$ m.

size, less than 0.5 mm long (adults of most *Cypridea* species are typically between 0.7 and 1.1 mm in length). The positions of its weak tubercles appear to match closely those seen in the subspecies of *C. clavata*. Some of our smaller specimens (e.g.,

Fig. 10 N, O) are very similar to *C. insulae*; they appear to lack the two short dorsomedian sulci that are characteristic of *C. insulae* (and hint that *Bisulcocypridea* Sohn, 1969 might be a more appropriate generic assignment for that species) but

Table 3  
Ostracoda recorded from Smokejacks Brickworks

Ostracod taxon	Sample number										
	10/1	10/2	10/3	10/4	10/5	10/6	10/7	10/8	10/9	10/10	10b
<i>Cypridea clavata</i> adult	0	0	0	0	3f	31c, 11rv, 8lv	17c, 5rv, 13lv	3c, 2rv, 5lv	5rv, 1lv	4c, 5rv, 2lv	3c, 7rv, 6lv
<i>Cypridea clavata</i> juvenile	0	0	0	0	0	0	3rv, 1lv	2lv	0	3rv, 1lv	10rv, 13lv
<i>Stenestroemia</i> cf. <i>cressida</i>	0	0	0	0	0	1c	2rv, 2lv	0	0	0	4c, 1rv
<i>Stenestroemia</i> sp. A	0	0	0	0	0	1c	1c, 1lv	0	0	0	0
<i>Damonella</i> cf. <i>pygmaea</i>	0	0	0	0	0	1c	0	1c	0	0	2c, 1lv
<i>Mantelliana?</i> sp.	0	0	0	0	0	0	8f	1?rv	2?dv	2?dv	1f, 2?dv

rv = right valve; lv = left valve; c = carapace; dv = damaged valve; f = fragment.

these are only weakly developed at best and may owe their appearance to flanking tubercles. We consider our specimens to represent juveniles of *C. clavata* and regard Anderson's *C. insulae* as representing juveniles, possibly of *C. clavata*, but perhaps of another species. Anderson himself (1967) noted the possibility that *C. insulae* might be a juvenile of *Cypridea warlinghamensis* Anderson, 1967, but concluded that differences in ornament pattern and the shape of the rostrum warranted the establishment of a new species.

According to fig. 5 of Anderson (1985) all of his subspecies of *C. clavata*, together with *Cypridea bogdenensis*, are confined to the Gillmans and Ditchling faunicycles of the Upper Weald Clay, except *C. clavata clavata* itself which ranges almost throughout both the Lower and Upper Weald Clay.

Family: Candonidae Kaufmann, 1900  
Subfamily: Cyclocypridinae Kaufmann, 1900  
Genus *Damonella* Anderson, 1966

*Damonella* cf. *pygmaea* (Anderson, 1941)  
Fig. 10 S, V

- ?1941 *Cypris pygmaea* sp. nov. Anderson, 379, pl. 19, fig. 17.  
?1966 *Damonella pygmaea* (Anderson, 1941); Anderson, 441, text-figs 22, 30.  
?1985 *Damonella pygmaea* (Anderson, 1941); Anderson, 34, pl. 2, fig. 7.

*Remarks.* Our specimens are closely similar in outline to *Damonella pygmaea* (Anderson, 1941) which has been recorded sporadically throughout most of the Purbeck-Wealden succession with its highest occurrence in the Upper Weald Clay Formation at the level of Anderson's Gillmans Faunicycle (Anderson, 1985).

Suborder: Cytherocopina Grunzel, 1967  
Superfamily: Cytheroidea Baird, 1850  
Family: Limnocytheridae Klie, 1938  
Subfamily: Limnocytherinae Klie, 1938  
Genus *Stenestroemia* Christensen, 1968

*Stenestroemia* cf. *cressida* Anderson, 1971  
Fig. 10 R, U

- ?1971 *Stenestroemia cressida* sp. nov. Anderson in Anderson & Bazley, 126, pl. 21, fig. 13.  
?1985 *Stenestroemia cressida* Anderson, 1971; Anderson, 37, pl. 12, fig. 13.

*Remarks.* Originally described from the Grinstead Clay Formation (Hastings Beds Group). Our specimens are less elongate than that illustrated by Anderson, pl. 12, fig. 13 (in Anderson and Bazley, 1971, and 1985) but otherwise similar in outline in lateral and dorsal view as well as in the pitted ornament, dorsomedian sulcus and weak ventrolateral alar protuberance. It is possible that Anderson's figured specimen is a male while all of ours are female, in which case they can be assigned to *S. cressida*; further material is needed to resolve this question. Anderson, in Anderson and Bazley (1971), briefly discussed possible sexual dimorphism in two other species of *Stenestroemia* from the Purbeck Limestone Group.

*Stenestroemia* sp. A  
Fig. 10 Q, T

*Remarks.* This species is distinguished from *S. cf. cressida* by the more tapered extremities in dorsal view and the curved, less abrupt posterior termination of the alar protuberance. It bears a superficial resemblance to *Wolburgia atherfieldensis* Anderson, 1966 (which may also be a limnocytherine) from the Barremian–earliest Aptian Vectis Formation on the Isle of Wight, but the latter is more tapered in lateral view, has a different ornament of pits and small, flat tubercles, and lacks a distinct dorsomedian sulcus.

Genus *Mantelliana* Anderson, 1966

*Mantelliana?* sp.

*Remarks.* Poorly-preserved, broken valves and fragments of relatively large, thin-shelled ostracod in Weald Clay deposits often belong to the genus *Mantelliana*, specimens of which are usually only seen in their entirety when preserved *in situ*, for example on bedding plane surfaces of sideritic mudstones and siltstones; however, a careful search of such material from the dinosaur bed failed to reveal any such material that would allow confident identification.



## 6.2. Taphonomy of ostracod assemblages

Samples 10/6–10/10 yielded broadly similar ostracod assemblages dominated by *Cypridea clavata*. Of the three richest samples, 10/6 contained a high proportion of complete carapaces, while 10/7 and 10/10 included juvenile valves as well as adult valves and carapaces (Table 3). The presence of juvenile valves as well as adult valves and carapaces in 10/7, 10/8, 10/10 and 10b (both washings) is interpreted as indicative of a thanatocoenosis (*in situ* death assemblage) from a low-energy environment, with little or no post-mortem transport or mixing (Boomer et al., 2003). The relative abundance of articulated carapaces and absence of juveniles in 10/6 is suggestive of a slightly higher energy thanatocoenosis from which the juvenile valves have been removed by current or wave action. The ostracod assemblages can therefore be considered to represent the local palaeoenvironment at the time of the death and immediate post-mortem burial of the *Iguanodon*.

In view of the fact that no well-preserved ostracods have been found in any other part of the Smokejacks Brickworks exposure we consider it probable that our assemblages were preserved because of special diagenetic conditions in close proximity to the *Iguanodon* skeleton. Samples collected subsequently (November 2004) from the same level, within approximately 10 m of the *Iguanodon* site, proved to be barren of ostracods although they contained abundant megaspores.

