FLORA OF THE WEALDEN PLANT DEBRIS BEDS OF ENGLAND

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ABSTRACT. Descriptions are presented of forty-one cuticle species, all of probable gymnosperm origin, from the English Wealden. The distribution of these species and other plant remains within seventy-one plant debris beds from the Dorset, Isle of Wight, and Sussex Wealden is analysed. Significant groupings and associations, which to some extent reflect the differing ages of the material examined and perhaps also association in nature, are detailed together with stratigraphic conclusions. Palynological data from thirty of the samples show that miospore content is not directly related to the diversity and preservation state of the cuticle assemblage. The character of the plant debris beds suggests a probable origin in a delta top and/or shore-face and delta-front environment. The Wealden flora may be compared with certain aspects of the vegetation of southern Florida.

THE Wealden flora has previously been described by Seward (1894, 1895, 1913) and this work has been revised, in part, by Watson (1969) and Alvin (e.g. 1974 and earlier papers). The fossils described by Seward are of uncertain location but it appears that they were mostly collected from five beds within the Fairlight Clay formation that outcrops along the cliff section from Hastings to Pett Level in Sussex. The so-called Wealden flora is therefore little more than the megafossil remains found in the lowest formation of the outcrop as developed in Sussex. The other six more extensive formations that make up the Wealden deposits in the south-east of England and the entire successions developed in Dorset and the Isle of Wight are relatively undescribed botanically.

More extensive collection of megafossils over the wider area cannot remedy the situation as beds containing such remains are very few, as for example in the Fairlight Clay. Deposits producing identifiable miospores are not so restricted. Couper's (1958) paper on such fossils covers, if somewhat briefly, the entire Wealden groups, and Batten's (1973*a*, *b*, 1975) researches into palynological facies utilize material from much of the south-eastern succession. This work, while giving a general picture of the flora, is limited in its botanical application because of the difficulty in assigning dispersed miospores to megafossil genera.

There occur through the Wealden deposits plant beds that offer much of botanical interest although not usually containing any large plant remains. These beds have a high content of fragmented leaves and shoots, rarely greater than 10 mm in length. Such beds relate to those described as lignite beds by White (1921, 1928) and Arkell (1947) but this term does not apply to all the beds encountered as true lignite is sometimes rare or absent. The term 'plant debris bed' is considered to have a more useful application and is adopted in this paper.

The leaf and shoot fragments found within these beds are most satisfactorily prepared for examination by bulk maceration techniques. As a result of this it is the structure of the cuticle rather than gross morphological form that is apparent and the material is better regarded as dispersed plant cuticle than leaves and shoots as such.

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THE GEOLOGY

South-eastern England

The Wealden deposits may be divided into six or seven formations depending upon whether the Fairlight Clay and Ashdown Sand are treated as two formations or joined into one. Gallois (1965) follows the latter course but in this paper they will be treated as two formations following White (1928) as much attention is paid to the Hastings area where they are distinct.

The sediments of the Wealden group have been described by Allen (1959, 1967*a*, *b*), Taylor (1963), and White (1928).

The Wessex basin

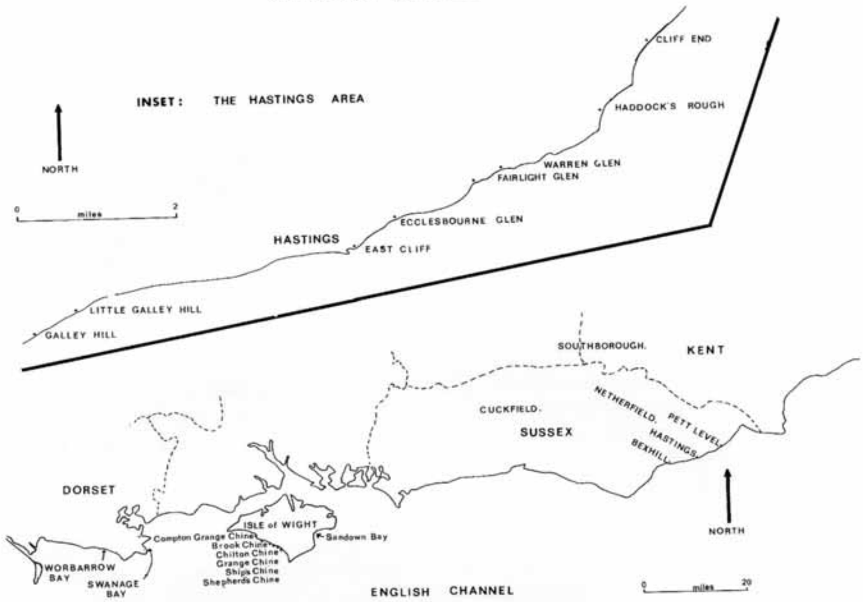
The two main areas of outcrop are in Dorset and the Isle of Wight. In both the sediments may be divided into two formations on lithological grounds; the Wealden Marls below and the Wealden Shales above. These sediments have received less attention than those of the south-eastern basin and the best descriptions remain those in the district memoirs of White (1921) and Arkell (1947).

In the Isle of Wight the beds outcrop in the south-western and south-eastern parts of the island where they are brought to the surface along the axes of two anticlinal folds. They occupy an area of less than 8 sq km and outcrop well only along the coast. They run for some 8 km between Compton Bay and Atherfield Point and for 1 km at Sandown Bay. Only the uppermost part of the Marls is exposed reaching a maximum development of 168 m (Arkell 1947). The Shales are better developed than in Dorset reaching a maximum of 60 m (Arkell 1947). The total thickness of Wealden sediment on the island, as revealed by the Arreton no. 1 Borehole, is 592 m (Falcon and Kent 1960).

The Marls consist of purple, red, green, and variegated clays with bands of sandstone. The absence of any band that can be traced over a considerable distance is particularly unfortunate as there are several faults that occur in the south-western section. Plant beds of the debris type are of regular occurrence especially on the south-western side of the island. Remains of vertebrates and molluscs occur. The Shales consist of stratified layers of dark clays with subordinate layers of clay-ironstone, sandstone, and shelly limestone. Plant remains, chiefly carbonized fragments of the fern *Weichselia reticulata*, occur rarely. Ostracods and molluscs dominate the fauna.

In Dorset the Wealden beds rest conformably upon the underlying Purbeckian strata. They exceed some 702 m thickness at Swanage but thin out westwards to 427 m at Worbarrow Bay and much less at Weymouth (Arkell 1947). Outcrops occur along the coast at Swanage Bay, Worbarrow Bay, Mupe Bay, Lulworth, and Durdle Door. The first two outcrops are the most useful as the sequence becomes increasingly confused westwards.

Lithologically and palaeontologically the Marls are similar to those of the Isle of Wight. Plant debris beds are slightly commoner but the fauna is less rich. As in the Isle of Wight there is rapid lateral variation of strata and correlation is difficult. Several bands of coarse quartz grit occur and according to Arkell (1947) one of these can be traced from Swanage to Durdle Door. The overlying Shales are poorly



TEXT-FIG. 1. Map of part of southern England showing the localities discussed in the text.

developed, being only 106 m thick at Swanage and absent at Worbarrow Bay. They resemble the Shales of the Isle of Wight but plant remains are rarer. Localities mentioned in the text are shown in text-fig. 1.

THE NATURE OF THE PLANT DEBRIS BEDS

Little has been written regarding the fragment composition of plant beds as opposed to their constituent floras, with the notable exception of coal strata. Harris (1953, 1963) refers to beds of dispersed plant fragments from the Jurassic of Yorkshire. He considers them to be mostly redeposited plant-bearing sediments of local origin, their constituent plants being of a rotted state prior to deposition and easily broken into small fragments as they were eroded out. His descriptions of the contents of these beds show them to be similar to those of the Wealden.

The distribution of the plant debris beds

They are best developed in the Fairlight Clay and Ashdown Sand formations of Sussex, especially along the cliff section from Hastings to Pett Level and at Galley Hill, Bexhill. They are, with the exception of beds of equisetalean remains, rare in the other formations of the Sussex Wealden. Some are found in the Tunbridge

Wells Sand but in the Wadhurst, Grinstead, and Weald Clay they appear to be absent. They are well distributed through the Wealden Marls of the Wessex basin but are not developed to any extent in the Wealden Shales.

Lithology

Beds containing small fragments of plant material can be found in most grades of sediment but where this is coarse the contained plant fragments are too poorly preserved to be of interest.

Medium to fine siltstones and claystones are the lithologies containing the better-preserved material. They are a medium to light-medium grey colour and often poorly consolidated. The best material comes from sediments soft enough to be cut with a knife.

Contents of the beds

Apart from the inorganic matrix, plant material is the sole component of the beds, animal remains not being found. The plant material consists of wood, both black and brown; cuticles of leaves, stems, and other plant organs; seeds; fruits; megaspores; miospores and charalean gyrogonites. The proportion of these varies from bed to bed. Miospores are usually the most important constituent in terms of number but rarely form much of the bulk of the bed. Wood also rarely forms the majority of the bulk and when it does plant cuticle material is scarce and the deposits are better termed lignite beds. Seeds and fruits are of little importance as are gyrogonites. Megaspores bear an inverse relationship to the richness of the cuticle remains but are normally present if only in small numbers.

It is the presence of large amounts of cuticular material that characterizes these beds and sets them apart from the lignite beds on the one hand and the megafossil beds on the other. This distinction is not absolute and a continuum of variation can be found. The cuticular material varies in size both within and between beds but is generally between 2 and 5 mm and rarely exceeds 10 mm. The material consists chiefly of leaves and pinnae but material relating to stems and reproductive structures also occurs. The leaf remains are usually fragmentary but occasionally complete leaves and sometimes branches can be seen.

Structure of the debris beds

Most of the beds comprise a complex of numerous individual beds, the whole structure ranging from a few centimetres to several metres in thickness. Isolated individual beds are rare. These complexes are separated by tens or even hundreds of metres of barren sediment.

The distinction of different sorts of debris beds

It was not considered wise to divide the beds up into different sorts as they varied along several independent parameters. These include the development of laminae, the proportion of plant material to inorganic matrix, the degree of cohesion of the matrix, the state of preservation of the contained plant material, the diversity of the contained plant matter, the amount of wood present, and the size of the cuticle fragments.

MATERIALS AND METHODS

Seventy-one samples from the plant debris beds of the Wealden group were examined in detail. These were collected from outcrops except for six samples from the Cuckfield no. 1 Borehole. Full details of the lithology and location of each of the samples is supplied in the appendix.

The methods employed in preparing the samples for examination were simple and gentle as much of the material was fragile. The samples were placed in 10 vol. hydrogen peroxide for an hour and the resulting slurry was sieved (250 μm sieve) and washed. The material remaining was placed in cold 60% hydrofluoric acid for three days and then sieved and washed as before. The mineral-free plant material that remained was cleaned by oxidation; 50 ml of concentrated nitric acid was added to 25 g of plant material. The length of time the material was left in the acid varied from sample to sample but twenty-four hours was usually the optimum time. The plant material was then again washed and placed in 5% ammonium hydroxide for ten minutes. After a final wash it was suitable for microscopic examination.

Individual specimens were mounted in 'Clearcol' and 'DePeX'. For examination under the scanning electron microscope specimens were mounted on 12 mm diameter aluminium stubs using 'Durofix' as the adhesive and 40% gold/palladium as the coating medium. Samples used for recording the miospore content were prepared following the methods of Dettmann (1963, p. 11).

SYSTEMATIC TREATMENT OF THE DISPERSED CUTICLES

The nature of the taxa

The taxa described are based upon the structure of the cuticle of plant organs; the cuticle being taken as the cutinized part of the epidermis and hypodermis. With much of the material gross morphological features could not be determined and what little information was available has been treated separately from the main diagnoses.

Each taxon is based upon ten, or in thirteen cases, five specimens, all from the same sample. Similar specimens from other samples are treated separately under comparison records, and so the taxa could be regarded as biorecords and not species in the usually accepted sense. The taxa are characterized by a serial number which would be prefaced by an author identifier outside this paper, an informal classificatory guide and the author's informal working reference (Hughes and Moody-Stuart 1967*b*, 1969).

Systematic position of the taxa

Three factors contrive to make it difficult to place every taxon within the existing hierarchical framework. First, few megafossil leaf taxa are based on cuticle characters alone, and many species have been described without reference to the cuticle at all. Second, a combination of cuticle features does not necessarily characterize a particular family or order. It is not therefore possible to place every taxon within even a major group. Third, the cuticle that can be prepared from the plant debris beds is often of considerably superior preservation and of a larger size than that which can be prepared from the megafossil leaves that form the basis of Seward's work. The diagnosis of a cuticle taxon will therefore differ somewhat from that of the cuticle prepared from a megafossil leaf even if they are of the same species.

Unsatisfactory though this may be, in practice most of the cuticle species can be referred to an order and often a leaf genus, but the slightly unusual taxonomic approach has been used for the reasons explained above.

The choice of cuticle characters

Thomas (1930), Florin (1931, 1958), and Harris (1932) have all considered the problem of the constancy of cuticle characters amongst the gymnosperms. They conclude that the cuticle is well suited to delimiting species and often genera and more rarely the larger taxonomic groupings. Meyen (1965) lists fifteen taxonomically important features of the cuticle, laying stress on those associated with the stomata.

All available features of the cuticle have been used in the diagnoses of the cuticle taxa presented here but the following requirements have been found necessary in order that the diagnosis can be considered reliable:

1. Preservation of the specimens must be sufficiently good to allow all structures to be clearly seen.
2. Stomata must be present.
3. A sufficiently large piece of cuticle must be available so that such features as stomatal arrangement can be determined.
4. Ten, or at the very least, five, specimens should be used for each diagnosis.
5. Preferably both surfaces of the leaf should be available for study.

SYSTEMATIC SECTION

Forty-one cuticle species are described, one from the Purbeck beds of Netherfield, twenty-five from the Fairlight Clay of the Hastings area, one from the Ashdown Sands of the Hastings area, twelve from the Wealden Marls of Dorset, and two from the Wealden Marls of the Isle of Wight. Only an outline is presented; full details of the diagnoses are deposited with the British Library, together with an explanation of the terms and abbreviations used (NLL SUP 14006).

The order and circumscription of the taxa is that adopted by Engler (1954). Sample details are given in the appendix (pp. 500–502).

