CHARCOAL-RICH PLANT DEBRIS ACCUMULATIONS IN THE LOWER CRETACEOUS OF THE ISLE OF WIGHT, ENGLAND

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ABSTRACT. The Wessex and Vectis Formations (Lower Cretaceous) of the Isle of Wight, England, contain abundant charcoal-rich plant debris accumulations. Two key samples are described (along with rare elements from other samples) in order to document the botanical affinity and diversity of this material. Charred coniferous wood and coalified wood occurs in both samples. At Hanover Point wood is the only charcoal whilst at Shepherds Chine charcoal of the fern *Weichselia* dominates over wood charcoal. The Shepherds Chine sample contains other plant debris (mostly uncharred) including cycad and bennettite cuticles, seeds and lycophyte megaspores, as well as arthropod cuticles and fish vertebrae. Both plant-debris associations are interpreted as representing low diversity fire-prone vegetation: Hanover Point a flood-plain conifer forest community and Shepherds Chine specialist coastal fern and conifer communities.

KEY WORDS: Cretaceous, charcoal, fire, conifers, wood, Weichselia, fern

INTRODUCTION

As part of a larger project investigating the conditions under which charcoal becomes entrained in sediment, we have studied charcoal-rich plant debris accumulations from the Lower Cretaceous (Wealden) Wessex and Vectis Formations (Hauterivian to Barremian) of the Isle of Wight, southern England. The Formations have been studied at Hanover Point and in the cliffs along the coastal outcrop between Cowleaze and Shepherds Chines. In this paper we concentrate on two key samples and use these to document the botanical affinity and diversity of the plant material. Rare material from other samples is also described in order to more fully document the botanical diversity in the sequence. The facies associations of plant debris accumulations throughout the sequence will be discussed elsewhere (Cripps et al. in prep.).

MATERIALS AND METHODS

The Hanover Point key sample, from the Wessex Formation, is from a foreshore exposure of a dark grey homogeneous mudstone facies which also contains large silicified logs 30–50 cm in diameter, known locally, and indicated on Ordnance Survey Maps, as the 'Pine Raft'. The logs represent large trees and the wood is of the araucaroid type (with biseriate alternate tracheid pitting), probably classifiable as *Dadoxylon* Endlicher (Alvin *et al.* 1981). This facies lies adjacent to a two metre thick channel-fill sandstone body which is ripple cross laminated on the upper exposed surface. This association of facies suggests that the logs and other plant material were deposited along the margins of a river channel and were preserved as the channel axis shifted laterally. There are no indicators of marine influence on the river channel.

The Shepherds Chine key sample from the Shepherds Chine Member (Stewart *et al.* 1991) of the Vectis Formation, consists of a fine-grained association of grey bioturbated mudstone, siltstone, ripple laminated and horizontally laminated fine sandstone beds. In areas with clear lamination plant debris is concentrated on bed-ding surfaces, especially in mudstone immediately above sand-stone, most is randomly orientated but some fragments show weak alignment. These beds occur 2.5 metres above the top of the Barnes High Sandstone, which is interpreted as having been deposited on a tidally influenced shoreface. The depositional environment of the sediments containing the charcoal is therefore interpreted as a shallow, low energy coastal lagoon (Cripps *et al.* in prep.).

Bulk sediment samples were collected, disaggregated whilst still damp using hydrogen peroxide of varying concentrations, and wet-sieve graded down to 63µm. Minimal agitation was used, always under water. Disaggregation in hydrofluoric acid (HF) was necessary for some well-cemented samples from the Vectis Formation. Specimens were sorted from the residues under a binocular microscope using a fine brush and cleaned in HF prior to mounting on stubs with carbon pads for study using a Hitachi 2400 or Philips 501 scanning electron microscope. Sorting and SEM study of the two key samples was undertaken initially by CF and subsequently samples were re-examined with SEM by MEC. 700 g of the Hanover Point sample and 2 kg of the Shepherds Chine sample were processed. Alvin (1974) and Harris (1981) studied sediment surfaces, not disaggregates, and this might yield different results. We compared phytoclasts visible on sediment surfaces prior to treatment and those found in the sieved residues. Disaggregation had little effect on the plant material and we saw nothing on surfaces that was not present in residues. We might have missed rare phytoclasts (if they broke up on disaggregation) by not studying sufficient sediment surface area, but these would be sufficiently rare to have minimal impact on interpretations. Plant material was identified as fusain (=charcoal) according to gross morphological features (black, silky/shiny lustre, brittle/friable, black smear) and anatomical criteria (three-dimensional preservation, homogenised cell walls) (see Scott 1989, Jones 1993).

BOTANICAL AFFINITIES OF PHYTOCLASTS

WOODS: GENERAL FEATURES

A few specimens of coalified woods were studied by SEM. They showed total compression of the cells in transverse section (TS) but radial (RLS) and tangential longitudinal sections (TLS) did reveal some anatomical detail. These very few specimens indicate that the coalified woods represent the same woods as the charred woods A or B below (resin ducts were not seen in coalified specimens but probably would not be for preservational reasons). Many more specimens need to be examined to confirm this interpretation. Approximately 80 charcoalified wood specimens were studied initially from each sample; 40 from Hanover Point and 30 from Shepherds Chine were subsequently re-examined. The text below combines these observations and uses Seward (1919), Jane (1956), Cope (1993) and Stewart & Rothwell (1993) for wood anatomical details.