## 7. Biostratigraphy and age determination

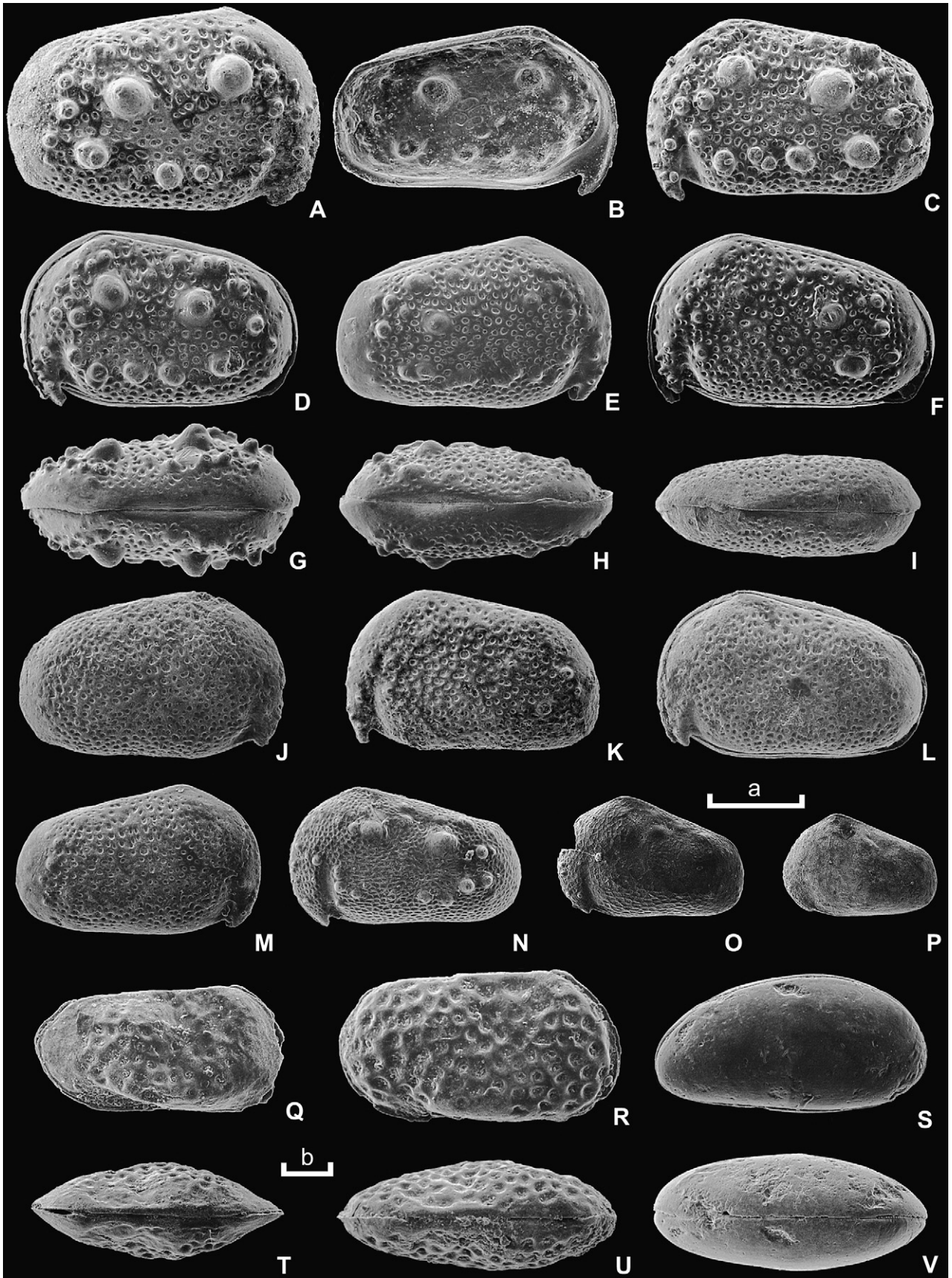
### 7.1. Palynological age determination

Previous attempts to either distinguish or subdivide the Purbeck-Wealden beds based on palynology have shown that there is little difference between the miospore assemblages of the British Jurassic and the Lower Cretaceous with the majority of genera first appearing in the Middle Jurassic and remaining present through into Albian or younger strata. In his classic work, Couper (1958) attempted to distinguish different miospore assemblages in the British Upper Jurassic and Lower Cretaceous through to the Lower Greensand (Aptian). He suggested that the first occurrence of several fern spore species distinguished Wealden microfloral assemblages from the underlying Purbeck assemblages; these included the following, found in the Smokejacks palynological assemblages: *Cicatricosisporites brevilaesuratus*, *Coronatispora valdensis* and *Impardecispora apiverrucata*. In his work on the Upper Jurassic of Southern England, Norris (1969) identified three microfloral suites A–C, and showed that Couper's 'Wealden' species are in fact present in the Middle to Upper Purbeck beds (Lower, Middle and Upper Purbeck beds are now referred to the Purbeck Limestone Group, subdivided into the Lulworth and Durlston formations and spanning the end-Jurassic (latest Portlandian) to earliest Cretaceous (Berriasian); see Westhead and Mather, 1996). Norris concluded, however, that the first occurrence of the many sculptured trilete spores that are typical of his suite C (upper part of middle Purbeck and upper Purbeck beds), including Couper's 'Wealden' species, can be used to

mark the base of the Cretaceous system. Also, the development of auriculae at the apices of schizaeaceous spores, as in *Plicatella*, first appears at the Jurassic/Cretaceous boundary (Batten, 1996b). *Cicatricosisporites* likely gave rise to *Plicatella* gradually by selection through the Early Cretaceous (Hughes in Tschudy and Scott, 1969). The auriculae on these schizaeaceous spores developed further into longer appendages as in *Appendicisporites*, known from the Albian to the Coniacian; none is present in the Smokejacks assemblages. The presence of *Cicatricosisporites angicanalis* suggests an age younger than mid Berriasian for the Smokejacks assemblage, as it occurs no earlier than the Upper Purbeck of Dorset (Norris, 1969) and first appears in the Wealden A in Germany (Döring, 1965). Fern spores were again the focus of an attempt to correlate Wealden assemblages when, due to the abundance and widespread distribution of the fern spore genus *Cicatricosisporites* in Lower Cretaceous sediments, Hughes and Moody-Stuart (1969) introduced 'biorecords' for stratigraphic correlation. They described a biorecord as a conceptual taxon approximating to a species, based on at least 100 specimens, from one sample or locality, judged to have a normal distribution of continuous variation. The use in stratigraphic correlation of these ordered events (as opposed to the use of biostratigraphic zones) was designed to provide more closely defined correlations. This work has been met with criticism; many of the biorecords described may in fact be spores from the same plant in different stages of maturity, or reflect different morphologies produced by individual plants within the same family. Fern spores can therefore only support an Early Cretaceous age for the assemblages.

On the other hand, the evolution of the early angiosperms and the first appearance of their distinctive pollen in Early Cretaceous assemblages provide useful stratigraphic markers within the Wealden (e.g., Hughes et al., 1979; Hughes and McDougal, 1990; Hughes, 1994). Although small numbers of pollen grains with angiosperm-like characteristics have been reported from as far back as the Middle Triassic (Hochuli and Feist-Burkhardt, 2004), a continuous record is not evident until the Hauterivian–Barremian (Batten, 1996b). Four species of pollen belonging to the early angiosperm pollen genus *Retimonocolpites* are present in the Smokejacks palynological assemblages at abundances of generally <1%, in common with other mid-latitude Barremian–Aptian pollen and spore assemblages (Batten, 1996b). Angiosperm pollen is distinguished by its wall structure where an outer layer of exine forms a roof-like structure (tectum) over the inner layers of the exine (endexine). The earliest angiosperm pollen was monosulcate with a tectum constructed of columellae which fuse at the tips forming a reticulum over the endexine. The term 'Monosulcate-Columellate-Tectate' (MCT) pollen used by Hughes (1994) is descriptive of the tectum morphology of the earliest angiosperm pollen.