GYMNOSPERMAE

Class CYCADOPSIDA

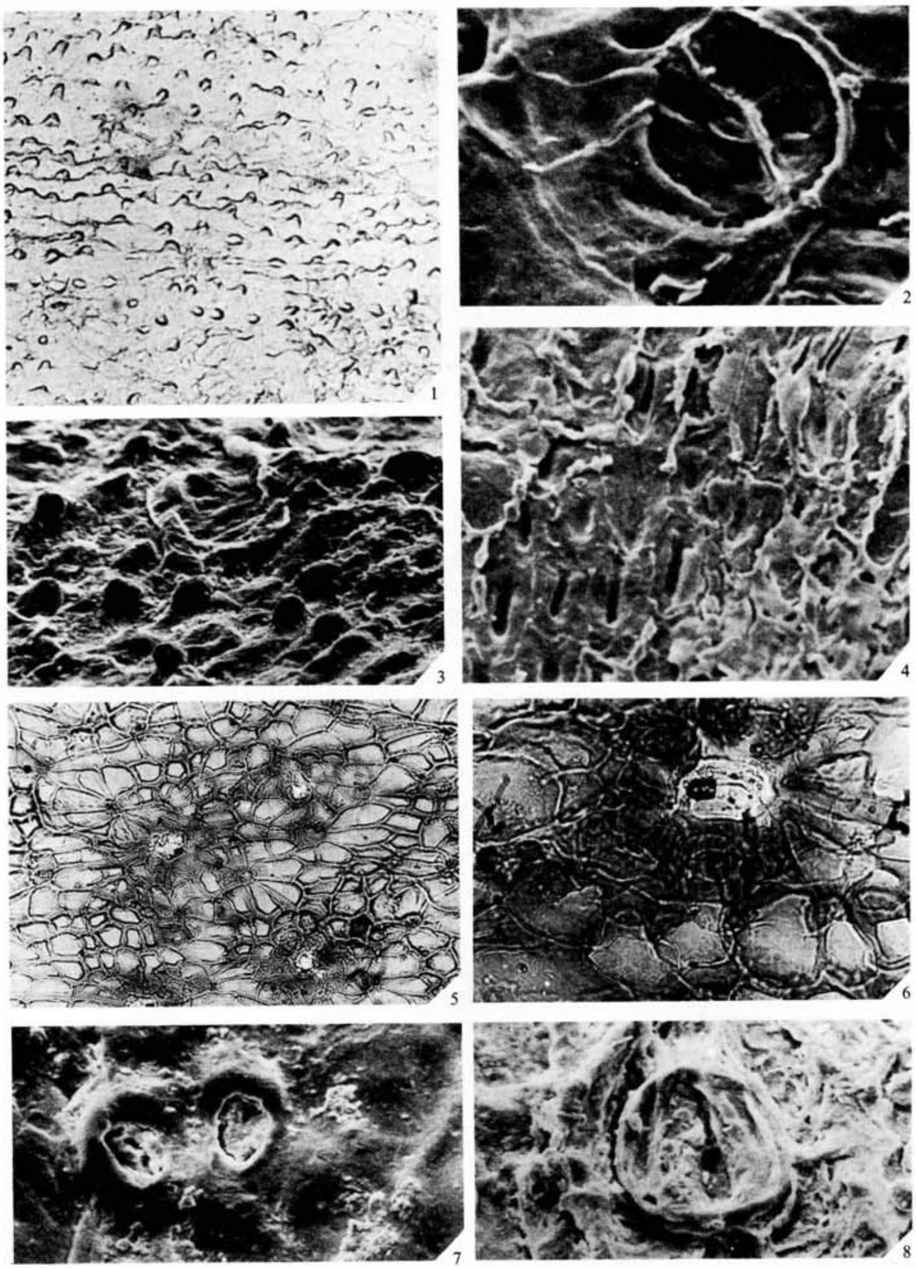
Order CAYTONIALES

This is an isolated order with a single leaf genus, *Sagenopteris* Presl in Sternberg 1838. Two species have been described from the English Wealden, *S. mantelli* (Dunker) Schenk and *S. acutifolia* Seward.

EXPLANATION OF PLATE 55

Figs. 1–4. 1 CAYT SaA. 1, ×500, LM., surface 2, stomata and papillae; P25: 5/2.2. 2, ×1000, SEM., surface 2, inside, stoma; B58. 3, ×500, SEM., surface 2, outside, papillae; B58. 4, ×500, SEM., surface 2, inside, epidermal cells, hypodermis; B58.

Figs. 5–8. 2 CYCAD PsA. 5, ×150, LM., surface 2, stomata; P49: 24/2. 6, ×500, LM., surface 2, stoma; P49: 24/2. 7, ×1000, SEM., surface 2, outside, stomatal apertures; B38. 8, ×1000, SEM., surface 2, inside, stoma; B38.



OLDHAM, 1 CAYT SaA and 2 CYCAD PsA

Cf. Genus SAGENOPTERIS Presl
1 CAYT SaA

Plate 55, figs. 1–4

Record sample. Ashdown Sand, Sample no. 7AH. From 300-mm plant debris bed complex, medium grey, fine siltstone, plant material in fine laminae. Ten specimens, P25: 5/2.1, 3.1, 4.1, 2.2, 4.2; 7/1.2; 17/2.1, 4.1, 1.2, 2.2.

Systematic position. The characters of the cuticle, especially the stomata, closely resemble those of the genus *Sagenopteris*. Jongmans and Dijkstra (1964) list over sixty species belonging to the genus. Of these cuticle is only known for six species and only one of these, *S. mantelli*, occurs in rocks of a relevant age. Carpentier (1939) describes the cuticle of this species and it differs from 1 CAYT in having no papillae and distinct subsidiary cells. *S. hallei* Harris is the only species with papillae in large numbers but it is a Liassic species and differs in several respects from 1 CAYT. *S. acutifolia*, the only other species recorded from the English Wealden, has not yielded any cuticle.

Order CYCADALES–NILSSONIALES

These two orders are not clear cut in terms of cuticle characters and so will be considered together. There are a considerable number of Mesozoic leaf genera belonging to this group and five of these have been recorded from the English Wealden. It is possible that some of the taxa described under this heading relate to the pteridosperms rather than the cycads but the two groups cannot be differentiated on cuticle characters alone.

Cf. Genus PSEUDOCTENIS Seward
2 CYCAD PsA

Plate 55, figs. 5–8

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 20/1; 24/1, 2, 3; 25/1, 2, 3; 26/1, 2, 3.

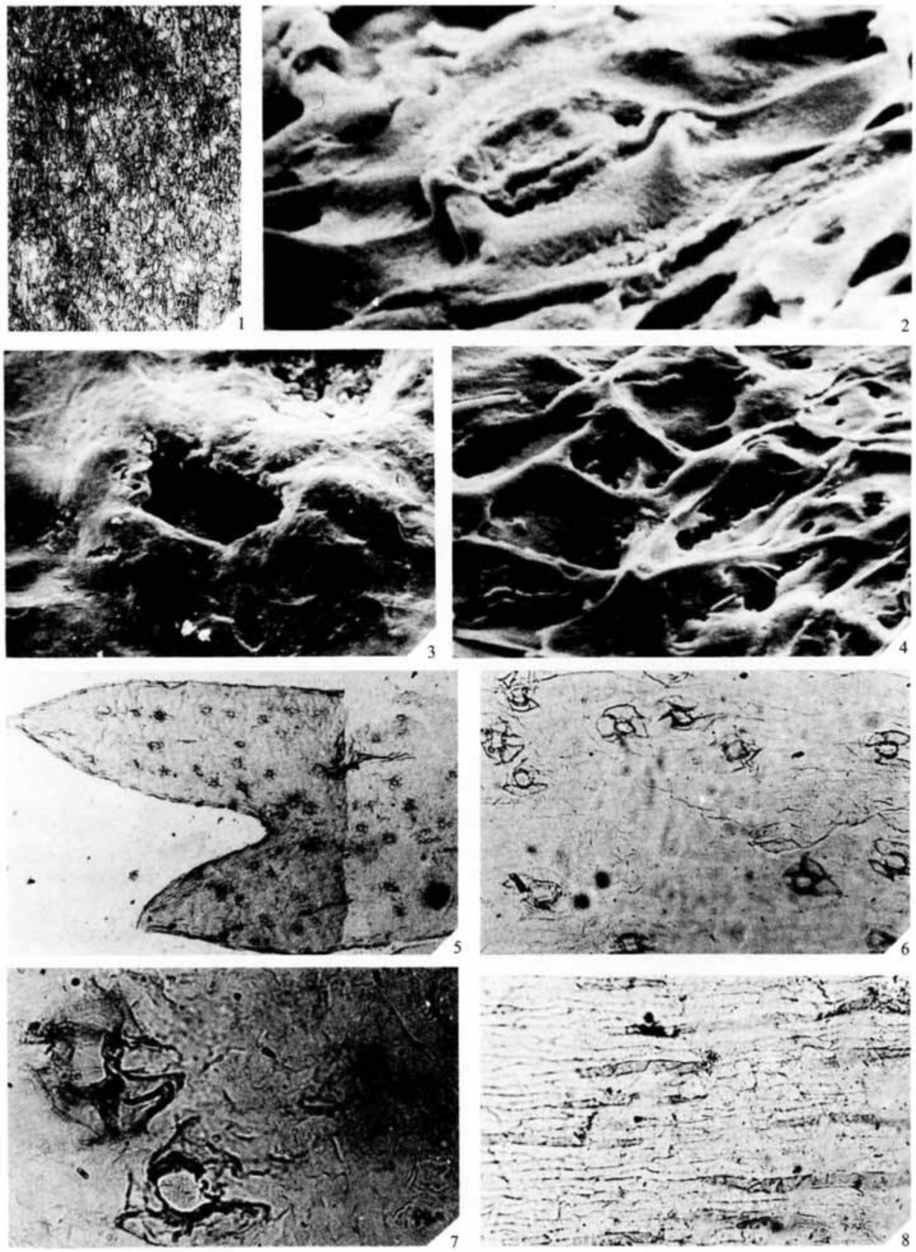
Systematic position. It relates to the cuticle of *Pachypteris* Brongniart to some extent but does not agree with *P. lanceolata* Brongniart, the single English Wealden species of this genus, nor does it agree in all respects with any member of that genus that has been described with reference to cuticle characters. Its resemblance to *Pseudoctenis* is also close, although this genus is hypostomatic as defined by Harris. Seward (1913) lists one specimen of *P. earthiensis* (Richard) Seward from Ecclesbourne Glen but it has not yielded cuticles. Carpentier (1939) describes a species of *Pseudoctenis*

EXPLANATION OF PLATE 56

Figs. 1–4. 3 CYCAD PsB. 1, × 50, LM., general view; P127: 7/1. 2, × 2000, SEM., surface 2, inside, stoma; B28. 3, × 1000, SEM., surface 2, outside, stomatal aperture; B28. 4, × 1000, SEM., surface 2, inside, epidermal cells and hypodermis; B28.

Figs. 5–8. 4 CYCAD CtA. 5, × 50, LM., both surfaces, general view; P59: 20/1.1. 6, × 150, LM., surface 2, stomata; P59: 20/1.1. 7, × 500, LM., surface 2, stomata; P59: 20/1.1. 8, × 150, LM., surface 1, epidermal cells and thickened cells; P59: 20/1.1.

PLATE 56



OLDHAM, 3 CYCAD PsB and 4 CYCAD CtA

giving full details of the cuticle structure from the French Wealden; this is similar to, but not the same as, 2 CYCAD. The same can be said of the *Pseudoctenis* species described by Benda (1961) from the German Wealden. The lack of evidence concerning the gross morphology of 2 CYCAD would make the placing of it in the genus *Pseudoctenis* premature.

3 CYCAD PsB

Plate 56, figs. 1–4

Record sample. Wealden Marls, Sample no. 27BD. From 100-mm band in 1-m plant debris bed complex, light grey, fine siltstone, plant material in irregular laminae. Ten specimens, P127: 5; 6; 7; 8; 9; 11; 12; 13; 14; 15.

Systematic position. This taxon is close to 2 CYCAD and remarks made with regard to its systematic position apply here.

Cf. Genus CTENIS Lindley and Hutton
4 CYCAD CtA

Plate 56, figs. 5–8; Plate 57, figs. 1, 2

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 16/3.2, 4.1; 20/1.1, 2.1, 2.3, 3.1; 23/2.3; 25/2.1, 2.2; 27/1.1.

Systematic position. This taxon is close to the genus *Ctenis*, important points of similarity being the structure and thickening of the guard cells and subsidiary cells. The major point of disagreement is the large number of stomata on both surfaces of 4 CYCAD and their virtual restriction to the lower surface in *Ctenis*. In its stomatal distribution 4 CYCAD bears some resemblance to *Stenopteris* Saporta but it differs in stomatal structure.

5 CYCAD CtB

Plate 57, figs. 3–6

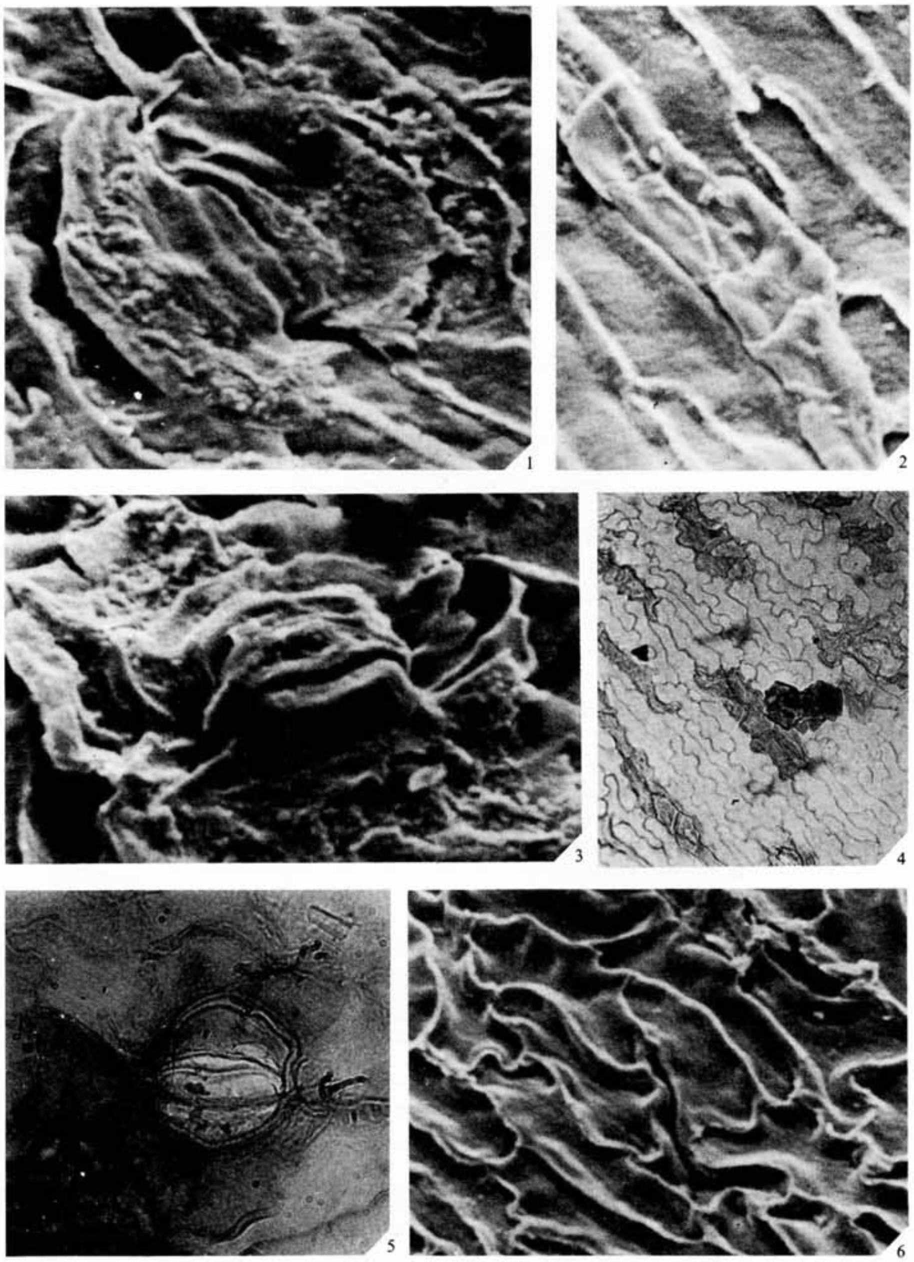
Record sample. Wealden Marls, Sample no. 18DD. From a 75-mm band in plant debris bed complex, light medium-grey claystone, plant material irregularly dispersed through the matrix. Ten specimens, P118: 1/4.2; 3/2.1; 5/4.1; 6/1.1, 4.1; 7/3.2; 11/4.1; 12/2.1, 2.2.