All wood charcoal (Pl. 1) is pycnoxylic and consists mainly of tracheids and parenchymatous rays. Tracheids vary from rounded to angular in TS, with and without intercellular spaces (Pl. 1, figs 1-3, 15, 18-20). Axial parenchyma and axial and transverse resin ducts occur in some wood specimens (Pl. 1, figs 1, 4, 10, 13, 14, 17). The tracheids have characteristic coniferous circular bordered pits, spaced or contiguous, typically in uniseriate rows (rarely biseriate opposite) on the radial walls (Pl. 1, figs 8, 9, 13). Sparse pitting occurs rarely on tangential walls . Rays range in height from 1-27 cells and are mostly uniseriate, rarely biseriate (Pl. 1, figs 4, 5, 6, 10, 11). Multiseriate fusiform rays occur in the wood with resin ducts (Pl. 1, figs 4, 17) and rarely in other wood (Pl. 1, fig. 5). All this wood is determined as coniferous, excluding an affinity with cycads (manoxylic) or bennettites (multiseriate bordered pits). Ginkgo wood is very similar to that of conifers but the presence of frequent/usual biseriate opposite bordered pits on tracheids and the very low height (1-3 cells) of the rays distinguishes Ginkgo from our charred woods. Amongst the conifers the Araucariaceae are excluded as they have frequent/usual biseriate alternate tracheid pitting. We have seen biseriate alternate pitting in only a few tracheids of one or two specimens and it is always concentrated in a few pit pairs at the very ends of the tracheids.

We have not been able to record numbers of tracheids or rays per unit area in any plane of section, or to measure sizes of tracheids, pits etc. due to time constraints. It is recognised that these characteristics can be important for species (or higher taxon) discrimination but in this project we are only documenting general wood characteristics rather than formally identifying the taxa.

Growth rings are distinct but uneven, varying considerably in width and character from year to year and specimen to specimen. In some cases (Pl. 1, figs 2, 12, 19) they consist of narrow zones (2-4 cells) of smaller late wood tracheids alternating with much broader zones of early wood tracheids with an abrupt transition. At the other extreme gradation between early and late wood is gradual to imperceptible (Pl. 1, figs 1, 3) and the ring may be broad (Pl. 1, fig. 1). Rings vary in width from year to year as shown in Pl. 1, fig. 12. There the central ring is complete and measures about 0.5 mm diameter whilst Pl. 1, fig. 1 seems to represent an almost complete ring (late wood thick-walled at right side) at least 1.5 mm in diameter. (Shrinkage due to charring should be considered when interpreting ring widths in terms of climate). As the specimens are very small some growth cessations may be false rings but none have been seen to fuse or disappear within the areas of wood available. No particular growth ring type is correlated with one wood type. The overall impression is of very variable extent of, and interruption to, favourable growing conditions, both between and within years, with growth interruption apparent in all specimens examined. The material provides the potential for a thorough evaluation of growth ring parameters.

WOODS: ANATOMICAL DETAILS

On the basis of anatomical differences three wood types can be recognised. All share the common features already listed above. The first (termed type A) occurs only in the Shepherds Chine key sample. Type A wood possesses common axial parenchyma as scattered cells (Pl. 1, fig. 4) and axial ducts (Pl. 1, figs 1, 10, 11) which has been seen in TS, TLS and RLS. The axial and ray parenchyma cells usually have contents, some of which are solid or 'bubbly' infills interpreted as resin. Type A wood also has multiseriate fusiform rays (Pl. 1, fig. 4 TLS, fig. 1 TS at mid-right) some of which show resin ducts of classical morphology seen in TLS (Pl. 1, fig. 17). Resin ducts have been confirmed in at least 8 specimens (which were randomly distributed through 10 stubs) out of 40 charred wood fragments. In RLS type A wood has a large, single, round, pit per cross field (Pl. 1, fig. 7), each pit has a narrow border and a wide aperture, very rarely two pits per cross field are encountered. Horizontal ray cell walls are pitted (seen as uneven thickening in Pl. 1, fig. 7) but vertical (tangential) ray cell walls do not seem to be pitted.

Wood types B & C occur only in the Hanover Point key sample. Type B wood usually has single pits per

cross field as in type A although two pits per field are more common and three per field occur (Pl. 1, fig. 8). Type B wood is otherwise like type A wood. However, axial parenchyma has only been clearly seen in three specimens (Pl. 1, fig. 14) and obvious axial or transverse resin ducts have not been recorded although rare (2 different specimens) fusiform rays do occur (Pl. 1, fig. 5). A subtle difference is that type B wood pieces may display only relatively low rays (up to 5 cells high) in TLS (Pl. 1, fig. 14) or RLS (Pl. 1, fig. 11), but a wide range of ray height is also seen (Pl. 1, fig. 5). The distinction between wood types A and B is tenuous, relying largely on the lack of observed resin ducts in B. This could be due to difficulties in recording ducts in the smaller more fibrous wood pieces from Hanover Point. Furthermore, as resin ducts occur in response to injury (Jane 1956) they are often unevenly distributed and lacking in parts of the wood. Resin ducts may be 'typical' in some woods and sporadic (following injury) in others (Jane 1956). The use of resin ducts as a taxonomic character in these charred woods may therefore be inappropriate. However, some authors distinguish normal from traumatic resin ducts; the former are elongate and occur singly, the latter are cyst-like and occur in tangential series (Phillips 1948, Jane 1956). On these criteria, as far as we can distinguish in small pieces, the resin ducts in the type A woods are normal. If the woods we identify as types A and B had been found together in the same sample it is possible that we would not have distinguished the two types, but we maintain the distinction here as, if nothing else, it may indicate differential 'injury' levels in the two wood samples.