Although the timing of the first continuous record of angiosperm pollen varies latitudinally, Hughes et al. (1979) attempted to put the Wealden early angiosperm pollen to some stratigraphic use, correlating what they referred to as the English 'upper Wealden Group' (which appears to





include the nonmarine Barremian Upper Weald Clay Formation through to the marine Early Aptian Atherfield Clay Formation) to Zone 1 of the Potomac Group of the north-eastern United States. They described different morphologies equivalent to species as ‘biorecords’ ranging from the mid Barremian to earliest Aptian of southern England. Hughes et al. (1979), Hughes and McDougal (1990) and Hughes (1994) use of SEM images to illustrate biorecords renders difficult the distinction of the very similar-looking grains using light microscopy alone. However, CLSM study of the Smokejacks specimens (Fig. 7) has allowed comparisons to be made more easily. Four MCT ‘phases’ defined by the abundance and diversity of early angiosperm biorecords were recognized by Hughes (1994) from the late Hauterivian to the early Aptian. By comparing angiosperm grains found in this study to Hughes’ biorecords, the Smokejacks assemblages may be constrained tentatively to within the early Barremian, under the definition of MCT phase 2 which states that there should be enough specimens to erect more than one taxon. However, MCT phases appear to have no definite boundaries and no correlations to other established zones have been made. Therefore the stratigraphic extent of MCT phase 2 is uncertain and its use in age determination should be with caution. *Retimonocolpites* sp. 1 was most abundant and can easily be assigned to the biorecord *Retisulc-dentata* (Hughes et al., 1979), and *Retimonocolpites* sp. 3 shows many similarities to biorecord *Retisulc-muribeaded* (Hughes, 1994; see section 5.1). Both these biorecords are characteristic taxa of MCT phase 2 (Hughes, 1994), however, *Retimonocolpites* sp. 3 appears to show the triangular suprategal elements comparable to biorecord *Superret-triang* (Hughes et al., 1979) although, according to Hughes (1994), these features did not appear until the early Aptian in MCT phase 4. *Retimonocolpites* sp. 4 does not compare well to any published biorecords. The simple, reticulate tectum morphology of *Retimonocolpites* sp. 1 and *Retimonocolpites* sp. 2 are typical of the first angiosperm pollen to appear in the Lower Cretaceous. The dinosaur site of Smokejacks Brickworks is therefore certainly older than the Bernissart *Iguanodon* site, which yielded angiosperm pollen with more intricate morphologies that were attributed to the MCT phases 3 and 4, dated mid-Barremian to earliest Aptian (Yans et al., 2004, 2005; Dejax et al., 2007).

## 7.2. Ostracod biostratigraphy

Anderson (1967) showed the short-ranging *Cypridea bogdenensis* as restricted to the base of his *Cypridea clavata*

Zone. That zone was later expanded downwards (Anderson, in Worssam and Ivimey-Cook, 1971) to take account of ostracod data from the Warlingham borehole, and *C. bogdenensis* was subsequently shown as occurring in both the Gillmans Faunicycle and the overlying Ditchling Faunicycle, near the top of the revised *Cypridea clavata* Zone (Anderson, 1985). The range of *Cypridea clavata* itself was shown by Anderson (1985) to extend well below and above the zone that bore its name; in the revised zonation scheme of Horne (1995) the first appearance of *C. clavata* marks the base of the *Cypridea fasciata* Subzone. Although *C. clavata clavata* is relatively long ranging in the Weald Clay Group, five of the six additional subspecies described by Anderson (1967) are restricted to the Gillmans Faunicycle, the sixth to the overlying Ditchling Faunicycle (Anderson, 1985). *Cypridea insulae* first appears immediately above this, in the Atherfield Faunicycle and is recorded again, higher up, in the Cuckmere Faunicycle (Anderson, 1985). Whether one accepts Anderson’s taxonomic scheme or the one proposed herein which accommodates all *C. clavata* subspecies, as well as *C. bogdenensis* and possibly *C. insulae*, within the intrapopulational variation of a single species, it seems probable that most of these forms except *C. clavata clavata* are restricted to a relatively small interval in the Barremian Upper Weald Clay Formation. It is, therefore, tempting to correlate the Smokejacks fauna directly with the Gillmans and Ditchling faunicycles as recorded in the Warlingham borehole in the Weald, and furthermore to suggest a tentative correlation with the lower part of the Vectis Formation on the Isle of Wight. Unfortunately, although they provide a valuable and detailed reference framework in his Purbeck-Wealden biostratigraphic scheme, Anderson’s faunicycles are not repeatable because they were never defined in a consistent way (Horne, 1995). Anderson never recorded any ostracods, let alone faunicycles, in Smokejacks Brickworks, so we can only guess at whether or not any particular faunicycle is represented there. There is, furthermore, the problem of preservational bias: if our Smokejacks fauna is only preserved by virtue of its association with an *Iguanodon* skeleton, it is entirely possible that other restricted occurrences of Upper Weald Clay Formation ostracod taxa owe their preservation to local and special diagenetic histories. The Smokejacks fauna may be contemporary with the Gillmans–Ditchling interval elsewhere in the western Weald, but it is not impossible that the fauna was longer-ranging, each occurrence at a different locality representing a preservational window on a different short time interval. Nevertheless, it can at least be said with confidence that the fauna is consistent with a Barremian age.

Fig. 10. Ostracods from the Upper Weald Clay Formation, Smokejacks Brickworks, Surrey, UK. A–P, *Cypridea clavata*; A–D, G, “*clavata*” variant, adults: A, right external lateral view of carapace; B, C, internal and external lateral views of same LV; D, G, left external lateral and dorsal views of same carapace; E, F, H, “*beltanalbogdenensis*” variant, adults: E, H, right external lateral and dorsal views of same carapace; F, left external lateral view of carapace; I–L, “*maleta*” variant, adults: I, L, dorsal and left external lateral views of same carapace; J, right external lateral view of carapace; K, external lateral view of LV; M–P, *Cypridea clavata* juveniles: M, right external lateral view of carapace; N, external lateral view of LV (“*insulae*”? variant); O, external lateral view of LV; P, external lateral view of LV; Q, T, *Stenestroemia* sp. A, right external lateral and dorsal view of same carapace; R, U, *Stenestroemia* cf. *crossida*, right external lateral and dorsal view of same carapace; S, V, *Damonella* cf. *pygmaea*, right external lateral and dorsal view of same carapace. A, D–I, J, L from sample 10/6; M from sample 10/7; B, C, K, R, U from sample 10/10; N–P, Q, S, T, V from sample 10b. Scale bar a = 200 µm (Figs A–P), scale bar b = 150 µm (Figs Q–V).

## 8. Discussion: palaeoclimate and palaeoenvironment

### 8.1. Palaeoclimate indications of the palynoflora

*Classopollis* pollen was produced by a member or members of the extinct conifer family Cheirolepidiaceae, many of which exhibit strong xeromorphic characters (Watson and Alvin, 1996), and the abundance of *Classopollis* has been used as an indicator of aridity (Vakhrameev, 1981; Batten and MacLennan, 1984). Forming the dominant component of many Triassic and Jurassic assemblages, abundances of *Classopollis* decrease until extinction in the Palaeocene. Although it was less common in the Early Cretaceous than in the Jurassic, it still formed an important part of Wealden conifer pollen assemblages. *Classopollis torosus* is present throughout the Smokejacks palynology assemblages and its maximum abundance may be used as an indicator of aridity.

Evidence of reworking is apparent in some samples in the form of marine, exclusively Middle to Upper Jurassic dinoflagellate cyst taxa, and the possibility that the relatively high percentage of *Classopollis torosus* in samples 1–6 could be partly due to reworking cannot be overlooked. However, since the other palynomorphs recognized as reworked, which are exclusively marine Jurassic taxa (see section 5.4), are not evident in these *Classopollis*-rich samples, we consider *C. torosus* to be *in situ*.