Systematic position. This taxon is close to 4 CYCAD and remarks made concerning the affinity of that taxon apply here. In its lack of stomata on one surface it is, however, even closer to the genus *Ctenis*.

EXPLANATION OF PLATE 57

Figs. 1–2. 4 CYCAD CtA. 1, ×1000, SEM., surface 2, inside, stoma; B42. 2, ×1000, SEM., surface 1, inside, thickened cells; B42.

Figs. 3–6. 5 CYCAD CtB. 3, ×1000, SEM., surface 2, inside, stoma; B56. 4, ×150, LM., surface 1, epidermal cells; P118: 6/4.1. 5, ×500, LM., surface 2, stoma; P118: 6/4.1. 6, ×500, SEM., surface 1, inside, epidermal cells; B56.



OLDHAM, 4 CYCAD CtA and 5 CYCAD CtB

Cf. Genus ALMARGEMIA Florin
6 CYCAD AlA

Plate 58, figs. 1–3

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 11/3.1; 20/3.2; 38/1.1, 1.3, 4.1.

Systematic position. This taxon agrees well with the diagnosis of the genus *Almargemia* Florin. The two species in the genus are *A. dentata* Florin from the Aptian of Portugal and *A. incrassata* Archangelsky from the Tico flora. 6 CYCAD has the characteristic rows of thickened cells of *A. incrassata* and has similar thickenings on the guard cells. The main point of divergence is the size of the subsidiary cells which are considerably smaller in 6 CYCAD. The genus *Stenopteris* is also similar but none of the published species agree with 6 CYCAD.

7 CYCAD AlB

Plate 58, figs. 4–8

Record sample. Fairlight Clay, Sample no. 18AH. From a 74-mm band in plant debrid bed complex, medium dark-grey siltstone plant material in laminae. Ten specimens, P81: 11/1.1, 2.1; 23/3.1; 25/1.2; 27/2.2; 28/1.2; 30/2.2, 3.2; 32/2.1; 34/4.1.

Systematic position. This taxon is close to 6 CYCAD in its stomatal structure and is likely to be of cycadalean affinity. It is not as close to *Almargemia* as 6 CYCAD.

8 CYCAD CeA

Plate 59, figs. 1–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 35/1.1, 2.1, 2.2; 59/1.1, 1.2, 1.3, 2.1, 2.2, 2.3.

Systematic position. This taxon is close to 9 CYCAD. The characteristic ring around the stomatal aperture is reminiscent of *Ctenozamites* and it agrees well with the diagnosis of that genus except in the factor of the stomata on both surfaces. A thickened ring is also characteristic of the genus *Mesosingeria* Archangelsky from the Tico flora, but it differs in other respects.

9 CYCAD CeB

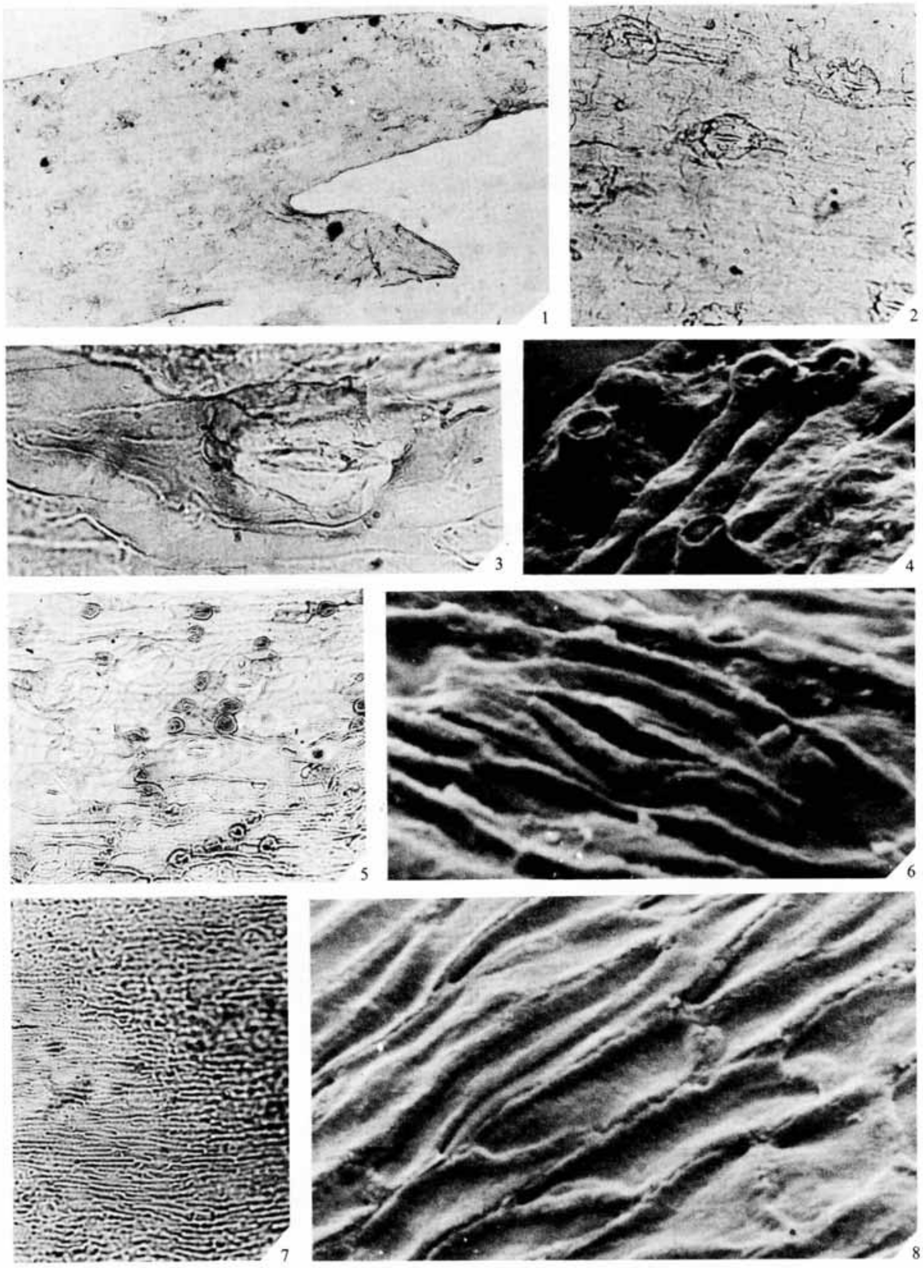
Plate 59, figs. 5–8

Record sample. Wealden Marls, Sample no. 7DD. From 75-mm band in plant debris bed complex, plant material irregularly dispersed through the matrix. Ten specimens, P100: 1/1.2; 2/3.1, 4.2; 4/3.2; 7/2.1; 8/1.1, 1.2; 10/1.1, 1.2; 11/3.1.

EXPLANATION OF PLATE 58

Figs. 1–3. 6 CYCAD AlA. 1, $\times 50$, LM., both surfaces, general view; P59: 41/1.1. 2, $\times 150$, LM., surface 2, stomata; P59: 41/1.1. 3, $\times 500$, LM., surface 2, stoma; P59: 41/1.1.

Figs. 4–8. 7 CYCAD AlB. 4, $\times 500$, SEM., surface 2, outside, papillae; B55. 5, $\times 150$, LM., surface 2, stomata and papillae; P81: 11/2.1. 6, $\times 2000$, SEM., surface 2, inside, stoma; B55. 7, $\times 150$, LM., surface 1, epidermal cells; P81: 11/2.1. 8, $\times 1000$, SEM., surface 1, inside, epidermal cells; B55.



OLDHAM, 6 CYCAD AlA and 7 CYCAD AlB

Systematic position. It is close to 8 CYCAD and remarks made concerning the affinity of that taxon apply here. Benda (1961) describes a cuticle which he does not place in any genus but refers to as Cycadee Form L; this appears very similar to 9 CYCAD.

Cf. Genus BECKLESIA Seward
10 CYCAD BeA

Plate 60, figs. 1–6

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 30/1.3; 31/1.1, 2.1, 2.2; 32/1, 2, 4; 48/2.1; 49/2.1.

Systematic position. Seward erected the genus *Becklesia* in 1895 and placed it in Gymnospermae incertae sedis. He described one species from the English Wealden, *B. anomola.* This species has been revised by Watson (1969) and in the same work she defines a new species from leaf fragments, *B. sulcata.* This is undoubtedly the same as 10 CYCAD.

11 CYCAD BeB

Plate 61, figs. 1–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Nine specimens, P49: 30/2; 32/3; 49/2.2; 51/1.2; 56/2.1, 2.2; 57/2.1; 58/2.

Systematic position. This is close to 10 CYCAD but does not agree completely with any of the published species of the genus *Becklesia.*

12 CYCAD BeC

Plate 61, figs. 5–9

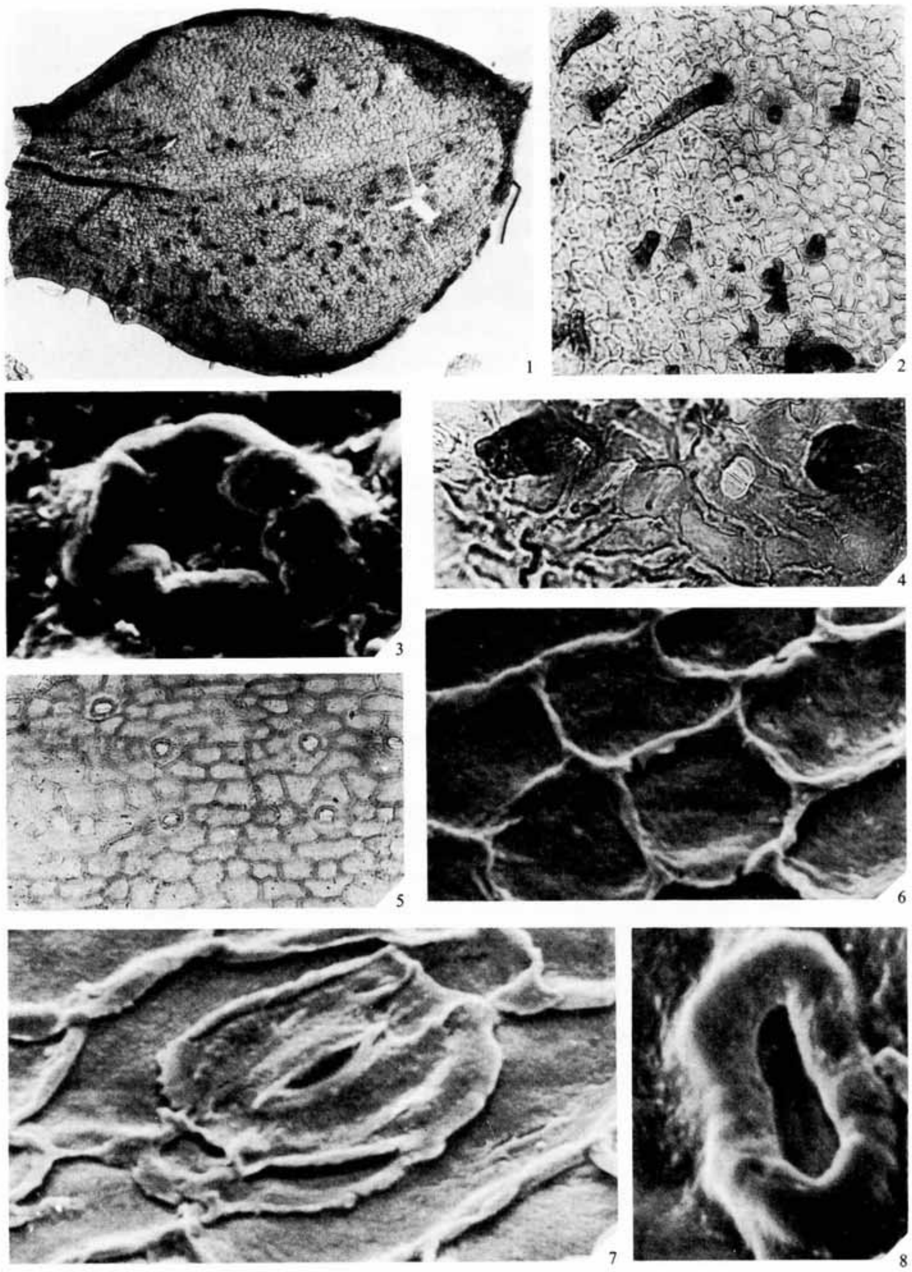
Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 2/4.1; 6/1.1, 1.2; 14/1.2, 2.2, 2.1; 15/1.1; 19/1.1, 3.2; 23/3.2.

Systematic position. This is close to 10 CYCAD and 11 CYCAD and remarks made concerning the affinity of those taxa to the genus *Becklesia* apply here. Like 11 CYCAD it does not agree completely with any of the published species of the genus.

EXPLANATION OF PLATE 59

Figs. 1–4. 8 CYCAD CeA. 1, ×50, LM., surface 2, general view; P49: 59/2.1. 2, ×150, LM., surface 2, hairs, papillae, and stomata; P49: 59/2.1. 3, ×2000, SEM., surface 2, outside, stomatal aperture; B41. 4, ×500, LM., surface 2, stoma; P49: 35/2.1.

Figs. 5–8. 9 CYCAD CeB. 5, ×150, LM., surface 2, stomata; P100: 2/3.1. 6, ×1000, SEM., surface 1, inside, epidermal cells; B48. 7, ×1000, SEM., surface 2, inside, stoma; B48. 8, ×1000, SEM., surface 2, outside, stomatal aperture; B48.



OLDHAM, 8 CYCAD CeA and 9 CYCAD CeB

Order BENNETTITALES

This group is well defined as a whole on cuticle characters but as Harris (1969) states there are no styles of cuticle-characterizing genera. The division into genera is on gross morphology although a few genera such as *Pseudocycas* and *Pterophyllum* can be identified without recourse to such information. The lack of information regarding the cuticle of the bennettitalean species described by Seward from the Wealden makes the task of placing isolated cuticles in their correct leaf genera more difficult.