Type C wood (Pl. 1, figs 3, 6, 9) is known from two fragments. The wood lacks axial parenchyma and resin ducts and has distinctive cross field pitting. There are (1-) 2-4 (-8) small cupressoid pits per cross field (Pl. 1, fig. 9), each pit bordered and with a narrow elliptical aperture in oblique orientation. The horizontal and vertical ray cell walls are not pitted. Ray cells have contents (Pl. 1, fig. 9, top right).

WOODS: STRUCTURAL VARIATIONS

Two wood specimens from Shepherds Chine which otherwise conform to wood type A have a TS with only thick-walled tracheids with exceptionally well-rounded, small lumina and a distinctive 'shattering effect' in the rays (Pl. 1, fig. 18). However, this ray shattering was also seen in one or two specimens lacking the distinctive TS and some areas of type A late wood TS do show rounded thick-walled tracheids. We therefore include all woods from Shepherds Chine in wood type A. One wood specimen of type B was striking in having pronounced helical structure in tracheids (Pl. 1, figs 19–21) only in particular growth increments (Pl. 1, fig. 19 upper part and 20 detail of upper part). Unlike this wood specimen, helical thickenings occur throughout the wood in the Taxales. However, helical thickenings are also recorded amongst a variety of conifers (Cupressaceae, Pinaceae, Cephalotaxaceae, Podocarpaceae) and often occur only in parts of the growth ring e.g. in *Pseudotsuga*, Pinaceae (Jane 1956: 86, Seward 1919: 134, Stewart & Rothwell 1993: 418). According to Jane (1956: 87) spiral thickening and checking (spiral cracks) are easily confused on superficial examination but distinction should be possible as thickenings are deposited upon the tracheid wall whilst checking 'splits' the wall thus creating pull apart depressions (Jane 1956: fig. 39, p. 89). This distinction has not proven simple in the charred woods but parts of Pl. 1, figs 20 and 21 suggest that the helical structures are due to splits or cracks in the wall rather than superficial deposits. Furthermore the helical structures show striation, variable thickness, separations and anastomoses, and are not seen 'overlying' any of the tracheid pits but rather cause splitting of the pits. These features are more clearly seen in other specimens (e.g. Pl. 1, fig. 16) and are generally unlike the thin, regular, evenly spaced, simple, spiral thickenings such as those in Pseudotsuga or Taxus illustrated by Jane (1956: fig. 38).

Compression wood, the reaction wood in conifers, forms on the lower surface of horizontal branches (Jane 1956). Well rounded tracheid lumina, intercellular spaces and oblique checking diagnose compression wood (Jane 1956), these occur in the unusual specimen (Pl. 1, figs 19-21) and in other specimens (e.g. Pl. 1, figs 15, 18). Compression wood is an expected component of fragmentary conifer wood material. Checking may result from drying cracks in normal wood (Jane 1956) which may be preserved by charcoalification (Jones 1993) but checking also occurs normally in compression wood (Jane 1956: 197, fig. 109). Use of checking in charcoal to infer charring of partially dried litter is therefore unreliable. Distinction may be possible based on the angle of checking $-10-20^{\circ}$ degrees in normal wood, about 45° in compression wood - due to the change in pitch of the microfibrils in the middle layer of the secondary cell wall (Jane 1956: 197). On this basis our helical structures (Pl. 1, figs 16, 19-21) represent compression wood checking preserved by charcoalification and do not reflect drying of normal wood.

Intercellular spaces, typical of compression wood, (and which occur in some normal conifer woods – Jane 1956: 81–82) could be confused with early stages of breakdown of the previously homogenised cell wall, a phenomenon noted by Jones (1993) as indicative of high temperature charring. Hanover Point wood is typically fibrous in character, sometimes breakdown of the previously homogenised cell wall is apparent (Pl. 1, fig. 15 center) and specimens have many intercellular spaces varying in size and shape. However, the fibrous wood character may be due to collapse and brittle shattering (see below) rather than splitting along the original site of the middle lamella. The intercellular spaces and wall splitting may be related to compression wood behaviour on charring. Thus, these specimens need not imply high temperature charring. Experimental charring of compression wood is necessary to resolve these issues.

A more reliable criterion to infer charring of litter may be the presence of obviously collapsed woody tissue. We have encountered this in about half the wood specimens studied. Within one wood fragment the larger-lumened, thinner-walled tracheids of the early wood are often seen to have partially collapsed and folded, whilst the thicker-walled late wood cells retain original shape. The collapsed cells often also show subsequent brittle shattering (e.g. Pl. 1, fig. 12 top right) due to post-charring compaction, presumably within the sediment. This brittle shattering often makes anatomical details difficult to see in some parts or planes of sections of wood specimens. Within our material we have charred fragments showing no collapse even of vulnerable cells, charred fragments with collapse in some areas, charred fragments with total collapse and uncharred fragments with total collapse. Rarely in an otherwise charred fragment collapsed cells may not be charred (cell walls not homogenised) showing that partial charring occurred originally. This range of material implies that wood charcoal was sourced from both old dried litter and either very fresh litter or directly from living plants (for further discussion see Cripps et al. in prep.).

WOODS: IDENTIFICATION

Wood is known for five species of the abundant Wealden conifer family Cheirolepidiaceae and attributed to the form genera Protocupressinoxylon or Protopodocarpoxylon (Watson 1988). These are characterised by mixed (semiaraucaroid or protopinaceous) pitting on the tracheids, absence of axial parenchyma or resin ducts, parenchymatous rays (some with resinous deposits), absence of pitting on the horizontal and tangential walls of ray cells and podocarpoid to cupressoid cross field pitting in the ray cells (Alvin et al. 1981, Watson 1988, Zhou Zhiyan 1983). The form genera and species have been distinguished by details of the cross field pitting (number and arrangement of pits; size and orientation of aperture and breadth of border) however, the distinction is difficult (Alvin et al. 1981, Watson 1988, Cope 1993) and these features may differ in early versus late wood.