Vakhrameev (1981) used *Classopollis* abundance data to define climatic belts crossing the former USSR and recording climatic fluctuation during the Mesozoic; with a maximum *Classopollis* content of 33%, the Smokejacks assemblage falls into his ‘warm subtropical zone’. Wealden vegetation was adapted to a seasonal climate of alternating wet and dry periods, including periods of marked aridity (Sladen and Batten, 1984; Allen, 1998). Wright et al. (2000) noted the abundance of fossil charcoal in Wealden deposits and the absence of *in situ* peat as evidence of seasonal aridity and wildfires. The significance of the xerophytic Cheirolepidiaceae producing *Classopollis* in the Smokejacks gymnosperm assemblage may indicate fire-adaptation as an advantage in the markedly seasonal climate described by Wright et al. (2000), in which wildfires were characteristic of the dry season. All extant gymnosperms, however, show xeromorphic features to a degree (Watson and Alvin, 1996), but other Wealden plants such as the bennettitales show xeromorphy which is more likely to have been an adaptation to the regional climate.

Cycads and ginkgoales were widely distributed in the high latitudes during the Mesozoic, but their pollen is absent from the Smokejacks palynological assemblages; microfossils of these taxa are rare in the Wealden (Watson and Alvin, 1996) and have not been found at Smokejacks. This may indicate that the temperatures were too high for ginkgoales, as suggested by Watson and Alvin (1996), and the climate perhaps too humid for cycads. The rare occurrences of *Ephedripites* in some of the Smokejacks samples (see Table 1), which was probably produced by an *Ephedra*-like plant, might have been wind blown from lower latitudes.

### 8.2. Vegetation reconstructed from pollen/spore relative abundance

The up-section change from principally gymnosperm-dominated assemblages to more diverse, principally pteridophyte-dominated assemblages in the Smokejacks palynological assemblages (Fig. 3) may be due to a drop in water level on the floodplain, the pollen/spore assemblages reflecting the extent of the vegetated floodplain at the time of deposition. The principally gymnosperm-dominated assemblages at the base of the section may reflect conifers inhabiting well-drained areas of relief including, perhaps, tree islands in times of flood. The ‘lowland’ areas, which seasonally would support pteridophyte vegetation, would be submerged, leaving water/air-transported conifer pollen from upland areas to dominate the miospore assemblages.

With a drop in water level on the floodplain, pteridophyte vegetation dominated by ferns, lycopods and to a lesser extent hepaticophytes inhabited the (seasonally) flooded mudflats, resulting in the increase in relative abundance of pteridophytes in the miospore assemblages. This coincides with a decrease in the relative abundance of the conifer pollen representing upland vegetation. This is a Wealden example of the ‘Neves effect’ sensu Chaloner and Muir (1968). The major shift to a pteridophyte-dominated assemblage is most clearly seen in sample 8 with a sudden high abundance of *Leptolepidites verrucatus*, which is rare or absent in the conifer-dominated assemblages below. The relative abundance of *Cicatricosisporites* spp. increases along with other fern spores in sample 8 and *Cicatricosisporites* also makes up most of the fern component of the conifer-dominated sediments. The number of *Cyathidites* specimens counted throughout the section is similar in both the gymnosperm-dominated and pteridophyte-dominated assemblages (Table 1). The tree fern which produced *Cyathidites* and the schizaceous fern which produced *Cicatricosisporites* may have formed the undergrowth in the better-drained areas of the basin where there was conifer forest. Their spores may have travelled some distance, along with the pollen produced by the conifers. The fern which produced *Leptolepidites verrucatus* is likely to have only grown on the poorly-drained open fluvial mudflats where it thrived and overtook the schizaceous ferns as the most important part of the vegetation.

The change in lithology through the section does not appear to have had a significant effect on the distribution of palynomorphs in the sediments. Although local vegetation may be reflected in palynomorph assemblages, Batten (1974) suggested that the distribution of miospores in the Wealden may be more closely related to sedimentary facies than to the distribution of parent vegetation. Jäger (2004) showed that the proportion of spherical grains increased with re-sedimentation, whereas the number of triangular spores decreased along with grain size. He observed higher abundances of trilete spores in medium silts – fine sandstones than in finer-grained deposits, this being partly due to many fern spores having a greater specific gravity than gymnosperm pollen. Our 10 m Smokejacks section generally coarsens-upwards (Fig. 2), with good

palynology assemblages from clays, silty clays through to the sandy clay of sample 11. With the exception of sample 12, where the scarcity of palynomorphs is likely to have been entirely due to the coarse grain size of the sediment, the distribution of the spores and pollen does not seem to show the sorting described by Jäger (2004). The relative abundance of the spherical pollen *Classopollis torosus* is noticeably higher in samples 3, 5 and 6. Samples 3 and 6 are both gymnosperm pollen-dominated silty clays, coarser than the gymnosperm pollen-dominated clay of samples 1, 2 and 4. However, sample 5 also shows a noticeably high abundance of *C. torosus* as it is dominated by pteridophyte spores which constitute 61%, but it is a clay deposit. The relative abundance of other spherical grains *Inaperturopollenites dubius* and *Taxodiaceapollenites hiatus* does not show the same distribution through the section as *Classopollis*; the highest numbers of *I. dubius* and *T. hiatus* are found in samples 1 (shaley clay), 4 (laminated silty clay) and 6 (silty clay). There is also no lithological reason why bisaccate pollen should form 50% of the conifer pollen in sample 2 but only constitute 27% and 20% of the conifer pollen in samples 1 and 3. The trends in the major plant groups from pollen/spore assemblages, as shown in Fig. 3, therefore probably represent direct changes in the vegetation of the area through time.

The plant macrofossil record at Smokejacks shows some differences from the flora inferred from the pollen/spore assemblage, suggesting that the proportions of different parent plant groups represented in the preserved miospore assemblage may not be representative of the local vegetation. Some plant groups may be over- or under-represented in the preserved palynology assemblage. Macrofossil remains of the horsetail *Equisetum* have been recorded but are rare at Smokejacks (Ross and Cook, 1995), and their pollen is absent from the palynological assemblages. Batten (1968) suggested that a low rate of spore production plus short-lived very local communities of these plants could explain the rarity of their spores in beds where their macrofossil remains are common. Some plant groups may therefore not be represented in the Smokejacks palynological assemblages, although they may have been important (but relatively short-lived) constituents of the local environment surrounding the *Iguanodon* when it was alive.

Alternatively, the absence of spores of certain plant groups in the palynological assemblages may indicate that they are representative of only the very local flora. On a broad scale, bennettitales formed an important part of the Wealden vegetation (Watson and Alvin, 1996), but their pollen is absent from the palynological assemblages at Smokejacks. This may indicate that the majority of spores and pollen preserved in the palynological preparations were produced by vegetation local to the dinosaur site and the inclusion of far-transported grains representing the regional vegetation was minimal. Ferns such as the common Wealden fossil fern *Weichselia reticulata*, formed a numerically important component of Wealden vegetation; burnt remains of *W. reticulata* were dominant in charred plant material described by Harris (1981) and remains have been found at Smokejacks Brickworks (Ross and Cook,

1995). Fossil conifer fragments were seen 4 m above bed 10 at Smokejacks and were probably transported onto the pteridophyte-dominated floodplain by flood from ‘upland’ areas in the region. Coniferalean twigs and cones are occasionally found from Smokejacks (Ross and Cook, 1995). Batten (1998) suggested the possibility that the lowland areas had no trees and that the small size and sparse distribution of coniferalean remains indicated that they were transported to the site of deposition and represented the more regional flora. The immediate vegetation on the area of the floodplain on which the *Iguanodon* was preserved was most likely made up primarily by ferns, with lycopods and hepaticophytes forming relatively minor components of the vegetation as reflected by the low relative abundance of their spores in the preserved palynological assemblages. Due to the development of structures both of the parent plant and of the pollen, encouraging biotic pollination, many angiosperms need only produce a small fraction of the amount of pollen produced by gymnosperms and pteridophytes. Therefore, it is likely that the earliest angiosperms constituted a more significant part of the vegetation than the rare occurrences implied by direct relative comparison with the other plant groups represented in the palynological assemblages, or that the plants were growing very close to the site of preservation. The angiosperms were possibly pollinated by digger wasps (Hymenoptera: Sphecidae), fossils of which have been found at Smokejacks Brickworks (Rasnitsyn et al., 1998). Macrofossil remains of the putative angiosperm *Bevhalstia pebja* are very abundant in ironstones at one horizon in Smokejacks Brickworks (Hill, 1996). They consist of small leafy stems with axillary or terminally enlarged structures; pollen of the plant is not known. *Bevhalstia* has previously been referred to as a “herbaceous aquatic or marsh-dwelling plant” in Ross and Cook (1995). Its affinity to angiosperms is uncertain and in debate, but there seems to be agreement about the aquatic habitat of this plant based on its morphology (Hill, 1996; Friis et al., 2006).