Cf. Genus PSEUDOCYCAS Nathorst
13 BENN PeA

Plate 62, figs. 1–3

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 40/1.2, 2.1, 2.2; 55/2.1, 3.1.

Systematic position. The presence of a stomatal groove places it within the genus *Pseudocycas*. It agrees well with *P. saportae* (Seward) Holden from Ecclesbourne and Hastings and an examination of the type material confirms this agreement.

14 BENN PeB

Plate 62, figs. 4–7

Record sample. Fairlight Clay, Sample no. 34AH. From 150-mm plant debris bed complex, medium light-grey siltstone, plant material in laminae. Ten specimens, P64: 4/1.1, 2.1, 1.2; 7/1.1, 2.1, 1.2, 2.2; 8/2.1; 9/2.2; 10/2.1.

Systematic position. Its cuticle characters and the possession of a stomatal groove places it in the genus *Pseudocycas*. It does not agree with any of the published species of this genus.

Cf. Genus ZAMITES Brongniart
15 BENN ZaA

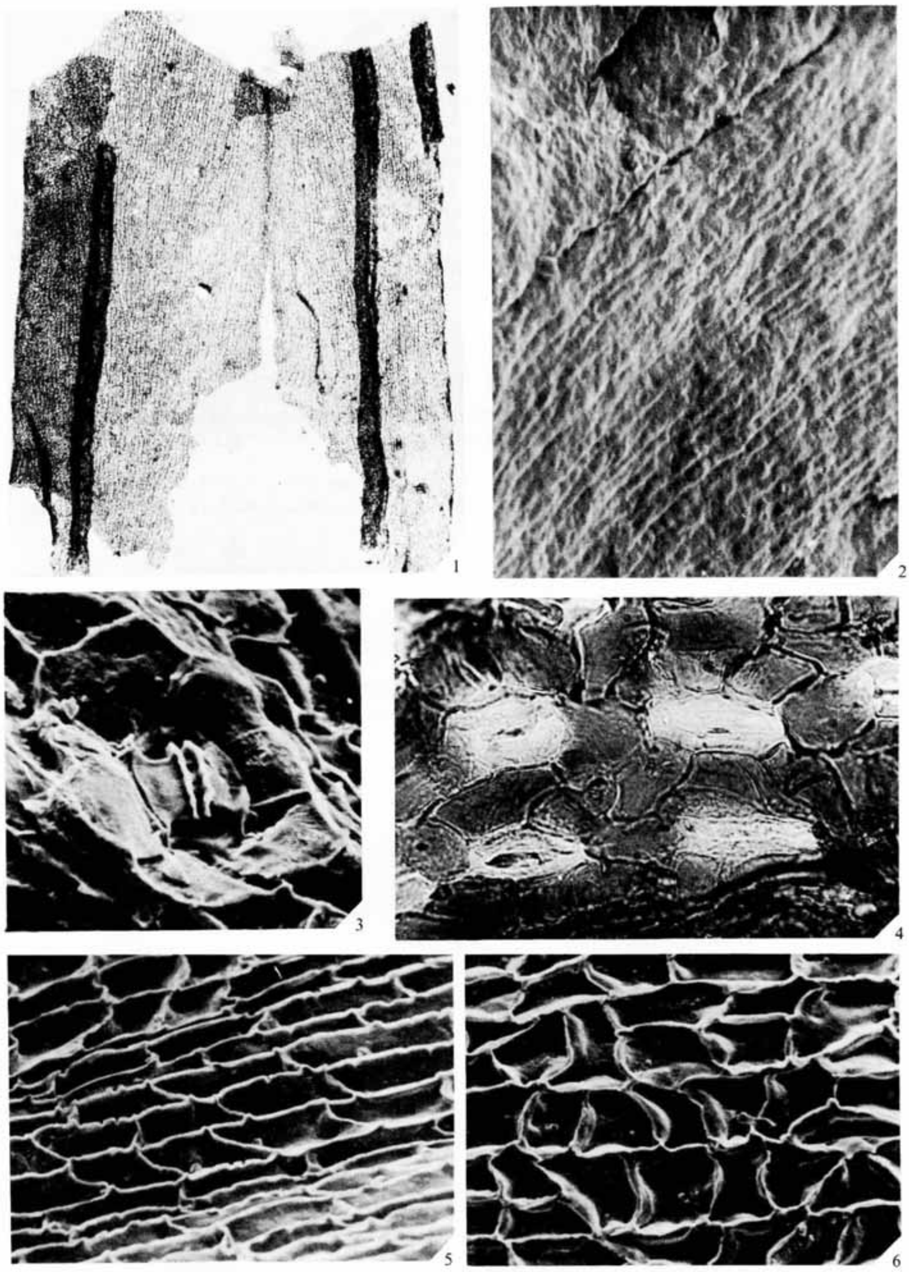
Plate 63, figs. 1–3

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 14/1.1; 34/1.2, 2.1; 36/2.2, 4.2; 37/2.2; 55/1.3; 60/1.1; 62/3.2; 63/3.2.

Systematic position. This taxon is close to the cuticles of specimens BMNH V2363, BMNH V2262, and BMNH V2698 which Seward included in *Zamites buchianus*. Some other specimens placed by Seward in the same species have totally different cuticles.

EXPLANATION OF PLATE 60

Figs. 1–6. 10 CYCAD BeA. 1, ×20, LM., both surfaces, general view; P49: 32/4. 2, ×100, SEM., surface 2, outside, groove; B50. 3, ×1000, SEM., surface 2, inside, stoma; B22. 4, ×500, LM., surface 2, stomata; P49: 32/1. 5, ×500, SEM., surface 2, inside, epidermal cells; B22. 6, ×500, SEM., surface 1, inside, epidermal cells; B22.



OLDHAM, 10 CYCAD BeA

16 BENN ZaB

Plate 63, figs. 4–7

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 36/3.2; 37/2.1; 61/3.3; 63/1.3, 3.1.

Systematic position. This relates well to the cuticle of specimens BMNH V2741 and BMNH V2360 which Seward placed in the species *Otozamites goppertianus.* It also resembles Daber's (1960) Blattfragment G which he does not place in any genus.

17 BENN ZaC

Plate 64, figs. 1–5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 34/3.1; 36/2.1, 4.2; 37/3.1; 63/2.1.

Systematic position. This taxon does not resemble the cuticles of any Wealden bennettitalean leaves examined. Its closeness to 15 BENN and 16 BENN, however, suggests an affinity with *Zamites.*

Cf. Genus OTOZAMITES Braun
18 BENN OtA

Plate 64, figs. 6–8

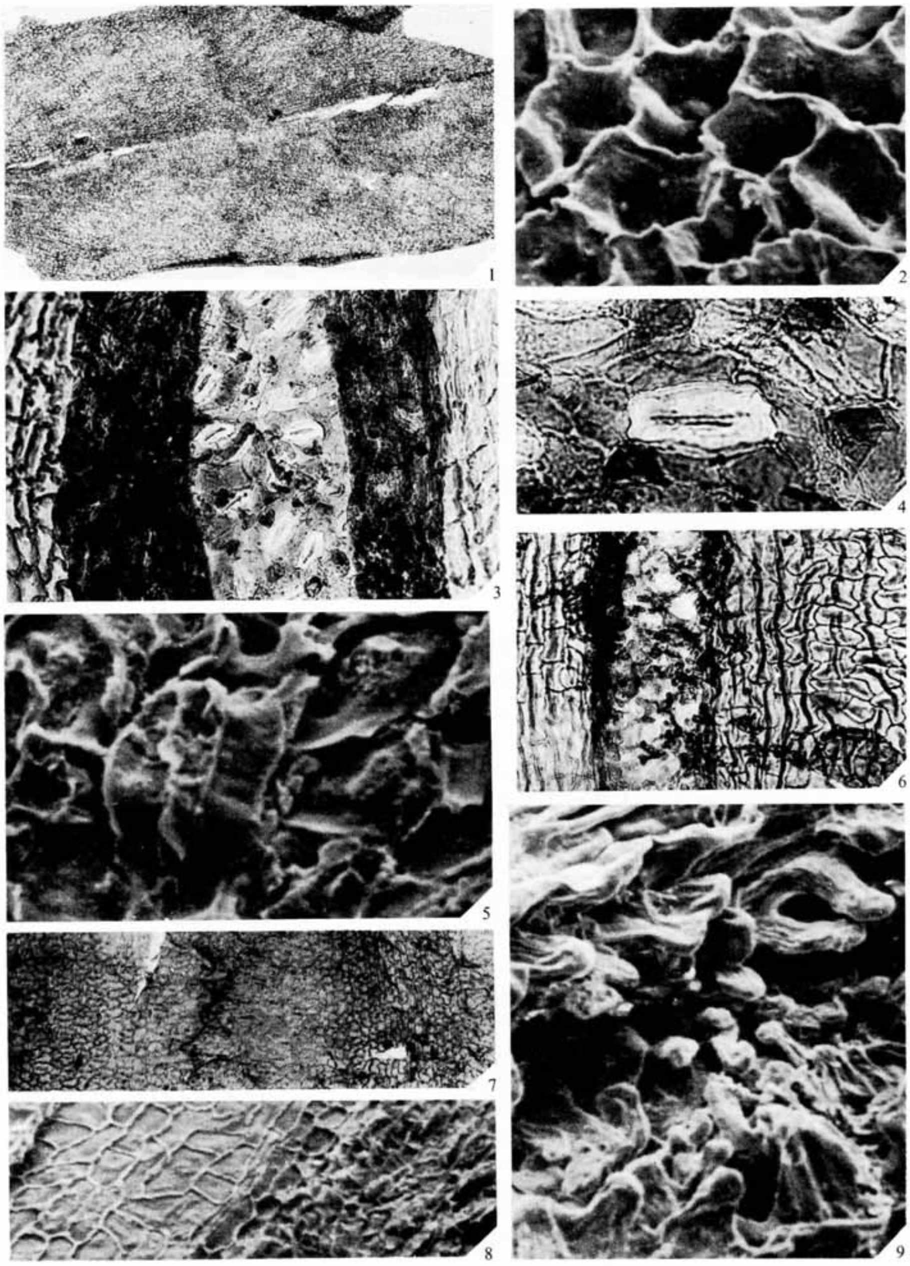
Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band plant in debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 15/2.2; 16/4.2; 17/1.1, 1.3; 22/1.2; 35/1.3; 36/3.1; 37/1.2, 3.1, 4.2.

Systematic position. This taxon agrees well with the cuticle of specimen BMNH V21222 which Seward places in *O. klipsteinii* var. *longifolia.* It also agrees with specimen BMNH V21222a which Seward places in *O. klipsteinii* var. *superba.* Unfortunately it also agrees with the cuticle of specimens BMNH 2123c and BMNH V2123d which Seward places in *Z. carruthersi* and with specimen BMNH V2120 which he places in *Z. buchianus.* This underlines the need for a thorough revision of Wealden bennettitalean leaves.

EXPLANATION OF PLATE 61

Figs. 1–4. 11 CYCAD BeB. 1, ×20, LM., surface 1, general view; P49: 53/1.1. 2, ×500, SEM., surface 1, inside, epidermal cells; B64. 3, ×150, LM., surface 2, groove; P49: 32/3. 4, ×500, LM., surface 2, stoma; P49: 32/2.

Figs. 5–9. 12 CYCAD BeC. 5, ×1000, SEM., surface 2, inside, stoma; B53. 6, ×150, LM., surface 2, groove; P98: 19/3.2. 7, ×50, LM., surface 1, epidermal cells; P98: 19/3.2. 8, ×500, SEM., surface 2, inside, epidermal cells and stomatal groove; B53. 9, ×500, SEM., surface 2, outside, groove; B53.



OLDHAM, 11 CYCAD BeB and 12 CYCAD BeC

Cf. Genus ANOMOZAMITES Schimper
19 BENN AnA

Plate 65, figs. 1-5

Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 2/2.2; 12/3.2; 13/4.2; 15/1.2; 16/1.2, 2.1; 18/1.2, 4.2; 21/1.1; 23/1.2.

Systematic position. It is close to the genus *Anomozamites* Schimper and relates to Wealden species *A. lyellianus* (Dunker) Seward, although this species has transversely orientated stomata borne in regular rows. It also resembles *A. nilsonni* (Phillips) Harris, although again the arrangement of stomata is somewhat different.

Cf. Genus PTEROPHYLLUM Brongniart
20 BENN PtA

Plate 65, figs. 6-8

Record sample. Purbeck, Sample no. 53H. From 250-mm plant debris bed complex, medium-grey claystone, plant material in irregular laminae. Ten specimens, P95: 1/1.3; 5/1.1; 11/1.1, 4.2; 12/4.1; 16/1.2; 17/2.1, 4.1; 19/2.1, 3.1.

Systematic position. The almost straight walls of the epidermal cells suggest an affinity with *Pterophyllum* but none of the published members of that genus agree with this taxon.

21 BENN PtB

Plate 66, figs. 1-5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 63/1.1, 2.2; 65/4.1; 66/2.1, 3.1.

Systematic position. Although bennettitalean in character it does not relate closely to any of the cuticles of Wealden leaves examined. Benda (1961) pictures a Bennettitee form 7, which resembles 21 BENN and Benda places his taxon in the genus *Pterophyllum*.