Cope (1993), Alvin *et al.* (1981), Francis (1983) and Zhou Zhiyan (1983) all recognised cupressoid pitting in cross fields (pits with an oblique, elliptical, narrow (slitlike) aperture contained within a border) in woods of *Cupressinoxylon, Protocupressinoxylon purbeckensis* Francis, *Pseudofrenelopsis intermedia* (Chow et Tsao) Watson 1988 and *Pseudofrenelopsis parceramosa* (Fontaine) Watson. Alvin *et al.* (1981) referred the latter to the form genus *Protopodocarpoxylon*. The latter three are known to be produced by members of the Cheirolepidiaceae. The number of pits per cross field is 2–7 in *P. purbeckensis*, 4–6 (2–8) in *P. intermedia* and (1) 4–10 (–17) in *P. parceramosa*.

Alvin et al. (1981) studied 26 pieces of charred (=fusainised) wood from the Wealden Wessex formation of Shiphards Chine to the west of Hanover Point. None of their specimens had resin ducts so they did not encounter our wood type A. Their type I (most abundant) wood was considered to be derived from Pseudofrenelopsis parceramosa on the basis of similarity with wood from in situ in a leafy shoot. This wood is very similar to our type C wood. We have not seen any specimens with the higher numbers of cross field pits (up to 16) which occurred in P. parceramosa charcoal. However 60% of P. parceramosa cross fields showed 2-4 pits (Alvin et al. 1981) consistent with our material. Type II wood of Alvin et al. (1981) possessed dacrydioid cross field pits which are circular and only narrowly bordered and in this respect is similar to our woods A & B. However, type II wood lacked axial parenchyma and resin ducts. Type III wood of Alvin et al (1981) was a single specimen distinguished from type I by having only 1-4 cross field pits and more rays per mm². Alvin et al. (1981) also examined six charred wood fragments from the 'Pine Raft' matrix at Hanover Point. Four they compared closely with the silicified araucaroid 'Pine Raft' logs and the other two were said to be similar to their type II wood. We have not found the araucaroid wood in our Hanover Point material but the cross field pits in our type A & B wood are very similar to those in the single figure of the other 'Pine Raft' wood shown by Alvin et al. (1981).

In summary, our type A wood, with prominent resin ducts, occurs only in the Shepherds Chine key sample where it is the only wood type recorded. The axial and transverse resin ducts tend to suggest affinity with Pinaceae and related conifers but, as noted above, the resin ducts may have been a sporadic wood feature. Furthermore, we have not recorded ray tracheids which are common in Pinaceae. Taxodiaceae and Cupressaceae are other possible affinities (Jane 1956, Seward 1919, Stewart & Rothwell 1993). Type B wood, (only from Hanover Point) assuming a genuine lack of resin ducts, is very similar to type II of Alvin et al. (1981) though the latter lacked axial parenchyma. Axial parenchyma is present in wood type B which may, therefore, have been produced by a member of the Podocarpaceae (Alvin et al. 1981). Our type C wood is identified as wood of the cheirolepidiaceous conifer Pseudofrenelopsis parceramosa. It occurs only in the Hanover Point key sample and is relatively rare.

FIBRE BUNDLES (Pl. 2, figs 1, 2)

Much material initially identified as woody in the Shepherds Chine sample was shown to be bundles of sclerenchyma fibres or mixed sclerenchyma and parenchyma when seen under SEM (Pl. 2, figs 1, 2). There are no taxonomically diagnostic features. However, Harris (1981: 52) and Alvin (1974: 588) noted 'sheets of fusain composed of bands of fibres' and 'larger usually striated pieces of fusain' which they suggested might be from the rachises or stems of the fern *Weichselia* which has 'erect stems up to 15cm thick with a broad sclerotic outer layer' (Watson & Alvin 1996). Futhermore, anatomical details shown in the more parenchymatous of these bundles are fully consistent with features illustrated by Alvin (1971, 1974). We interpret this material as *Weichselia* rachis or stem fragments.

FOLIAGE (Pl. 2, figs 3-7, 24)

The most common foliage encountered is charred fern pinnules (Pl. 2, figs 3, 4). These show identical anatomical features to pinnules of the fern Weichselia reticulata (Stokes et Webb) Fontaine as described by Alvin (1974) and Harris (1981). Diagnostic features include shape and size of pinnules, thick pinnules, frequently inconspicuous main veins (Pl. 2, figs 3-5), lateral veins forming a coarse meshwork with rhomboidal, polygonal or elongate rectangular inter-vein areas (Pl. 2, figs 3, 5), exposure by loss of upper cuticle of regular palisade cells and vein sheaths (Pl. 2, figs 5, 6; cf. to Alvin 1974: pl. 87, fig. 6) and a lower cuticle (Pl. 2, fig. 7) with closely spaced sunken stomata with two specialised subsidiary cells forming an epistomatal pit (Pl. 2, fig. 7; cf to Alvin 1974, Pl. 89, fig. 1). Alvin (1974) noted digitate subepidermal cells in Weichselia and we have seen this feature (Pl. 2, fig. 5) as well as digitate epidermal cells of the intact upper and lower cuticles (Pl. 2, figs 6, 7) (not clearly recorded by Alvin (1971, 1974)).