The *Iguanodon* probably moved out onto the exposed floodplain for the only available fresh water during the dry season and fed on the available plants. The diet of herbivorous dinosaurs has been, and still is, of great interest (e.g., Weaver, 1983; Weishampel, 1984; Farlow, 1987; Taggart and Cross, 1997; Chin and Kirkland, 1998; Barrett and Willis, 2001) and several authors have speculated about the preferences of dinosaurs for feeding on certain plant groups. Taggart and Cross (1997) suggest conifers as the primary food source for Early Cretaceous duck-billed dinosaurs and possibly iguanodonts, while ferns and other pteridophytes, which made up the majority of the ground-level vegetation, were also probable food sources for Early Cretaceous herbivorous dinosaurs. Remains of conifers and other gymnosperms have been reported to constitute entirely some rare finds of Late Cretaceous coprolites of herbivorous dinosaurs (Chin, 1990 and Chin and Gill, 1996). There is no living reptile that lives entirely on conifers, which would have been the dominant plants emergent during wet seasons; the lowland mudflat vegetation represented in the palynology assemblage surrounding the *Iguanodon* at Smokejacks may, therefore, have provided a major



source of its food. Many modern ferns accumulate toxic compounds, probably developed in response to grazing attack from insects (Coe et al., 1987); high levels of unpalatable tannin today are efficient in preventing grazing by mammals. Coe et al. (1987) suggest however that similar levels of chemical defence in Mesozoic ferns may not have prevented grazing by herbivorous dinosaurs if they shared a trait in common with modern reptiles, such as the giant tortoise, which tolerate higher tannin concentrations than warm-blooded mammals. Ferns certainly would have provided large quantities of vegetation easily available to herbivorous dinosaurs. The remains of Cretaceous ferns (along with angiosperm and gymnosperm fragments) have been described from coprolites from the Maastrichtian of India (Mohabey and Samant, 2003), which the authors claim to have been produced by a sauropod. Pteridophytes have been shown to have a higher calorific value than conifers (Weaver, 1983) and therefore would constitute a better, more nutritious fodder than fibre-rich conifers. The relatively large *Iguanodon* (approximately 4.5 tonnes) is likely to have eaten all available vegetation, perhaps favouring marsh plants over conifers.

### 8.3. Palynological evidence of temporary freshwater conditions

The occurrences of the green algae taxa *Pediastrum*, *Scenedesmus* and *Tetraedron* in the Smokejacks assemblages indicate the presence of freshwater habitats in the depositional environment. All the genera are extant, inhabiting freshwater lakes, ponds and slow-moving rivers (Batten, 1996a) and although some species (*Tetraedron paraincus*, *Scenedesmus novilunaris*) are known only from the fossil record, they are always associated with freshwater sediments. In the living genus *Scenedesmus*, dried resting cells may remain viable for years (Batten, 1996a), so the algae can colonize ephemeral waterbodies. The dramatic increase in abundance of *S. novilunaris* in sample 10b (in the *Iguanodon* bed) was not encountered in any of the samples in the more detailed subset (sample set 2) of the same unit, suggesting that it occurs in a very thin layer and represents a short-lived bloom, perhaps representing only a single (particularly hot?) season. The elevated abundances seen in samples 10/4 and 10/6 may indicate that 10b is best correlated to a level just below 10/4 on the detailed section (Fig. 4). The algal cyst *Tetraguladinium conspicuum* is known only from Cretaceous freshwater sediments; its association with *Scenedesmus* here may indicate that it too was capable of inhabiting ephemeral water bodies.

An interesting point is that the *Scenedesmus* signal was strong in sample 10b (from the sediment associated with the *Iguanodon* skull) but absent in samples 10c and 10d (from sediment associated with the right tibia and fibula). It is beyond the scope of this paper to discuss in detail the taphonomy of the *Iguanodon* remains, but we speculate that the skull may have still been exposed above the sediment-water interface at the time of the algal bloom, while the limbs were already buried.

### 8.4. Ostracod palaeoecology

The ostracod-bearing samples were closely spaced and the differences between the assemblages are minor, so it is reasonable to amalgamate the results and consider them as a single assemblage associated with the *Iguanodon* skeleton. The genus *Cypridea* belongs to an extinct cypridoidean family, the Cypridoidea, members of which are considered to have inhabited non-marine waters (possibly including athalassic saline lakes as well as fresh waters) (Horne, 1995, 2002). Like other, extant families of the superfamily Cypridoidea, they are thought to have possessed desiccation-resistant eggs, enabling them to colonize temporary waterbodies and achieve wide dispersal (Horne and Martens, 1998), although some species may have lived in permanent waters. We consider the dominance of a single *Cypridea* species in the Smokejacks assemblage to be indicative of an ephemeral habitat such as a seasonal pond or small lake. We doubt that the *Iguanodon* horizon palaeoenvironment was a permanent lake because the ostracod assemblage lacks examples of species such as *Alicenula leguminella* (formerly assigned to *Darwinula* – see Martens et al. (2003); a darwinuloid) and *Theriosynoecum fittoni* (a cytheroidean limnocytherid), both of which had brood care of eggs and juvenile instars, confining them to permanent waterbodies. Both of these species are relatively common in other Weald Clay Group faunas, including the Hauterivian Lower Weald Clay Formation at Clockhouse Pit in Surrey and the Barremian–earliest Aptian Vectis Formation on the Isle of Wight (Anderson, 1967, 1985; Horne, 1988, 1995). A lake assemblage might also be expected to have higher diversity (species-richness). The other cypridoidean genus in the Smokejacks assemblage (*Damonella*), by analogy with living representatives, probably had desiccation-resistant eggs and could inhabit temporary waters (Horne, 2002) (this would also apply to *Mantelliana* if the occurrence of that genus were confirmed). The only other ostracod genus in the fauna is *Stenestroemia*; it belongs to the Superfamily Cytheroidea, a group widely considered to lack resting eggs, and this is undoubtedly true of those with brood care. However, there are two cytheroidean (limnocytherid) subfamilies in Mesozoic nonmarine ostracod faunas, the Timiriaseviinae (e.g., *Theriosynoecum*, *Timiriasevia*) with brood care, and the Limnocytherinae (e.g., *Limnocythere*, *Stenestroemia*) without brood care. Several examples have been reported of modern limnocytherine species inhabiting temporary ponds (e.g., Horne and Martens, 1998; Smith and Horne, 2004), implying that they too have desiccation-resistant eggs. The presence of species of *Stenestroemia* is therefore not inconsistent with a temporary pond palaeoenvironment.

In summary, the low diversity of the Smokejacks ostracod fauna, the overwhelming dominance of a single *Cypridea* species and the absence of taxa indicative of permanent waters are all suggestive of an ephemeral waterbody, probably existing for only a few weeks or months at a time. The taphonomic considerations mentioned above suggest a slightly higher-energy environment for sample 10/6 than for the overlying samples. This could be consistent with the littoral zone of an



initially large pool, where even limited wave action could suspend smaller valves and allow them to be redeposited in slightly deeper water in the middle of the pool; as the pool dried up and shrank the succeeding assemblages would all remain *in situ*. An alternative possibility is that smaller valves were removed from the lowest assemblage by wind, following drying on the exposed margins of a shrinking pool. There is supporting evidence for drying as we found a few desiccation cracks in the sediments of the *Iguanodon* bed.