Cf. Genus CYCADOLEPIS Saporta
22 BENN CyA

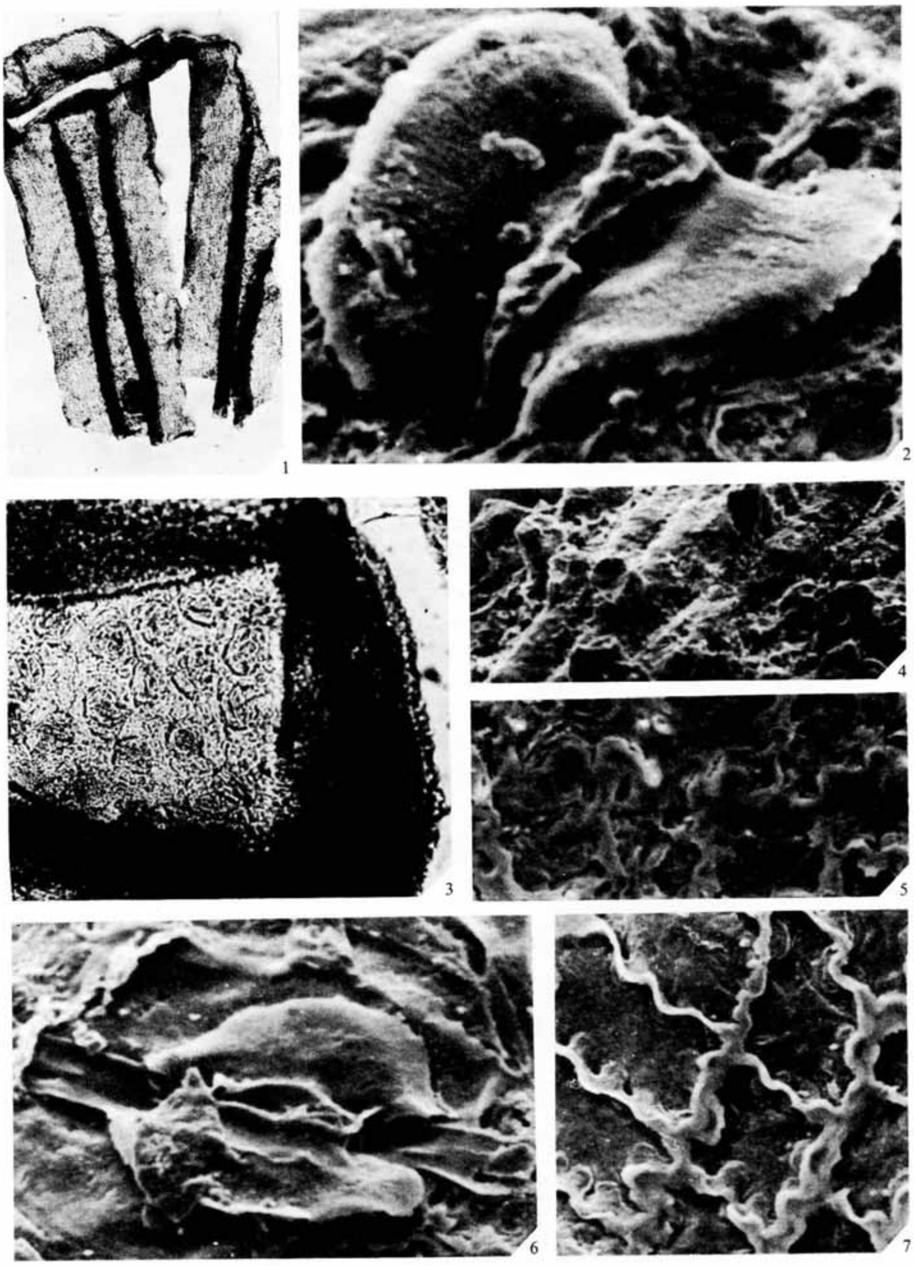
Plate 66, figs. 6-8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band from plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 12/1.2, 3.1; 14/1.2; 15/3.2; 36/3.2.

EXPLANATION OF PLATE 62

Figs. 1-3. 13 BENN PeA. 1, ×20, LM., surface 2, general view; P49: 40/1.2. 2, ×2000, SEM., surface 2, inside, stoma; B63. 3, ×150, LM., surface 2, groove; P49: 40/1.2.

Figs. 4-7. 14 BENN PeB. 4, ×200, SEM., surface 2, outside, papillae; B57. 5, ×500, SEM., surface 2, inside, hypodermis; B57. 6, ×1000, SEM., surface 2, inside, stoma; B57. 7, ×500, SEM., surface 1, inside, epidermal cells; B57.



OLDHAM, 13 BENN PeA and 14 BENN PeB

Systematic position. The stomata are bennettitalean in character and the straight walled epidermal cells and the scarcity of stomata suggest an affinity with *Cycadolepis* Saporta. Seward (1913) describes a *Cycadolepis* species from the English Wealden but the cuticle prepared from this is very poor. Daber's (1960) Blattfragment E is similar.

BENNETTITALES Incertae sedis
23 BENN BnA

Plate 67, figs. 1–8

Record sample. Wealden Marls, Sample no. 50CIOW. From 150-mm band from plant debris bed complex, medium light-grey siltstone, plant material in fine laminae. Five specimens, P153: 2/1.2; 3/3.1; 7/1.2, 3.2, 4.2.

Systematic position. It is bennettitalean in many of its characters but the stomata are not fully typical of the group.

Order GINKGOALES

Until Watson (1969) described *Pseudotorellia heterophylla*, no member of this order had been recorded from the English Wealden. The following six taxa relate to the Ginkgoales in varying degrees, but all fit in here better than with any other group.

Cf. Genus PSEUDOTORELLIA Florin
24 GINK ToB

Plate 68, figs. 1–3

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band from plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 9/1.2; 13/1.1; 19/3.2, 3.3; 24/4.1.

Systematic position. This taxon agrees with *P. heterophylla* Watson and an examination of the type material confirms this.

25 GINK ToA

Plate 68, figs. 4–8

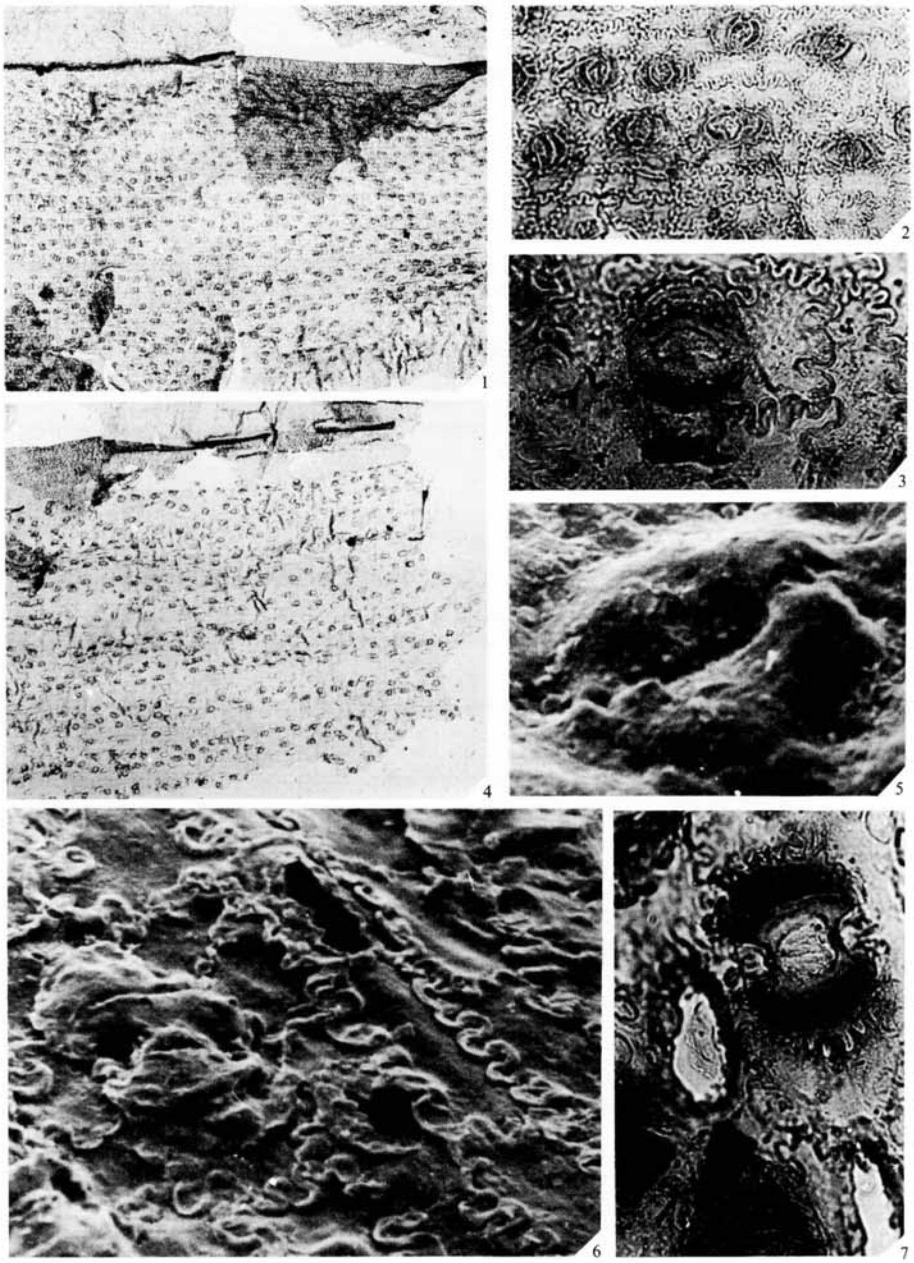
Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 9/1.1, 1.2, 2.1, 2.2; 16/1.2, 2.1, 3.2; 12/1.1; 45/1.1, 2.2.

Systematic position. This taxon agrees well with Watson's emended diagnosis of the genus *Pseudotorellia* (1969). Of the seven species described by Lundblad (1968)

EXPLANATION OF PLATE 63

Figs. 1–3. 15 BENN ZaA. 1, ×20, LM., surface 2, general view; P49: 14/1.1. 2, ×150, LM., surface 2, stomata; P49: 14/1.1. 3, ×500, LM., surface 2, stoma; P49: 13/2.2.

Figs. 4–7. 16 BENN ZaB. 4, ×20, LM., surface 2, general view; P49: 63/3.1. 5, ×1000, SEM., surface 2, outside, stomatal aperture; B62. 6, ×500, SEM., surface 2, inside, stoma, bordered holes; B62. 7, ×500, LM., surface 2, stoma; P49: 36/1.2.



OLDHAM, 15 BENN ZaA and 16 BENN ZaB

none agree completely with 25 GINK. It should be noted that specimens described as *Abietites linki* (Rom)Dunker by Michael (1936) and Benda (1961) appear to be identical with 25 GINK.

Cf. Genus GINKGOITES Seward
26 GINK GiA

Plate 69, figs. 1–6

Record sample. Wealden Marls, Sample no. 48CIOW. From 150-mm band from plant debris bed complex, medium light grey, fine siltstone, plant material in fine laminae. Five specimens, P147: 2/4.2; 4/4.2; 5/1.2; 6/2.2; 8/1.2.

Systematic position. It relates well to the ginkgoalean genera *Ginkgoites* Seward and *Baiera* Braun. It is not possible to distinguish these two genera apart on cuticle ground but the number of vein traces in the specimens of 26 GINK suggest a closer affinity to *Ginkgoites*. All the cuticle characters of these two genera that are described by Oishi (1933) are present in 26 GINK.

GINKGOALES Incertae sedis
27 GINK GkA

Plate 70, figs. 3–6; Plate 71, figs. 1, 3, 5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 10/1.2, 2.1, 3.2; 11/1.2, 2.2, 2.1; 17/1.2, 2.2; 46/2.1.

Systematic position. This taxon is of ginkgoalean affinity but does not agree specifically with any of the published taxa.

28 GINK GkB

Plate 71, figs. 2, 4, 6, 7, 8

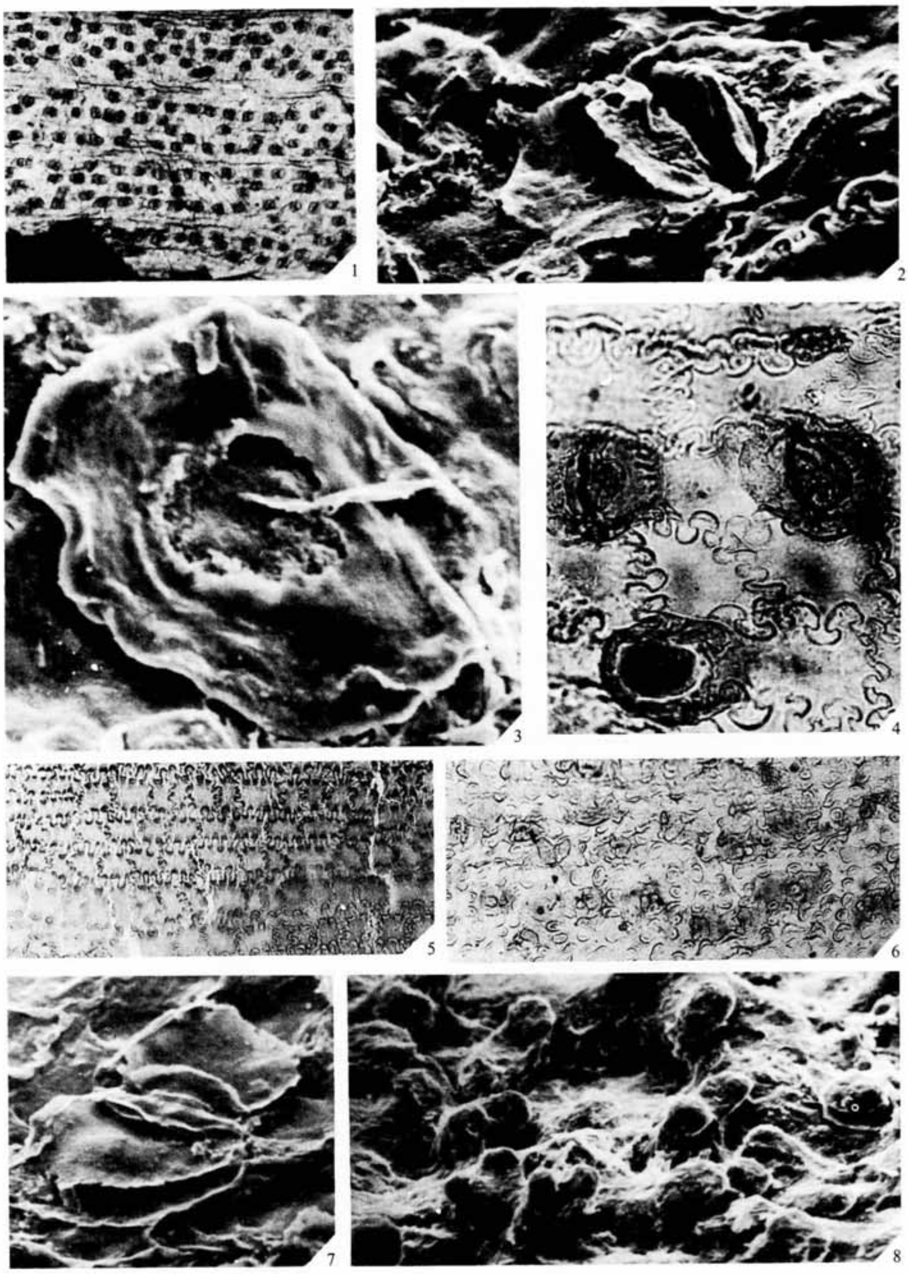
Record sample. Wealden Marls, Sample no. 20BD. From 300-mm plant debris bed complex, light grey, fine siltstone, plant material in irregular laminae. Five specimens, P121: 1/3.2; 2/1.1; 4/1.1; 6/1.1; 7/1.1.

Systematic position. It is closely related to 27 GINK and remarks made concerning the affinity of that taxon apply here.

EXPLANATION OF PLATE 64

Figs. 1–5. 17 BENN ZcC. 1, ×20, LM., surface 2, general view; P49: 63/2.1. 2, ×1000, SEM., surface 2, inside, stoma; B17. 3, ×2000, SEM., surface 2, inside, intracellular, circular, cutinized bodies; B17. 4, ×500, LM., surface 2, stomata and intracellular, circular, cutinized bodies; P49: 36/3.1. 5, ×150, LM., surface 1, epidermal cells; P49: 63/2.1.

Figs. 6–8. 18 BENN OtA. 6, ×150, LM., surface 2, stomata and papillae; P59: 37/4.2. 7, ×500, SEM., surface 2, inside, stoma; B16. 8, ×100, SEM., surface 2, outside, papillae; B16.