Along with *Weichselia*, Harris (1981) described charred *Gleichenites* and *Phlebopteris* fern pinnules from the Wealden of Surrey whilst Alvin (1974) noted charred *Phlebopteris* and *Cladophlebis* in material from Shepherds Chine. *Gleichenites* and *Cladophlebis* are distinguished by having open dichotomous or forking lateral venation. *Phlebopteris* has a distinct main vein and major lateral veins which fork about half way between the margins and the midrib and subsequently anastomose to form small irregular meshes. Furthermore the pinnules are long, charred fragments lack apex and base and are more or less parallel-sided. We have only found *Weichselia* in the Shepherds Chine sample documented here.

Four specimens of minute, uncharred, narrow cylindrical leafy shoots with spirally arranged scale leaves, one per node, were found in the Hanover Point key sample. The illustrated specimen (Pl. 2, fig. 24) is the bestpreserved example which was found in a Shepherds Chine sample, from a different facies, stratigraphically higher than the key sample studied here. This type of foliage occurs only in the Cheirolepidiaceae and Brachyphyllum (Watson 1988) amongst the Wealden floral elements listed by Watson & Alvin (1996). Amongst the foliage illustrations in Watson (1988: figs 9.1-9.3) our specimens show similarity with the Brachyphyllum/Hirmeriella type and the Pseudofrenelopsis type. Leaves of the former are longer, with longer free tips and do not ensheath the stem whilst leaves of the latter are short, have a very small free tip and ensheath the stem. Our specimens are fragments and we have not dissected them but the leaves do appear to ensheath the stem. They strongly resemble the small shoots of the Wealden Pseudofrenelopsis parceramosa having 'open' types of leaf and short sutures, such as those figured by Watson (1977: Pl. 85, fig. 5 and text-fig. 2A) and which are reconstructed as the ultimate branchlet tips by Alvin (1983). We also note that non-sheathing Brachyphyllum-like leaves are recorded on lateral buds of extension shoots in P. parceramosa (Alvin 1983) and that 'open' type leaves which do not fully ensheath the stem, hence resembling Brachyphyllum, are also recorded in P. parceramosa by Watson (1977: 717). Taking all these features into account we conclude that our leafy shoots can be determined as shoot tips of Pseudofrenelopsis parceramosa (Fontaine) Watson. Unfortunately, loss of cuticle detail has prevented us confirming the identification by observing features such as rows of stomata, papillate subsidiary cells and the hairy leaf margin (Watson 1977, 1988). It is notable that we have not recovered any internodal fragments, long 'closed' leaves or any other leafy shoots.

INDUSIA (Pl. 2, figs 8-12)

Small peltate structures (Pl. 2, figs 8–10) from the Shepherds Chine sample show similarity to the sporangiophores of Equisetales or pollen/ovule-bearing organs of some gymnosperms. They lack evidence of former sporangial, pollen sac or ovule attachment which should be obvious on well-preserved material.

The peltate structures are, therefore, interpreted as fern indusia. They have a short stalk (about 650 μ m long) and a pentagonal to hexagonal head (about 0.9 to 1.5 mm wide) with slightly recurved margins (Pl. 2, figs 8–10). The texture is woody and the cells seen at the base of the stalk include thick-walled sclerenchyma (Pl. 2, figs 11, 12). The sclerenchyma cells show homogenised walls (Pl. 2, figs 11, 12), the underside of the indusium shows cell inflation (Pl. 2, fig. 8) and the anatomy is preserved in three dimensions (e.g. Pl. 2, fig. 11). All these features indicate that the indusia are charred al-

though some collapse clearly occurred before charring in some specimens (Pl. 2, figs 9, 12 stalks). This collapse need not indicate that indusia were charred in litter after shedding as our experimentally produced fern charcoal always shows some tissue collapse even when placed in the kiln immediately after removal from the plant. These indusia are identical in every respect with the indusia of Weichselia illustrated and reconstructed in Alvin (1968) and Watson & Alvin (1996) and their faceted head shape (Pl. 2, figs 8, 10) is consistent with close-packing in the soral cluster of Weichselia. The distribution of cells in the stalk is consistent with detachment at or near the base of the thick-walled tissues. Alvin (1971: 22 footnote) recorded a fragment with two soral clusters recovered by bulk macerating a Weichselia-containing matrix from the Isle of Wight but Watson (1969) noted that none of the English Weichselia material was fertile and Watson and Alvin (1996) stated that Weichselia soral clusters have never been reported amongst charred material. These points need not pose a problem with our determination. Fire may have induced detachment of indusia enabling release of spores or, alternatively, indusia may have been charred in the litter after shedding. In both these cases entire charred soral clusters would not be preserved. Charred axial material of fertile fronds would not be distinctive. The absence of sporangia can be explained if they were protected in the enclosed soral cluster whilst fire charred the indusium, inducing its detachment, enabling post-fire spore release. This would represent a fire-adapted reproductive biology similar to that suggested by Watson and Alvin (1996). Alternatively, charred sporangia may have fragmented before or during deposition. We studied residues to 63 µm and should have recorded isolated sporangia had they been present.

Weichselia is assigned to the modern fern family Matoniaceae or to an extinct sister family (Collinson 1996). Modern Matoniaceae have peltate indusia such as those described here. Harris (1981) and Alvin (1974) recorded *Phlebopteris* (Matoniaceae) as a component of charred Wealden ferns. However, it is an extinct genus which lacked indusia. Indusia have been discovered subsequently in several *Phlebopteris* species leading to their transfer to the modern genus *Matonia* (Harris 1980) but indusia have not been discovered on the Wealden species *P. dunkeri* Schenk.