### 8.5. Preservation

The palaeotopography at the time of the dinosaur's burial was likely a series of shallow ponds in hollows in what once may have been a freshwater lake basin. Mud cracks are rare; the lake probably silted up in a waterlogged marshy environment rather than dried up completely. The presence of ironstone (siderite: iron carbonate) immediately beneath the *Iguanodon* bed, traceable around the claypit, could suggest that the ground over quite a large area was a marsh in which anoxia and alkaline conditions favoured the formation of siderite over goethite (which forms in well-aerated palaeosols). The rapid accumulation of clay and silt in these water bodies may have contributed to the diagenetic environment; high burial rates have been linked to high rates of sulphate reduction (Berner, 1985), while iron carbonates are derived from sediments depleted in sulphate and hydrogen sulphide. The sediments immediately surrounding the *Iguanodon* itself are very distorted; this is likely a combination of trampling in what was probably an area of animal activity at the time the *Iguanodon* was living, and the behaviour of the soft sediment during compaction compared to the more competent bones. Nevertheless, bioturbation from invertebrates was minimal (although small tubular burrows are in evidence, for example in the top of the underlying ironstone) and fine laminations, ripples and a thin layer recording an algal bloom are all preserved in the *Iguanodon* bed. Thin laminations near the base of the sandstone (sample 11) overlying the *Iguanodon* bed had a well preserved pollen/spore assemblage, while near the top of the same sandstone, 31% of the total palynomorphs counted from sample 12 were recognised as reworked (Table 2) and only a few large fern spores and bisaccates were preserved; the latter assemblage had likely been subjected to winnowing and oxidation.

## 9. Conclusions

Samples from the Smokejacks *Iguanodon* site have yielded the first useful ostracods from the locality, consistent with a Barremian age. Distinct forms of early angiosperm pollen present in the palynological assemblages are consistent with Hughes' (1994) MCT phase 2, which supports the early Barremian age previously determined by Ross and Cook (1995). The change from principally gymnosperm-dominated palynological assemblages to principally pteridophyte-dominated assemblages up the section agrees with the general shallowing-upwards trend previously suggested on sedimentological grounds by Ross

and Cook (1995). At the time the *Iguanodon* lived, schizaceous ferns represented by spores *Cicatricosisporites* spp., together with tree ferns, formed dense undergrowth in conifer forests on the better-drained areas, while an indeterminate fern which produced spores (*Leptolepidites*) dominated the marshy floodplain on which the *Iguanodon* died. The ostracod assemblage is confined to the *Iguanodon* bed, which we interpret to represent a temporary, shallow water body on a marshy floodplain, in which a bloom of green algae (*Scenedesmus novilunaris*) occurred, probably after the death of the dinosaur but before its carcass was completely buried.

## Acknowledgements

We would like to thank all our many colleagues at the Natural History Museum who were involved in the *Iguanodon* excavation in 2001 and were available for discussion on all sorts of aspects concerning the dig, the fossils recovered and the Weald Clay geology. We are grateful to Jonah Chitolie (NHM and Geotechniques Research) for his expert processing of the palynology samples, to David Gray (then NHM Palaeontology Conservation Unit) for access to the *Iguanodon* specimen, to Nick Hayes (NHM Photo Unit) for his assistance with the ostracod SEM images, to Jackie Skipper (formerly NHM, now GCG Geological Consulting Group, London) for providing an unpublished detailed field log of the dinosaur site, to Paul Barrett (NHM Palaeontology Department) for advice on dinosaur diet, to Bill Chaloner (Royal Holloway) for his guidance on the palynology, and to John E. Williams (NHM Palaeontology Department) for valuable advice and access to his library and reference system. We are most grateful to David Batten for his advice on the identification of the megaspores and also to an anonymous reviewer for constructive comments on the manuscripts. We thank Chelwood Brick and The Brick Business Ltd., and Tim Burgess, for provision of aerial photographs and allowing unrestricted access to the claypit and generous provision of assistance. This contribution is based in part on the Master's project report by the first author (EN) carried out in the framework of the MSc course in Micropalaeontology at University College London (UCL) whilst in receipt of a 50% NERC studentship.

## References

- Allen, P., 1976. Wealden of the Weald: a new model. *Proceedings of the Geologists' Association* 86 (4), 389–437.
- Allen, P., 1981. Pursuit of Wealden models. *Journal of the Geological Society of London* 138 (4), 375–405.
- Allen, P., 1990. Wealden research — ways ahead. *Proceedings of the Geologists' Association* 100 (4), 529–564. 1989.
- Allen, P., 1998. Purbeck-Wealden (Early Cretaceous) climates. *Proceedings of the Geologists' Association* 109 (3), 197–236.
- Anderson, F.W., 1939. Wealden and Purbeck Ostracoda. *Annals and Magazine of Natural History* 11 (3), 291–310. pls 12–13.
- Anderson, F.W., 1966. New genera of Purbeck and Wealden Ostracoda. *Bulletin of the British Museum, Natural History, Geology* 11, 435–446.
- Anderson, F.W., 1967. Ostracods from the Weald Clay of England. *Bulletin of the Geological Survey of Great Britain* 27, 237–269.