OLDHAM, 17 BENN ZaC and 18 BENN OtA

29 GINK GkC

Plate 69, figs. 7, 8; Plate 70, figs. 1, 2

Record sample. Fairlight Clay, Sample no. P49. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 9/3.1; 12/1.2, 3.1, 3.2; 13/1.2, 3.1, 3.2; 14/2.1, 2.2; 21/3.

Systematic position. This is ginkgoalean in character and is close to the genera *Ginkgoites* and *Baiera*, although not agreeing sufficiently well to be placed in either genera.

Class CONIFEROPSIDA

Several species belonging to this class have been described from the English Wealden by Seward (1895, 1913) but many only relate to reproductive structures. In all he describes nine species that are defined by, or at least possess, leaves.

Order CONIFERAE

Family CHEIROLEPIDIACEAE Hirmer and Höurhammer emend. Takhtajan

30 CHEIR MaA

Plate 72, figs. 1–8

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 4/3.1, 4.1; 5/1.1, 2.1, 1.2; 6/1.1, 2.1, 2.2, 3.2, 4.2.

Systematic position. The cuticle structure resembles *Frenelopsis* but the phyllotaxis of 30 CHEIR is quite distinct. Its close association with *Classopollis* Pflug pollen in nearly every sample suggests an affinity with the family Cheirolepidiaceae. Archangelsky (1968) assigned this pollen grain to the family.

Family TAXODIACEAE

Cf. Genus SCIADOPITYTES Goeppert et Menge

31 TAXOD ScA

Plate 73, figs. 1–6

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 40/1.1, 3.1; 53/1.1; 55/1.1; 57/1.2.

Systematic position. This taxon agrees well with Florin's (1922) diagnosis of the genus *Sciadopitytes*. It does not, however, agree in detail with any of the fourteen

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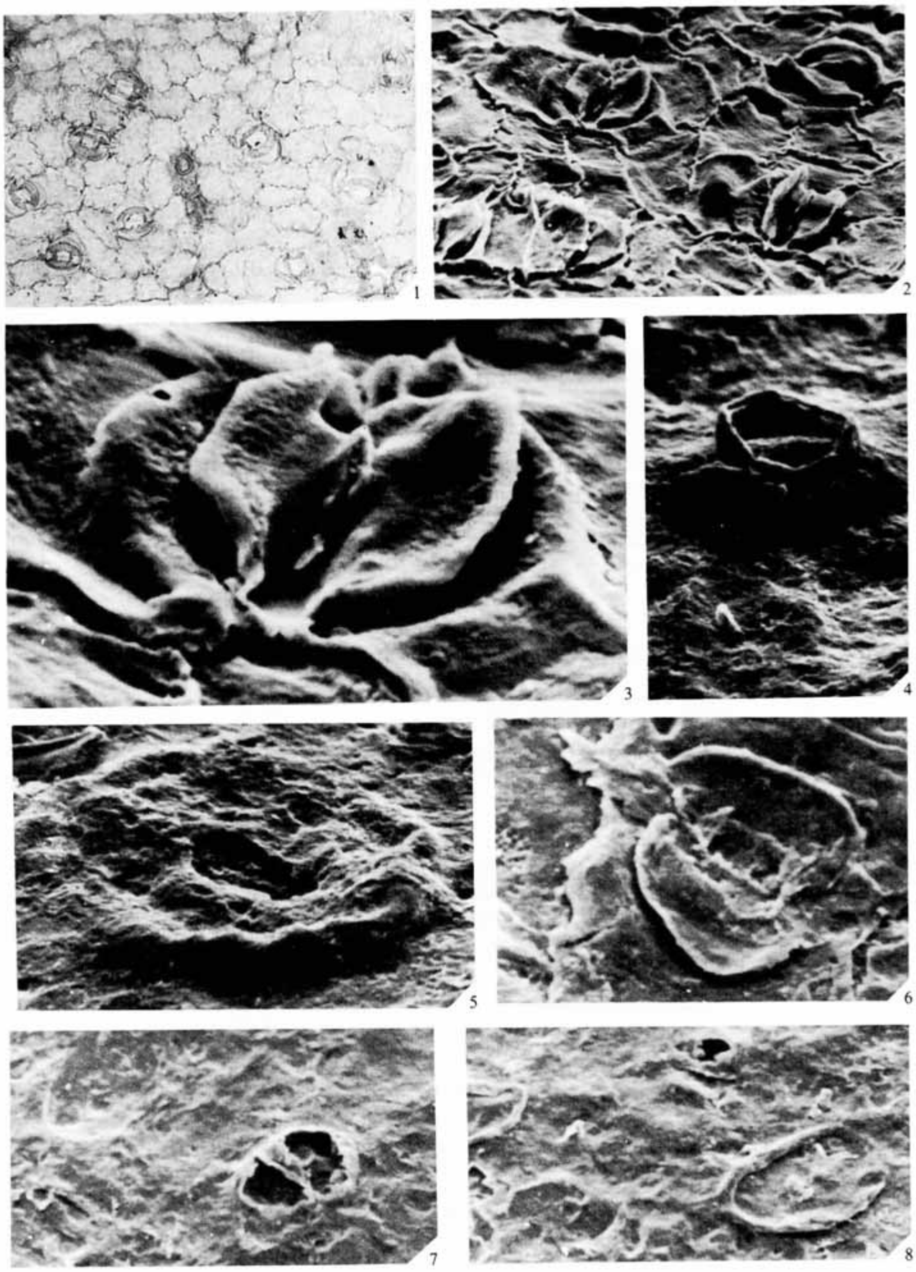
EXPLANATION OF PLATE 65

Figs. 1–5. 19 BENN AnA. 1, ×150, LM., surface 2, stomata; P98: 18/1.1. 2, ×500, SEM., surface 2, inside, stomata; B27. 3, ×2000, SEM., surface 2, inside, stoma; B27. 4, ×1000, SEM., surface 2, outside, hair base; B27. 5, ×1000, SEM., surface 2, outside, stomatal aperture; B27.

Figs. 6–8. 20 BENN PtA. 6, ×1000, SEM., surface 2, inside, stoma; B61. 7, ×500, SEM., surface 2, outside, ahir base; B61. 8, ×500, SEM., surface 2, outside, papillae, hair bases; B61.



OLDHAM, 19 BENN AnA and 20 BENN PtA

species he describes. It most resembles *S. macrophylla* but this species has no hairs along the stomatal groove and possesses a wider leaf. Gothan (1954) pictures a species of *Sciadopitytes* from the Wealden of Spain but his description is poor.

TAXODIACEAE Incertae sedis
32 TAXOD SpA

Plate 78, figs. 1–3

Record sample. Fairlight Clay, Sample no. 44H. From 50-mm band from plant debris bed complex, medium-grey siltstone, plant material in thick laminae. Ten specimens, P55: 5/4.1; 7/1.2, 2.2, 4.2; 9/3.2; 10/2.2, 3.2; 12/1.1, 1.2, 3.2.

Systematic position. The structure and arrangement of the stomata suggests a taxodiaceous affinity. It resembles the living genus *Athrotaxis* but the sinuous walled epidermal cells of 32 TAXOD are not a feature of this genus or indeed the family. Comparison with Mesozoic taxodiaceous genera shows this taxon to be distinct from most of them. It could be placed in *Sphenolepis* Schenk but this is a genus for leaves with a known cone, also the sinuous walls of the epidermal cells, the occasional sharing of subsidiary cells, and the presence of stomata on both surfaces are not characteristic of this genus. Similar arguments can be used against placing it in the genus *Elatides* Keer.

Family CUPRESSACEAE
Cf. Genus CUPRESSINOCLADUS Seward
33 CUPR CuA

Plate 74, figs. 1–7

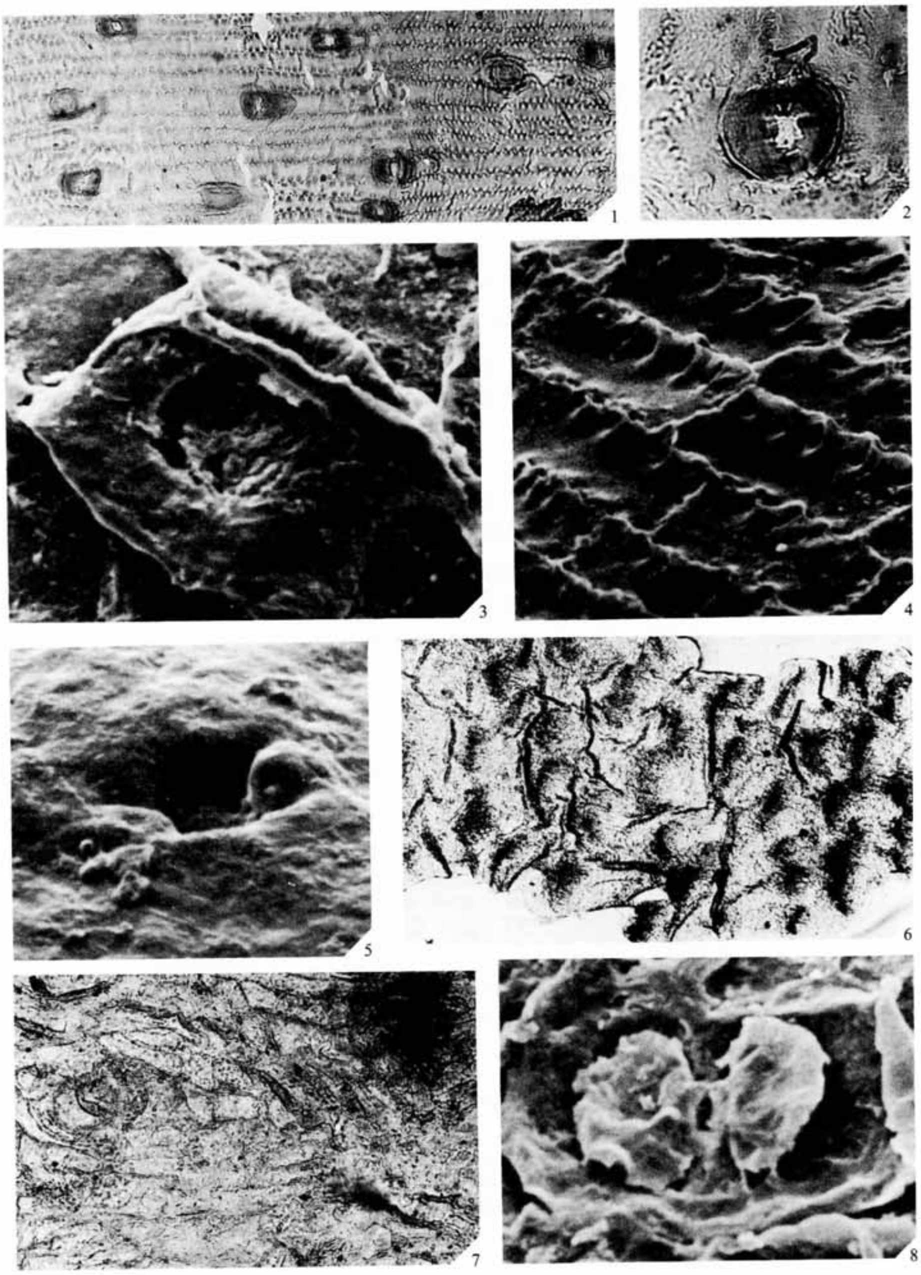
Record sample. Wealden Marls, Sample no. 3AD. From 300-mm plant debris bed complex, light grey, coarse siltstone, plant material concentrated in laminae. Ten specimens, P93: 5/1.1, 2.1, 3.1, 4.1, 1.2, 2.2; 8/2.1, 4.1, 2.2, 4.2.

Systematic position. The decussate arrangement of leaves in this taxon is reminiscent of the Cupressaceae. The genus *Cupressinocladus* was erected by Seward in 1919 for vegetative shoots showing such characters. This was slightly emended by Chaloner and Lorch (1960) and 33 CUPR agrees with the diagnosis. The several published species belonging to this genus agree in many respects with 33 CUPR but are all distinct in some features.

EXPLANATION OF PLATE 66

Figs. 1–5. 21 BENN PtB. 1, ×150, LM., surface 2, stomata; P49: 63/2.2. 2, ×500, LM., surface 2, stoma; P49: 63/2.2. 3, ×1000, SEM., surface 2, inside, intracellular, circular, cutinized bodies; B62. 4, ×500, SEM., surface 2, inside, epidermal cells; B62. 5, ×1000, SEM., surface 2, outside, stomatal aperture; B62.

Figs. 6–8. 22 BENN CyA. 6, ×20, LM., general view; P59: 12/3.1. 7, ×150, LM., stoma; P59: 12/3.1. 8, ×1000, SEM., inside, stoma; B45.



OLDHAM, 21 BENN PtB and 22 BENN CyA

CONIFERAE Incertae sedis
Cf. Genus BRACHYPHYLLUM Brongniart
34 CONIF BrA

Plate 75, figs. 1–8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 11/2.2; 31/1.1, 2.1, 1.3, 1.2, 2.2, 3.2; 32/1.1, 2.1, 2.2.

Systematic position. This taxon agrees with the diagnosis of this genus but does not agree specifically with any of the published taxa.

35 CONIF BrB

Plate 76, figs. 1–6

Record sample. Wealden Marls, Sample no. 7AD. From 25-mm band in plant debris bed complex, medium light-grey siltstone, plant material concentrated in laminae. Ten specimens, P101: 3/1.2, 2.2, 3.2; 4/4.1, 1.2; 5/2.1, 3.1, 4.1, 2.2, 3.2.

Systematic position. This is a leaf of the *Brachyphyllum* type but it does not agree with any of the published species. The combination of a frilled margin, papillate subsidiary cells, and papillate epidermal cells mark it off as a distinct new taxon.

36 CONIF BrC

Plate 77, figs. 1–7

Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 15/3.2, 4.1; 16/1.1; 17/1.1, 3.2; 18/2.1, 3.2; 20/2.2, 3.1; 21/2.2.

Systematic position. This resembles the cuticle that can be prepared from the specimens placed by Seward (1895) in *B. obesum* Heer. The preservation of the cuticle from Seward's specimens is poor, however, and will not allow an adequate comparison.