Amongst ferns not hitherto represented by charcoal, *Matonidium* is another Matoniaceae listed in the Wealden flora list (Watson & Alvin 1996) which might have yielded these indusia. Watson (1969) stated that the Wealden material agreed in all available characters with the Yorkshire Jurassic material studied by Harris (1961). Harris (1961: 114, 116) described indusia on uncharred *Matonidium* as 0.25 mm wide, the peltate head mostly a single cell thick with a delicate membranous margin and a rather slender stalk. These characteristics differ from our indusia which are more than four times larger (and this without allowance for shrinking on charring) and tough, woody in texture. *Aspidistes sewardii* is known only from a single pinnule (Watson 1969). Lovis suggested that it should be included in Matoniaceae (Collinson 1996: 367). It has a thick indusium, probably attached by a central stalk, but the head is circular (Watson 1969).

Gleichenites is recorded amongst Wealden fern charcoal (Harris 1981) and Gleichenia occurs in other charcoal floras (Collinson 1996: 360) however modern Gleicheniaceae are exindusiate and no indusia are recorded on any fertile fossil specimens (Collinson 1996). Of the other ferns listed in the Wealden floral list (Watson & Alvin 1996) the Dicksoniaceae and Schizaeaceae have specialised lamina forming enrolled, enfolding, pod-like or box-like protection to the sorus, nothing like a peltate structure. Cladophlebis is a form genus for sterile fossil foliage thought to be produced by Osmundaceae. In modern and fossil Osmundales sporangia are not grouped into sori hence there are no indusia. Sorus details of the extinct Tempskyaceae are not known (Collinson 1996). Modern Dipteridaceae are exindusiate and the extinct Hausmannia is very similar to modern Dipteris (Collinson 1996). It is represented in the Wealden only by a few imperfect sterile leaves (Watson 1969).

Thus almost all alternative candidates for parentage of these fossil indusia can be eliminated on the basis of a) the ferns lack indusia, b) the ferns have distinctive and different soral protection or c) the ferns have peltate stalked indusia but these differ from our specimens. Of course, we cannot rule out the possibility of these indusia having been produced by a Wealden fern for which fertile material is unknown or by an as yet unrecorded Wealden fern. However, given the fact that all characters of our fossil indusia are found in those of *Weichselia*, and that they are closely associated with charred *Weichselia* foliage, we consider determination to *Weichselia* to be strongly-supported.

MEGASPORES (Pl. 2, figs 14-17)

Four types of megaspore (all rare) have been recorded all except one specimen from Shepherds Chine. All were recorded by Batten (1974) in his study of Wealden flora. The first (Pl. 2, fig. 14) was formerly named *Arcellites pyriformis* but has subsequently been revised to *Bohemisporites pyriformis* (Dijkstra) Knobloch. It is characterised by a relatively short elongate apical neck consisting of three major folds and a spore body ornamented by short, broad, blunt appendages. Specimens are very similar to that figured by Batten *et al.* (1996: fig. 10a) though the ornament is apparently worn. The second megaspore type (Pl. 2, fig. 16) is characterised by a sur-

face reticulum with elevated narrow and wavy muri and by elevated trilete laesurae. It can be determined as Erlansonisporites and is very similar to specimens figured by Batten (1974: Pl. 13, fig. 6). The third type (Pl. 2, fig. 15) is characterised by a spore body covered in fine, long hairy ornament which obscures the main spore body. This can be determined as *Echitriletes* and is very similar to specimens figured by Batten (1974: Pl. 13, fig. 4). A single specimen of a fourth megaspore type (Pl. 2, fig. 17) was found in another sample from a minor channel in the Cowleaze Chine Member. It has a reticulate body with a wide equatorial flange, the outer corona of which is ragged and uneven, broken down into discrete, variable appendages. The inner zona is undulating, has rays of thickening and an uneven outer margin. The triradiate flange is subtended by appendages. This is determined as Dijkstraisporites (probably D. helios Dijkstra) following the revision by Batten & Koppelhus (1993). All of these megaspores are attributed to lycophytes and are likely to have been produced by herbaceous plants that lived near to, or perhaps in, water (Batten et al. 1996, Batten 1974).

CUTICLES (Pl. 2, figs 18-20)

Dispersed uncharred cuticles can be compared with those figured by Oldham (1976) from Wealden plant debris beds. Using his work, personal observations by SEM of Yorkshire Jurassic material (Stanhope & Collinson pers. obs.) and references cited by Watson and Alvin (1996) we consider that one type of cuticle, with straight epidermal walls and simple stomata (Pl. 2, fig. 20), may have affinities with cycads though it is also very similar to 41 GYMN GyD (Gymnospermae Incertae Sedis) of Oldham (1976). Another cuticle, with undulating epidermal walls and sunken stomata (Pl. 2, fig. 18), has affinities with bennettites. Both these cuticle types occurred in the Shepherds Chine key sample (and rarely in other levels of the Vectis Formation) where they were very rare. A third cuticle (Pl. 2, fig. 19) (single specimen) from a sample from the Cowleaze Chine Member resembles cuticles assigned to the conifers Cheirolepidiaceae and Brachyphyllum figured by Oldham (1976) and Watson (1988). Indeterminable, translucent, featureless (in LM and SEM) cuticle sheets occurred in the Hanover Point Sample.