- Anderson, F.W., 1985. Ostracod faunas in the Purbeck and Wealden of England. *Journal of Micropalaeontology* 4 (2), 1–68.
- Anderson, F.W., Bazley, R.A.B., 1971. The Purbeck beds of the Weald. *Bulletin of the Geological Survey of Great Britain* 34, ix + 174 pp.
- Austen, P., 2001. The day of the *Iguanodon*. *The Geologists' Association Circular* 948, 13.
- Baltanás, A., Alcorlo, P., Danielopol, D.L., 2002. Morphological disparity in populations with and without sexual reproduction: a case study in *Eucypris virens* (Crustacea: Ostracoda). *Biological Journal of the Linnean Society* 75 (1), 9–19.
- Barrett, P.M., Willis, K.J., 2001. Did dinosaurs invent flowers? Dinosaur-angiosperm coevolution revisited. *Biological Reviews* 76, 411–447.
- Batten, D.J., 1968. Probable dispersed spores of Cretaceous *Equisetites*. *Palaeontology* 11 (4), 633–642.
- Batten, D.J., 1969. Some Wealden British megaspores and their facies distribution. *Palaeontology* 12, 333–350.
- Batten, D.J., 1974. Wealden palaeoecology from the distribution of plant fossils. *Proceedings of the Geologists' Association* 85 (4), 433–458.
- Batten, D.J., 1996a. Colonial Chlorococcales. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*, vol. 1. American Association of Stratigraphic Palynologists Foundation, pp. 191–203.
- Batten, D.J., 1996b. Upper Jurassic and Cretaceous miospores. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*, vol. 2. American Association of Stratigraphic Palynologists Foundation, pp. 807–830.
- Batten, D.J., 1998. Palaeoenvironmental implications of plant, insect and other organic-walled microfossils in the Weald Clay Formation (Lower Cretaceous) of southeast England. *Cretaceous Research* 19, 279–315.
- Batten, D.J., MacLennan, A.M., 1984. The palaeoenvironmental significance of the conifer family Cheirolepidiaceae in the Cretaceous of Portugal. In: Reif, W.-E., Westphal, F. (Eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, pp. 7–12.
- Berner, R.A., 1985. Sulphate reduction, organic matter decomposition and pyrite formation. *Philosophical Transactions of the Royal Society of London* A315, 25–38.
- Boomer, I., Horne, D.J., Slipper, I.J., 2003. The use of ostracods in palaeoenvironmental studies, or what can you do with an ostracod shell? In: Park, L.E., Smith, A.J. (Eds.), *Bridging the Gap: Trends in the Ostracode Biological and Geological Sciences*. The Paleontological Society Papers, vol. 9, pp. 153–179.
- Chaloner, W.G., Muir, M., 1968. Spores and floras. In: Murchison, D., Westoll, T.S. (Eds.), *Coal and Coal-Bearing Strata*. Oliver & Boyd, Edinburgh, pp. 127–146.
- Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum, London, Geology Series* 53 (1), 11–70.
- Chin, K., 1990. Possible herbivorous dinosaur coprolites from the Two Medicine Formation (Late Cretaceous) of Montana. *Journal of Vertebrate Paleontology* 10 (3 Suppl.), 17A.
- Chin, K., Gill, B.D., 1996. Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaios* 11, 280–285.
- Chin, K., Kirkland, J.I., 1998. Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore quarry, western Colorado. *Modern Geology* 23, 249–275.
- Coe, M.J., Dilcher, D.L., Farlow, J.O., Jarzen, D.M., Russell, D.A., 1987. Dinosaurs and land plants. In: Friis, E.M., Chaloner, W.G., Crane, P.R. (Eds.), *The Origins of Angiosperms and their Biological Consequences*. Cambridge University Press, pp. 225–258.
- Couper, R.A., 1958. British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontographica Abteilung B* 103, 75–179. pls. 15–31.
- Dejax, J., Pons, D., Yans, J., 2007. Palynology of the dinosaur-bearing Wealden facies in the natural pit of Bernissart (Belgium). *Review of Palaeobotany and Palynology* 144, 25–38.
- Dettmann, M.E., 1963. Upper Mesozoic microfloras from south-eastern Australia. *Proceedings of the Royal Society of Victoria* 77 (1), 148, pp. 27 pls.
- Dijkstra, S.J., 1949. Megaspores and some other fossils from the Aachenian (Senonian) in South Limburg, Netherlands. In: *Mededelingen van de geologische Stichting, Nieuwe Serie*, 3, 19–32.
- Dijkstra, S.J., 1951. Wealden megaspores and their stratigraphic value. In: *Mededelingen van de geologische Stichting, Nieuwe Serie*, 5, 7–21.
- Döring, H., 1965. Die sporenpaläontologische Gliederung des Wealden in Westmecklenburg (Structur Werle). *Geologie* 14, 1–117. pls 1–23.
- Farlow, J.O., 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. *Paleobiology* 13 (1), 60–72.
- Feist-Burkhardt, S., Pross, J., 1999. Morphological analysis and description of Middle Jurassic dinoflagellate cyst marker species using confocal laser scanning microscopy, digital optical microscopy, and conventional light microscopy. *Bulletin du Centre de Recherches Elf Exploration Production* [1998] 22 (1), 103–145.
- Friis, E.M., Raunsgaard Pedersen, K., Crane, P.R., 2006. Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232, 251–293.
- Gallois, R.W., Worssam, B.C., 1993. *Geology of the country around Horsham*. Memoir of the British Geological Survey, Sheet 302 (England and Wales), viii + 130 pp.
- Haywood, A.M., Valdes, P.J., Markwick, P.J., 2004. Cretaceous (Wealden) climates: a modelling perspective. *Cretaceous Research* 25, 303–311.
- Harris, T.M., 1981. Burnt ferns from the English Wealden. *Proceedings of the Geologists' Association* 92, 47–58.
- Hill, C.R., 1996. A plant with flower-like organs from the Wealden (Lower Cretaceous) of southern England. *Cretaceous Research* 7, 27–38.
- Hochuli, P., Feist-Burkhardt, S., 2004. A boreal early cradle of Angiosperms? Angiosperm-like pollen from the Middle Triassic of the Barents Sea (Norway). *Journal of Micropalaeontology* 23, 97–104.
- Hodgkinson, R.L., 1991. Microfossil processing: a damage report. *Micropalaeontology* 37, 320–326.
- Horne, D.J., 1988. Cretaceous Ostracoda of the Weald. In: *British Micropalaeontological Society Field Guide*, No. 4, 42.
- Horne, D.J., 1995. A revised ostracod biostratigraphy for the Purbeck-Wealden of England. *Cretaceous Research* 16, 639–663.
- Horne, D.J., 2002. Ostracod biostratigraphy and palaeoecology of the Purbeck Limestone Group in southern England. In: *Special Papers in Palaeontology*, 68, 1–18.
- Horne, D.J., Martens, K., 1998. An assessment of the importance of resting eggs for the evolutionary success of Mesozoic non-marine cypridoidean Ostracoda (Crustacea). In: *Archiv für Hydrobiologie, Special Issues. Advances in Limnology*, 52, 549–561.
- Hughes, N.F., 1969. Lower Cretaceous miospores. In: Tschudy, R.H., Scott, A.C. (Eds.), *Aspects of Palynology*. Wiley Interscience, pp. 311–329.
- Hughes, N.F., 1994. *The Enigma of Angiosperm Origins*. Cambridge University Press, Cambridge, 303 pp.
- Hughes, N.F., Moody-Stuart, J.C., 1969. A method of stratigraphic correlation using early Cretaceous microspores. *Palaeontology* 12, 84–111.
- Hughes, N.F., Drewry, G.E., Laing, J.F., 1979. Barremian earliest angiosperm pollen. *Palaeontology* 22 (3), 513–535.
- Hughes, N.F., McDougal, A.B., 1990. New Wealden correlation for the Wessex Basin. *Review of Palaeobotany and Palynology* 65, 145–151.
- Jäger, H., 2004. Facies dependence of spore assemblages and new data on sedimentary influence on spore taphonomy. *Review of Palaeobotany and Palynology* 130, 121–140.
- Kemp, E.M., 1968. Probable angiosperm pollen from the British Barremian to Albian strata. *Palaeontology* 11, 421–434.
- Lupia, R., 2004. Megaspores and palynomorphs from the Lower Potomac Group of Maryland, U.S.A. *International Journal of Plant Sciences* 165 (4), 651–670.
- Martens, K., Rossetti, G., Horne, D.J., 2003. How ancient are ancient asexuals? *Proceedings of the Royal Society of London, Series B (Biological Sciences)* 270, 723–729.
- Mohabey, D.M., Samant, B., 2003. Floral remains from Late Cretaceous faecal mass of sauropods from Central India: implication to their diet and habitat. In: Kundal, P. (Ed.), *Recent Developments in Indian Micropalaeontology*. Gondwana Geological Magazine, Special, vol. 6, pp. 225–238.