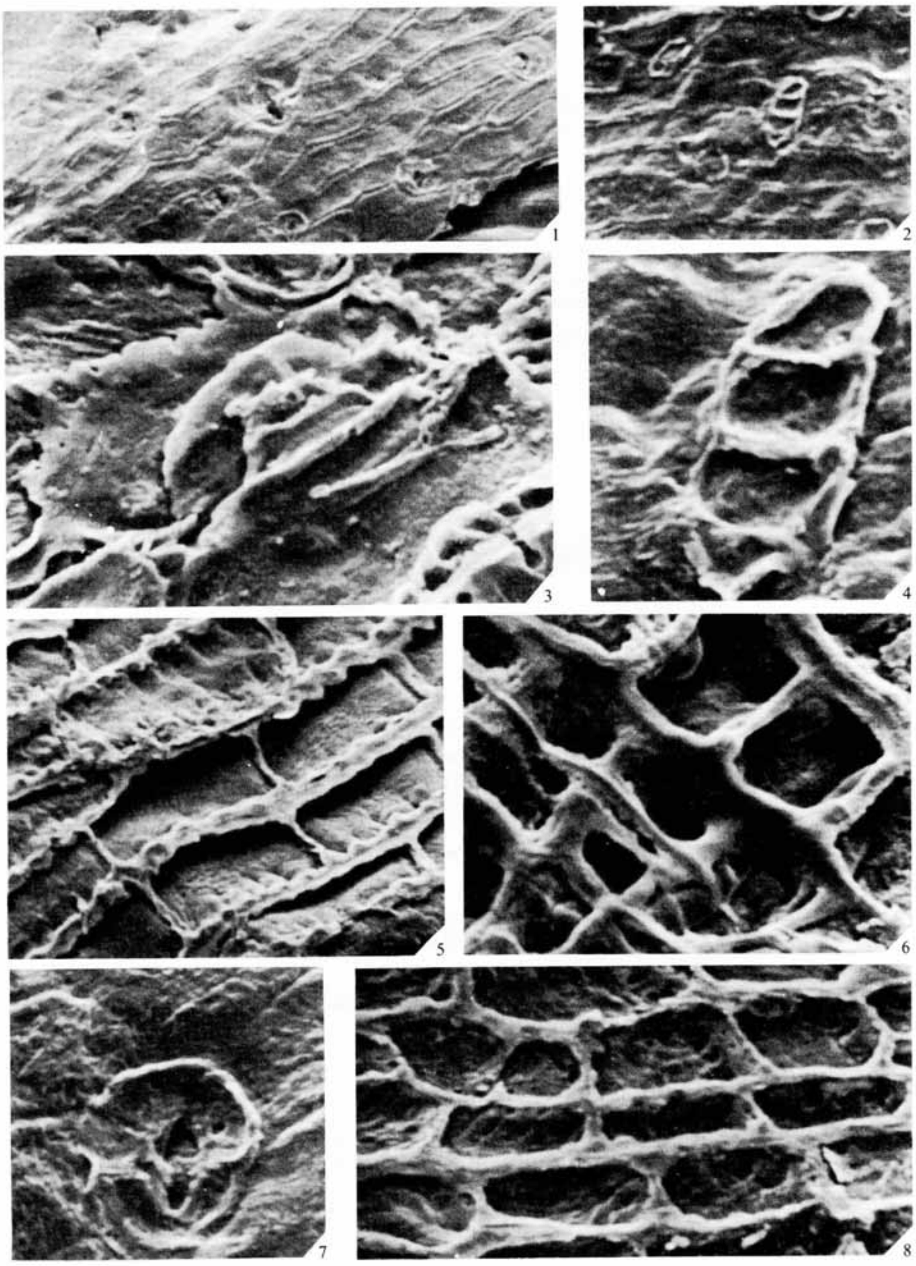
Class TAXOPSIDA
Order TAXALES
Cf. Genus TOMHARRISIA Florin
37 TAXAC ThA

Plate 78, figs. 4–8; Plate 79, fig. 1

Record sample. Wealden Marls, Sample no. 6D. From 300-mm plant debris bed complex, light-grey siltstone, plant material irregularly dispersed through the matrix. Ten specimens, P99: 2/3.1, 2.1; 5/1.2; 6/1.1, 1.2; 8/2.1; 9/1.2, 2.1; 10/2.2, 1.2.

EXPLANATION OF PLATE 67

Figs. 1–8. 23 BENN BnA. 1, ×200, SEM., outside, general view, hair bases; B60. 2, ×200, SEM., outside, general view, hair bases; B60. 3, ×1000, SEM., inside, stoma; B60. 4, ×1000, SEM., outside, hair base; B60. 5, ×500, SEM., inside, epidermal cells; B60. 6, ×1000, SEM., inside, epidermal cells and hypodermis; B60. 7, ×1000, SEM., outside, hair base; B60. 8, ×500, SEM., inside, epidermal cells; B60.



OLDHAM, 23 BENN BnA

Systematic position. This taxon could belong in either the Coniferales or Taxales in terms of its cuticle characters. It does, however, resemble several Mesozoic genera that Florin (1958) relates to the Taxales. It is closest to *Tomharrisia* but does not agree completely with any of the published members of that genus.

GYMNOSPERMAE Incertae sedis

38 GYMN GyQ

Plate 79, figs. 2–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 18/2, 3; 27/1, 2, 3; 28/1, 2; 29/1, 2, 3.

Systematic position. This taxon does not appear to resemble any Mesozoic gymnosperm in its cuticle structure.

39 GYMN GyI

Plate 79, figs. 5–8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 7/4.2; 14/3.2; 18/3.2; 33/3.2; 39/1.2.

Systematic position. This taxon does not appear to resemble any Mesozoic gymnosperm in its cuticle structure.

40 GYMN GyH

Plate 80, figs. 5–8

Record sample. Wealden Marls, Sample no. 20AD. From 300-mm plant debris bed complex, light grey, fine siltstone, plant material in fine laminae. Five specimens, P120: 1/2.1, 3.1; 6/1.1, 2.2, 3.2.

Systematic position. Little is known of the gross morphology of this taxon and the cuticle structure is unusual. It may relate to the cycadalean genus *Deltolepis* Harris but there is insufficient evidence to make a valid comparison.

41 GYMN GyD

Plate 80, figs. 1–4

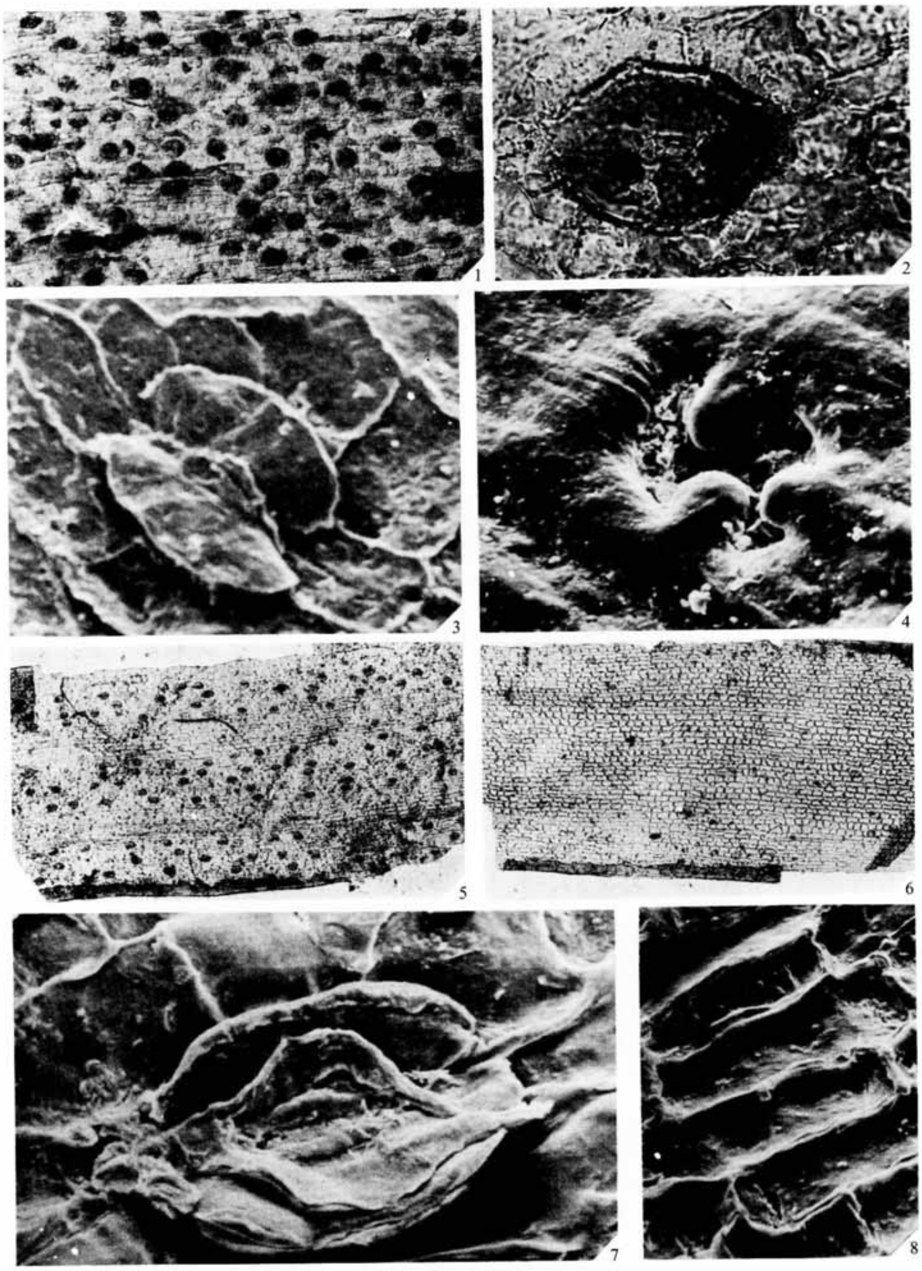
Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material in laminae. Ten specimens, P98: 6/4.2, 2.2; 13/3.1; 16/2.2, 4.2; 17/1.2, 2.2; 19/3.1; 20/2.1; 21/1.3.

Systematic position. This taxon is of uncertain affinity though it is possibly coniferalean.

EXPLANATION OF PLATE 68

Figs. 1–3. 24 GINK ToB. 1, ×50, LM., surface 2, general view; P59: 13/1.1. 2, ×500, LM., surface 2, stoma; P59: 13/1.1. 3, ×500, SEM., surface 2, inside, stoma; B44.

Figs. 4–8. 25 GINK ToA. 4, ×1000, SEM., surface 2, outside, stomatal aperture; B6. 5, ×20, LM., surface 2, general view; P49: 9/2.1. 6, ×20, LM., surface 2, general view; P49: 9/2.1. 7, ×1000, SEM., surface 2, inside, stoma; B6. 8, ×500, SEM., surface 2, inside, epidermal cells; B6.



OLDHAM, 24 GINK ToB and 25 GINK ToA

CLUSTER ANALYSIS OF DATA

A quantitative analysis of the contents of seventy-one samples from plant debris beds of the English Wealden is presented in Tables 1–3. These data were subjected to a cluster analysis following the methods of Bonham-Carter (1967). The resulting

TABLE 1. Analysis of the content of samples from the Isle of Wight succession.

	40IOW	39IOW	41IOW	42BIOW	43IOW	44IOW	47IOW	48DIOW	48CIOW	48AIOW	49AIOW	49BIOW	50EIOW	50DIOW	50CIOW	50BIOW	50AIOW
3 CYCAD	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–
4 CYCAD	3	3	–	–	–	–	3	–	3	–	–	–	3	3	3	3	3
6 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	2	2	3	2	–
8 CYCAD	–	–	–	–	–	2	–	2	2	2	–	–	2	2	2	2	2
12 CYCAD	–	–	–	–	–	2	–	–	2	2	–	–	–	–	–	–	3
13 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2	–
14 BENN	–	–	–	–	–	2	–	–	–	–	–	–	2	–	2	2	–
16 BENN	–	–	–	–	–	–	–	–	–	2	–	2	–	2	–	2	–
17 BENN	–	–	–	2	–	2	–	–	2	3	2	–	3	3	3	3	3
18 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	3	–
19 BENN	–	–	–	–	–	–	–	2	2	–	2	–	3	2	3	2	3
21 BENN	–	–	–	–	–	–	–	2	2	–	2	–	–	–	–	–	–
22 BENN	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
23 BENN	–	–	–	–	–	–	–	–	2	2	–	3	3	3	3	3	3
25 GINK	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26 GINK	–	2	–	–	–	2	–	2	2	–	2	–	–	–	–	–	3
28 GINK	2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
30 CHEIR	4	3	–	–	–	–	2	–	–	2	5	5	1	1	2	–	–
32 TAXOD	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–
36 CONIF	4	4	3	4	4	5	–	5	5	5	4	3	4	4	4	3	5
37 TAXAC	2	2	–	–	2	2	–	–	2	–	–	–	2	2	2	2	2
40 GYMN	–	–	–	2	–	2	–	–	–	–	–	–	–	–	–	–	–
41 GYMN	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–
WOOD Bl	3	3	5	4	3	3	5	3	3	3	4	2	4	4	4	4	4
WOOD Br	4	4	3	3	5	3	2	2	3	2	5	2	3	3	3	4	3
MEGASPR	1	1	1	2	2	3	–	2	2	1	1	1	2	3	3	3	2
SEEDS	3	2	1	2	2	3	2	2	2	2	2	2	3	3	3	3	2

All plant material present in the samples is scored on a five-point abundance scale. 1 = rare, 2 = occasional, 3 = frequent, 4 = abundant, 5 = very abundant.

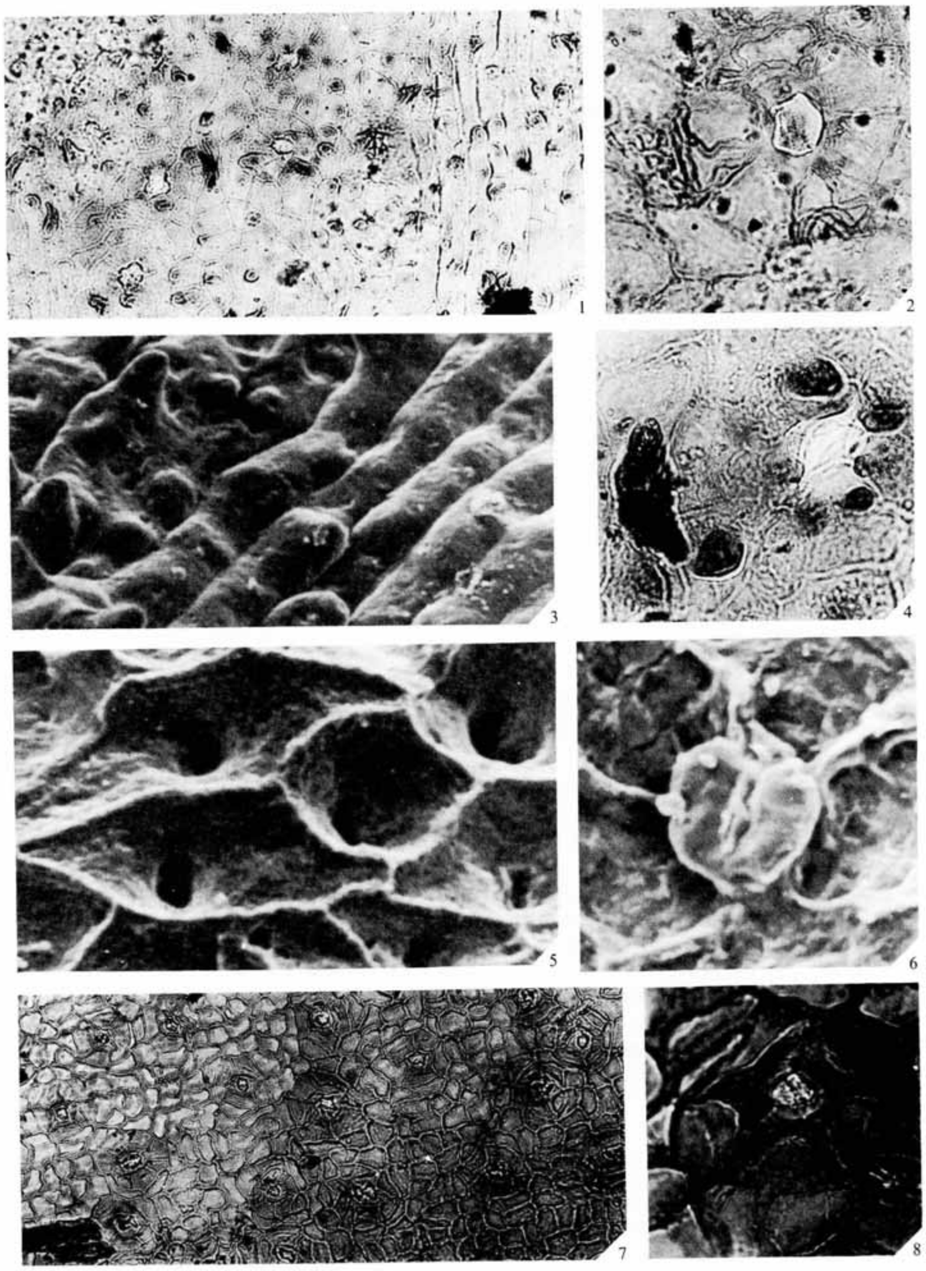
Abreviations used: WOOD Bl = Black wood, WOOD Br = Brown wood, MEGASPR = Megaspores.