SEEDS (Pl. 2, fig. 13)

A number of uncharred, small (1 mm or less) thin, ovoid translucent envelopes (Pl. 2, fig. 13), with impressions of cellular structure and with basal and/or apical darkenings, constrictions or scars, are interpreted as seed cuticles. They are poorly preserved and hence we refer to them as *Spermatites*-like (see Batten & Zavattieri 1996). It is not known which plant group or how many plant types are represented.

OTHER MATERIAL (Pl. 2, figs 21-23, 25-28)

Two examples of uncharred narrow cylindrical specimens (Pl. 2, fig. 27) up to 5 mm long and 1 mm diameter, with uniseriate rows of stomata (single stoma detail Pl. 2, fig. 28) have not been determined. They may be from a very small photosynthetic stem or leaf-stalk. Woody coprolites (Pl. 2, fig. 21) are discussed below under Hanover Point.

One charred fragment (Pl. 2, figs 22, 25), from the Shepherds Chine key sample, is flattened, covered with collapsed short trichomes, and carries several round scars each revealing dominantly round, thick-walled cells (detail in Pl. 2, fig. 25). Another two samples, from stratigraphically higher levels at Shepherds Chine, yielded a comparable fragment as well as two short cylindrical structures (?spines/leaves/branches) tapering to a point (Pl. 2, fig. 23), the anatomy of which (Pl. 2, fig. 26) resembles that of the scars on the flattened fragments. One of these appendages shows a tiny central strand of probable xylem elements (Pl. 2, fig. 26 center). We cannot identify the parent plant group. Together these specimens may represent the stem (s) of a xeromorphic herb (s), though there are no obvious stomata on the flattened pieces or the cylindrical structures.

DIVERSITY AND VEGETATION

HANOVER POINT PLANT DEBRIS ASSOCIATION

The Hanover Point key sample residue was dominated by woody phytoclasts, both coalified and charred, with a ratio (estimated by eye) of about 3:1. The phytoclasts showed no preferential alignment in the sediment. Pyrite (especially framboids) was commonly found in association with charred and uncharred material, particularly in the parenchyma of both. Few charred fragments were larger than 1.0 mm in smallest dimension, and these varied in size, shape and degree of rounding. Small fragments were typically thin, flat slivers with fibrous appearance due to cell shattering. Charcoal consisted only of wood. This wood is not the same as that of the associated silicified logs. One rare charred wood type was produced by Pseudofrenelopsis parceramosa (Cheirolepidiaceae), the more abundant charred wood was produced by another conifer (possibly of the Podocarpaceae).

Four fragmentary specimens of uncharred leafy shoots, bearing adpressed scale-like leaves, were also found. These are interpreted as the ultimate tips of leafy branches of *Pseudofrenelopsis parceramosa*. A few indeterminable featureless uncharred cuticles and a single *Erlansonisporites* megaspore were found.

Common trace fossils occurred in the form of uncharred, woody, hexagonally faceted coprolites (Pl. 2, fig. 21). These are identical to those of wood-digesting dry wood termites (Collinson 1990, in press). Animal fossils are represented by a beetle elytron and a few fragmentary fish vertebrae.

The Hanover Point association thus represents a low diversity, woody, conifer vegetation, with at least some trees (*Pseudofrenelopsis*). The vegetation was fire prone but also yielded uncharred litter in the form of wood, a few ultimate tips of leafy branches and termite coprolites.

SHEPHERDS CHINE PLANT DEBRIS ASSOCIATION

The Shepherds Chine key sample yielded a diverse range of material with 'woody' phytoclasts and charred fern foliage co-dominant. Charcoal included wood, fibre bundles, fern foliage and indusia (the latter three attributed to Weichselia). Woody phytoclasts were both coalified and charred with a ratio (estimated by eye) ranging from about 5:1 (mudstones) to 3:1 (sandstones and mudstone/sandstone laminations). Charred wood ranged from rounded to jagged, from thin slivers to cuboid pieces and from several millimetres to less than 0.5 mm in minimum dimension. All is attributed to one species of conifer. About half of the woody phytoclasts were in fact not secondary wood but have been termed fibre-bundles (see botanical affinity). Charred Weichselia pinnules ranged from complete to fragmentary and with or without cuticles. Cuticles may have been lost through brittle fracture after charring or by virtue of the passage of the fracture plane within the leaf when sediment surfaces are examined (see also Alvin 1974).

We have only recorded the one fern, *Weichselia*, in this Shepherds Chine sample. Ferns of the genera *Gleichenites* and *Phlebopteris* were also found in Wealden charcoal-rich debris associations from Surrey, although *Weichselia* represented about 80% of determinable fern fragments (Harris 1981). Alvin (1974) studied charred material from a siltstone in the Shepherds Chine Member from Shepherds Chine. This too was dominated by *Weichselia* with only 'occasional' other plants, the ferns *Phlebopteris* and *Cladophlebis* and one fragment probably representing *Ruffordia*.

Other uncharred material in the Shepherds Chine key sample included cuticles of both bennettite and cycadophyte affinity (several specimens), *Spermatites*-type seeds (four specimens) and megaspores belonging to the genera *Bohemisporites* (6 specimens), *Erlansonisporites* and *Echitriletes* (one specimen each). Three axial fragments (one type xeromorphic and charred (Pl. 2, figs 22, 25), the other not (Pl. 2, figs 27, 28)) were also recorded. Animal fossils were not charred and were mostly fragmentary. They included beetle elytra, other arthropod cuticle fragments and fish vertebrae.