- Norris, G., 1969. Miospores from the Purbeck Beds and marine Upper Jurassic of southern England. *Palaeontology* 12 (4), 574–620.
- Nye, E., 2004. Palynology of the Ockley dinosaur site. MSc in Micropalaeontology, Report (unpublished), University College London, 74 pp.
- Pierce, R.L., 1961. Lower Upper Cretaceous plant microfossils from Minnesota. *Minnesota Geological Survey Bulletin* 42, 1–86.
- Pocock, S.A.J., 1962. Microfloral analysis and age determination of strata at the Jurassic Cretaceous boundary in the western Canada Plains. *Palaeontographica Abteilung B* 111, 1–95.
- Rasnitsyn, A.P., Jarzembowski, E.A., Ross, A.J., 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research* 19, 329–391.
- Ross, A.J., Cook, E., 1995. The stratigraphy and palaeontology of the Upper Weald Clay (Barremian) at Smokejacks Brickworks, Ockley, Surrey, England. *Cretaceous Research* 16, 705–716.
- Sladen, C.P., Batten, D.J., 1984. Source-area environments of Late Jurassic and Early Cretaceous sediments in Southeast England. *Proceedings of the Geologists' Association* 95 (2), 149–163.
- Smith, R.J., Horne, D.J., 2004. First British record of *Paralimnocythere psammophila* (Flössner, 1965) (Crustacea, Ostracoda, Cytheroidea, Limnocytheridae) from the British Isles. *Journal of Micropalaeontology* 23, 133–134.
- Taggart, R.E., Cross, A.T., 1997. The relationship between land plant diversity and productivity and patterns of dinosaur herbivory. In: Wolberg, D.L., Stump, E., Rosenberg, G.D. (Eds.), *Dinofest International, Proceedings of a Symposium Sponsored by Arizona State University*. Academy of Natural Sciences, Philadelphia, pp. 403–416.
- Tang, F., Luo, Z.-X., Zhou, Z.-H., You, H.-L., Georgi, J.A., Tang, Z.-L., Wang, X.-Z., 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Research* 22, 115–129.
- Thurrell, R.G., Worssam, B.C., Edmonds, E.A., 1968. Geology of the country around Haslemere. *Memoirs of the Geological Survey of Great Britain* 301, 169.
- Topley, W., 1875. *The Geology of the Weald*. Memoirs of the Geological Survey, England and Wales, 503 pp.
- Vakhrameev, V.A., 1981. Pollen *Classopollis*: Indicator of Jurassic and Cretaceous climates. *The Palaeobotanist* 28–29, 301–307.
- Van Itterbeeck, J., Markevich, V.S., Horne, D.J., 2004. The age of the dinosaur-bearing Cretaceous sediments at Dashuigu, Inner Mongolia, P.R. China based on charophytes, ostracods and palynomorphs. *Cretaceous Research* 25, 391–409.
- Watson, J., Alvin, K.L., 1996. An English Wealden floral list, with comments on possible environmental indicators. *Cretaceous Research* 17, 5–26.
- Weaver, J.C., 1983. The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*. *Paleobiology* 9 (2), 173–182.
- Weishampel, D.B., 1984. Interactions between Mesozoic plants and vertebrates: fructifications and seed predation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 167 (2), 224–250.
- Westhead, R.K., Mather, A.E., 1996. An updated lithostratigraphy for the Purbeck Limestone Group in the Dorset type-area. *Proceedings of the Geologists' Association* 107, 17–128.
- Worssam, B.C., 1978. The stratigraphy of the Weald Clay. *Institute of Geological Sciences, Report*, 78/11, 23 pp.
- Worssam, B.C., Ivimey-Cook, H.C., 1971. The stratigraphy of the Geological Survey borehole at Warlingham, Surrey. *Bulletin of the Geological Survey of Great Britain* 36, 1–146.
- Wright, V.P., Taylor, K.G., Beck, V.H., 2000. The palaeohydrology of Lower Cretaceous seasonal wetlands, Isle of Wight, southern England. *Journal of Sedimentary Research* 70, 619–632.
- Yans, J., Pons, D., Dejax, J., 2004. Palynological study of the dinosaur-bearing Wealden facies sediments of Bernissart (Belgium). *Polen* 14, 177–178; Cordoba (Abstracts of the XIth IPC, International Palynological Congress, 4–9 July 2004 in Granada, Spain).
- Yans, J., Dejax, J., Pons, D., Dupuis, C., Taquet, P., 2005. Implications paléontologiques et géodynamiques de la datation palynologique des sédiments à faciès wealdien de Bernissart (bassin de Mons, Belgique). *Comptes Rendus Palevol* 4 (1–2), 135–150.

## Appendix 1

List of recorded palynomorphs and megaspores with full author reference

### Spores:

- Aequitriradites verrucosus* Cookson & Dettmann, 1961  
*Baculatisporites comaumensis* (Cookson, 1953) Potonié, 1956  
*Cicatricosisporites angicanalis* Döring, 1965  
*Cicatricosisporites australiensis* (Cookson, 1953) Potonié, 1956  
*Cicatricosisporites brevilaesuratus* Couper, 1958  
*Cicatricosisporites hallei* Delcourt & Sprumont, 1955  
*Cicatricosisporites hughesii* Dettmann, 1963  
*Cicatricosisporites mohrioides* Delcourt & Sprumont, 1955  
*Cicatricosisporites myrtilii* Burger, 1966  
*Concavissimisporites* sp.  
*Contignisporites dorsostriatum* (Bolkhovitina, 1956) Dettmann, 1963  
*Coptospora striata* Dettmann, 1963  
*Coronatispora valdensis* (Couper, 1958) Dettmann, 1963  
*Couperisporites complexus* (Couper, 1958) Pocock, 1962  
*Cyathidites australis* Couper, 1953  
*Cyathidites minor* Couper, 1953  
*Dictyophyllidites equixinus* (Couper, 1958) Dettmann, 1963  
*Distaltriangulisporites perplexus* (Singh, 1964) Singh, 1971  
*Echinatisporis varispinosus* (Pocock, 1962) Srivastava, 1977  
*Foveotrilites subtriangularis* Brenner, 1963  
*Gleicheniidites circinidites* (Cookson, 1953) Brenner, 1963  
*Impardecispora apiverrucata* (Couper, 1958) Venkatachala, Kar & Raza, 1968  
*Klukisporites foveolatus* Pocock, 19652  
*Kraeuselisporites hastilobatus* Playford, 1971  
*Leptolepidites verrucatus* Couper, 1953  
*Microreticulatisporites crassixinus* Brenner, 1963  
*Pilososporites trichopapillosus* (Thiergart, 1949) Delcourt & Sprumont, 1955  
*Pilososporites verus* Delcourt & Sprumont, 1955  
*Plicatella concentrica* (Kemp, 1970) Davies, 1985  
*Plicatella robusta* (Kemp, 1970) Davies, 1985  
*Plicatella tricornitata* (Weyland & Greifeld, 1953) Deak & Combaz, 1968  
*Retitriletes austroclavatidites* (Cookson, 1953) Döring et al. in Krutzsch, 1963  
*Tauocusporites reduncus* (Bolkhovitina, 1953) Stover, 1962  
*Tauocusporites segmentatus* Stover, 1962  
*Triporoletes reticulatus* (Pocock, 1962) Playford, 1971  
*Undulatisporites undulapolus* Brenner, 1963  
*Verrucosisporites obscurilaesuratus* Pocock, 1962

### Gymnosperm pollen:

- Abietinaepollenites microreticulatus* Groot & Penny, 1960  
*Alisporites bilateralis* Rouse, 1959  
*Callialasporites dampieri* (Balme, 1957) Sukh Dev, 1961  
*Cerebropollenites mesozoicus* (Couper, 1958) Nilsson, 1958  
*Classopollis torosus* (Reissinger, 1950) Couper, 1958  
*Ephedripites patapscoensis* Brenner, 1963  
*Eucommiidites troedssonii* Erdtman, 1948  
*Inaperturopollenites dubius* (Potonié & Venitz, 1934) Thomson & Pflug, 1953  
*Perinopollenites elatoides* Couper, 1958  
*Podocarpidites radiatus* Brenner, 1963  
*Taxodiaceapollenites hiatus* (Potonié, 1931) Kremp, 1949

### Angiosperm pollen:

- Retimonocolpites* sp.1  
*Retimonocolpites* sp.2  
*Retimonocolpites* sp.3  
*Retimonocolpites* sp.4

### Green algae:

- Foveoinaperturites forameniferus* Pierce, 1961  
*Leioletes calvatus* Singh, 1964  
*Scenedesmus bifidus* Batten & Lister, 1988b  
*Scenedesmus novilunaris* He Cheng-quan et al., 1992

*Schizosporis parvus* Cookson & Dettmann, 1959

*Tetraedron paraincus* Batten & Lister, 1988b

*Tetranguladinium conspicuum* Yu Jingxian, Guo Zhengying & Mao Shaozhi, 1983 ex Chen et al., 1988

Megaspores:

“*Clockhousea*” of Batten, 1998

aff. *Flabellisporites* sp. of Lupia, 2004

*Erlansonisporites* sp.

*Minerisporites* sp.

*Ricinospora* sp.

*Striatriletes sulcatus* (Dijkstra, 1951) Potonié, 1956