This Shepherds Chine association thus contains coastal fire prone plants of two kinds. One represents monotypic woody conifers and the second Weichselia-dominated ferns, monotypic in this sample. Collinson (1996: 374–375) discussed the concept of 'fern savannas and/or prairies' which has been applied to Mesozoic fern-dominated vegetation and (1996: 376) summarised arguments that Weichselia was tolerant of arid conditions in a fire-prone coastal floodplain (see also Watson & Alvin 1996). Further facies analyses are required to judge whether the fire-prone Weichselia and conifers coexisted or grew on separate sites as separate communities. Other vegetation within the catchment area of the Shepherds Chine sample included cycads, bennettites and lycophytes which were apparently not part of fire prone vegetation.

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PLATES

Plate 1

Charred woods, for detailed explanation see text . In LS the axial system is orientated from top to bottom of illustration except in 4, 6, 11 and 21 where it runs across the illustration. Figs 1, 4, 7, 10, 13, 16, 17, 18 wood type A from Shepherds Chine key sample, all others from Hanover Point key sample; 3, 6, 9 wood type C, remaining numbers wood type B. Scale bar on fig. 1 represents 300 μ m in figs 1; 220 μ m in figs 3, 10, 12; 120 μ m in figs 2, 4, 5, 6, 11; 65 μ m in figs 8, 9, 13, 14, 17, 19; 35 μ m in figs 7, 15, 18 and 15 μ m in figs 16, 20, 21

- 1. TS with gradual transition to late wood at right, several axial resin ducts, horizontal duct at right
- 2. TS showing abrupt growth interuption with only two cells of late wood
- 3. TS showing gradual change in growth conditions
- 4. TLS showing axial parenchyma and rays. Rays are uniseriate and rarely biseriate, with one fusiform ray (top left). Rays have varying heights
- 5. TLS showing uniseriate and rarely biseriate rays with one fusiform ray (top left). Rays have varying heights
- 6. TLS showing rays, mostly uniseriate, with varying heights, section unclear due to shattering
- 7. RLS showing cross fields with single round, narrowly bordered pits
- 8. RLS showing cross fields, many with single pits like those in 7 but several fields have two pits (e.g. towards top right and in lowest ray row) whilst one has three pits (center of lowest ray row). Uniseriate circular bordered pits are evident on radial tracheid walls
- 9. RLS showing cross fields with (1-) 2-4 (-8) small cupressoid pits per field. Uniseriate circular bordered pits on radial tracheid wall at left
- 10. RLS showing rays of varying height and elongate axial resin duct (towards right)
- 11. RLS showing relatively low rays. Compression wood checking occurs towards top of figure
- 12. TS showing three growth increments, the central one complete with abrupt transitions and small amounts of late wood. Inner increment (top right) shows collapse and shattering of early wood cells, outer increment (bottom left) also shattered and torn away as a result at the ring boundary
- 13. RLS showing axial duct and uniseriate circular bordered pits on tracheid radial walls
- 14. TLS showing low heights of rays and axial parenchyma with contents
- 15. TS showing intercellular spaces (variable) and breakdown of previously homogenised cell walls. Possibly compression wood
- 16. RLS Checking in wood interpreted as compression wood
- 17. TLS fusiform ray with horizontal resin duct in section
- 18. TS Slightly unusual wood type A with very rounded lumina and shattered ray. Possibly compression wood
- 19. TS detail from fig. 2 showing typical cells in lower growth increment, abrupt growth ring transition with 2 cells of late wood, and atypical cells with helical structures (causing wavy inner cell outline) in the upper growth increment
- 20. TS detail of upper growth increment in 19 showing rounded cell lumina, thick walls, intercellular spaces and helical structures. Interpreted as compression wood
- 21. TLS detail from 11 showing helical structures seen in TS in 20



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Plate 2

For discussion, detailed explanation and justification of determinations see text. All figures from Shepherds Chine key sample except figs 17, 18, 19 from the Cowleaze Chine Member; figs 23, 24, 26 from a stratigraphically higher sample of the Shepherds Chine Member at Shepherds Chine; figs 16, 21 from the Hanover Point key sample. Scale bar on figure 23 represents: $-600 \mu m$ in figs 3, 4, 8, 22, 24; 400 μm in fig. 23; 300 μm in figs 14, 15; 250 μm in figs 1, 9, 10, 13, 16, 17, 21; 180 μm in fig 5; 160 μm in figs 25, 26; 130 μm in figs 6, 7, 19, 20, 27; 80 μm in figs 2, 18; 35 μm in fig. 28 and 15 μm in figs 11, 12

- 1, 2. Charred fibre bundle; lateral view (1) and oblique TS showing sclerenchyma fibres (2)
- 3-7. Charred Weichselia pinnules; 3, 5, 6 upper surface, 4, 7 lower surface
- 8–12. Charred *Weichselia* indusia; 8 viewed from attachment point, 9 lateral view, 10 view onto surface of peltate head. 11, 12 cell detail from the bases of stalks of two different specimens
- 13. Uncharred seed cuticle
- 14-17. Uncharred lycophyte megaspores
 - 14. Bohemisporites
 - 15. Echitriletes
 - 16. Erlansonisporites
 - 17. Dijkstraisporites
- 18-20. Uncharred cuticles, inner surfaces; 18 bennettite, 19 conifer, 20 cycad
- 21. Uncharred termite woody coprolite
- 22, 25. Unidentified charred flattened fragment with scars
- 23, 26. Unidentified charred cylindrical appendage (23) with tiny central xylem strand in TS (26)
- 24. Uncharred *Pseudofrenelopsis*, tip of leafy shoot
- 27, 28. Unidentified, uncharred cylindrical specimen (27) and detail of stoma (28)