Samples are arranged in ascending stratigraphic order from left to right.

EXPLANATION OF PLATE 69

Figs. 1–6. 26 GINK GiA. 1, × 150, LM., surface 2, general view; P147: 2/4.2. 2, × 500, LM., surface 1, stoma; P147: 2/4.2. 3, × 500, SEM., surface 2, outside, stomatal aperture, papillae; B66. 4, × 500, LM., surface 2, stoma; P147: 2/4.2. 5, × 1000, SEM., surface 2, inside, epidermal cells; B66. 6, × 1000, SEM., surface 2, inside, stoma; B66.

Figs. 7, 8. 29 GINK GkC. 7, × 150, LM., surface 2, general view; P49: 9/3.1. 8, × 500, LM., surface 2, stoma; P49: 9/3.1.



OLDHAM, 26 GINK GiA and 29 GINK Gkc

TABLE 2. Analysis of the content of samples from the Dorset succession. See Table 1 for key to abundance scale.

	SWANAGE BAY									WORBARROW BAY															
	8D	7AD	7BD	7DD	6D	5D	3BD	3AD	2AD	22D	20BD	20AD	18DD	18CD	18BD	18AD	17D	27DD	27CD	27BD	27AD	13D	11BD	11AD	10D
1 CAYT	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
3 CYCAD	2	2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	3	–	3	–	–	–	–	–
4 CYCAD	3	–	3	2	2	2	–	–	3	–	2	3	2	–	2	2	–	–	–	–	–	–	–	–	–
5 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
6 CYCAD	–	–	2	2	2	–	–	–	2	–	2	–	–	–	–	–	–	–	2	–	–	–	–	–	–
8 CYCAD	–	–	–	–	2	2	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2	1
9 CYCAD	2	2	2	2	–	2	–	–	–	–	–	2	2	–	3	2	–	–	–	–	–	–	2	–	3
12 CYCAD	2	–	4	3	–	3	–	–	–	–	3	2	3	2	–	–	–	–	–	–	–	–	2	3	–
13 BENN	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16 BENN	2	–	–	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17 BENN	3	–	3	–	2	–	–	–	3	–	3	3	–	–	–	–	–	–	2	–	–	2	–	–	3
18 BENN	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
19 BENN	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2
21 BENN	2	–	–	2	–	–	–	–	2	–	–	2	2	–	2	–	–	–	2	2	2	–	–	–	2
22 BENN	2	–	2	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
23 BENN	–	–	–	–	–	2	–	2	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	3
25 GINK	2	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26 GINK	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
27 GINK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
28 GINK	–	–	–	2	–	–	–	–	–	–	3	3	–	–	2	2	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	2	2	2	–	–	–	–	–	–	–	–	2	–	–	–	–	2	–	3	2	3	2
30 CHEIR	4	4	4	4	4	2	–	2	–	4	3	4	5	5	5	5	5	5	5	5	5	5	5	5	–
31 TAXOD	–	–	–	–	–	–	–	–	–	–	4	2	2	–	–	–	–	–	–	–	–	–	–	–	–
33 CUPR	–	–	–	–	–	4	5	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
34 CONIF	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35 CONIF	3	4	3	2	3	–	–	–	–	–	–	2	–	–	–	–	2	–	1	1	1	–	3	–	–
36 CONIF	4	2	2	3	–	4	2	1	3	–	3	3	2	–	–	–	2	–	–	–	–	2	3	2	4
37 TAXAC	2	2	2	2	3	2	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
40 GYMN	–	–	–	–	–	2	–	–	–	–	2	3	2	–	2	–	–	–	–	–	–	–	–	–	–
41 GYMN	2	–	–	–	2	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
WOOD Bl	1	1	2	1	2	2	–	–	4	2	2	2	3	2	1	2	3	3	3	3	3	2	2	2	4
WOOD Br	3	4	3	3	4	3	3	3	2	5	3	3	4	4	4	4	4	4	3	3	3	4	4	3	2
MEGASPR	2	–	2	2	2	–	–	–	3	2	3	4	3	2	2	2	–	–	–	–	–	2	2	2	1
SEEDS	1	1	1	2	2	2	–	1	2	–	2	2	2	2	2	2	1	–	2	–	2	2	2	2	2

dendrograms (deposited with the British Library) were examined for meaningful associations. No single factor was found to explain all the groups but stratigraphic proximity, geographical location, and the cuticle species richness of the samples were all important.

Comparison of the samples on the basis of their total cuticle assemblage did not bring about an ordering of them in a precise stratigraphic fashion. This is best explained by the fact that so many of the samples contained so few species they

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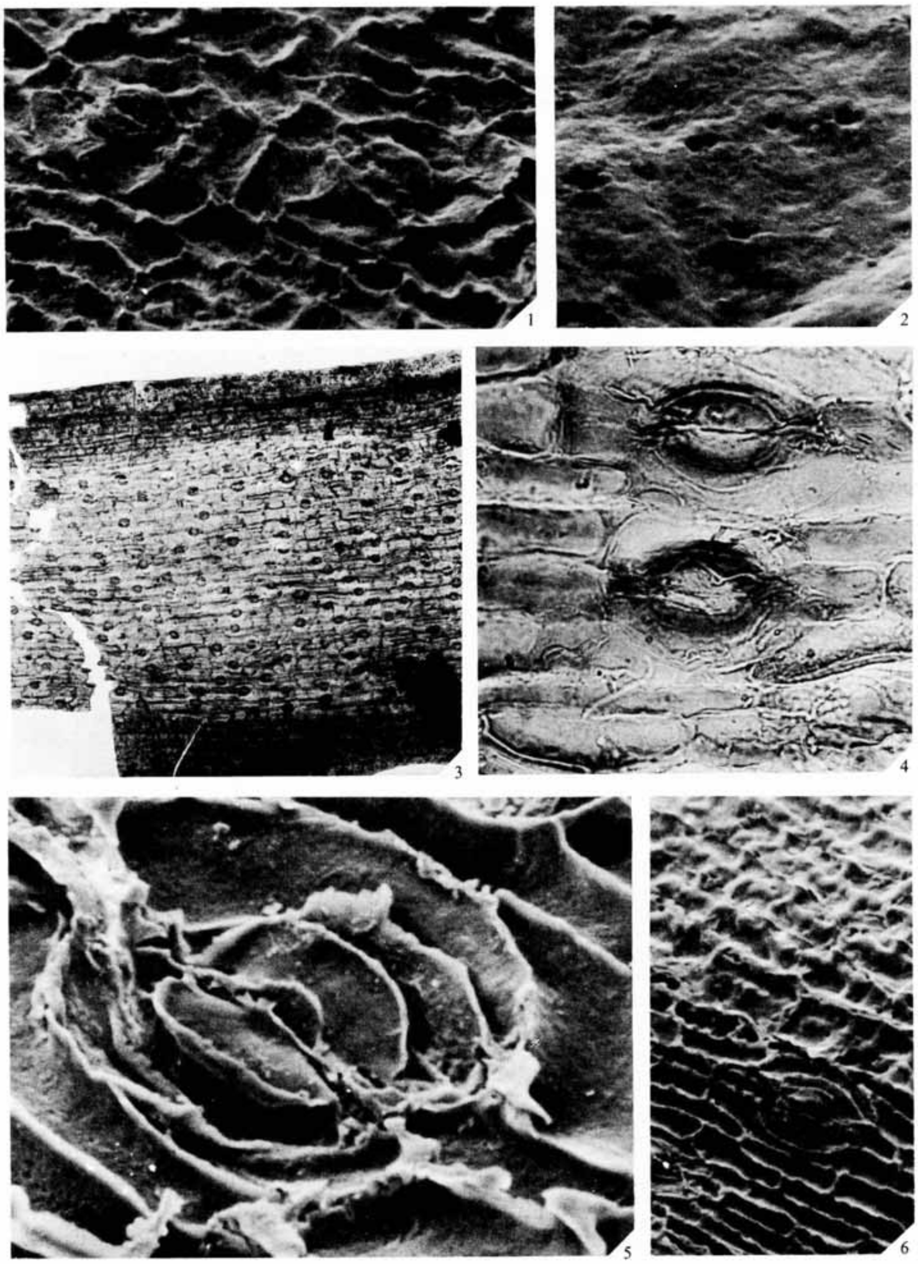
EXPLANATION OF PLATE 70

Figs. 1, 2. 29 GINK GkC. 1, ×500, SEM., surface 2, inside, stomata; B40. 2, ×200, SEM., surface 2, outside, stomatal apertures; B40.

Figs. 3–6. 27 GINK GkA. 3, ×50, LM., surface 2, general view; P49: 10/2.1. 4, ×500, LM., surface 2, stomata; P49: 10/2.1. 5, ×1000, SEM., surface 2, inside, stoma; B39. 6, ×200, SEM., surface 2, inside, groove and non stomatal area; B39.



OLDHAM, 29 GINK Gkc and 27 GINK GkA

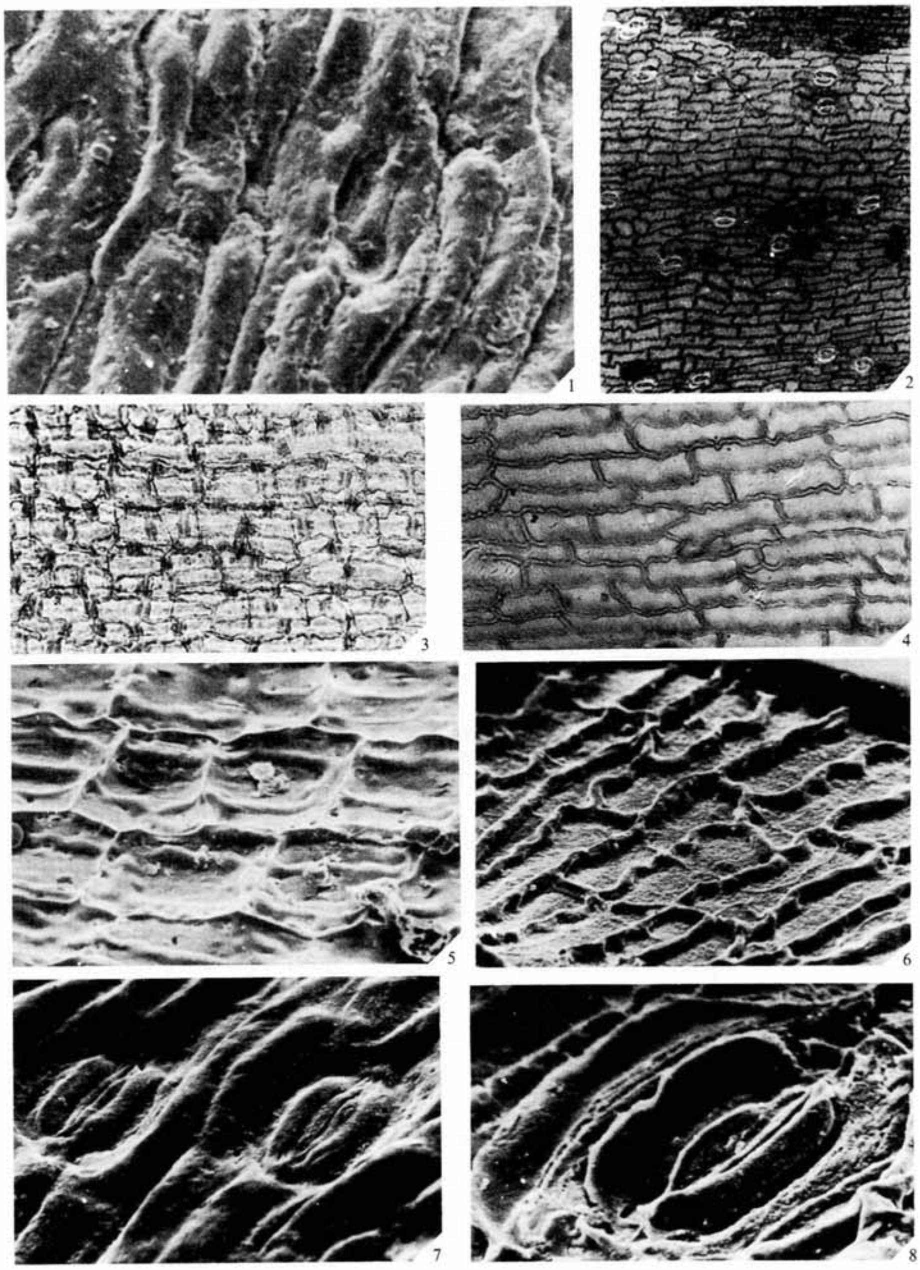
TABLE 3. Analysis of the content of samples from the South-eastern succession. See Table 1 for key to abundance scale.

	53H	21BH	19H	22H	18AH	25H	26H	27H	28H	30H	32H	33H	23H	13H	41H	34AH	44H	51BH	15AH	7AH	14H	47H	CUC931	54H	CUC635	CUC634	CUC443	CUC434	CUC431
1 CYAT	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	4	1	–	–	–	–	–	–	–	–
2 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–
3 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	2	3	–	–	–	–	–	–	–	–	–
4 CYCAD	3	–	–	3	4	–	2	–	–	–	–	–	–	4	3	–	–	3	3	–	2	2	–	3	–	–	–	2	–
6 CYCAD	–	–	2	2	3	–	–	–	–	–	2	2	–	3	2	–	2	–	2	–	–	–	–	–	2	2	–	–	–
7 CYCAD	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8 CYCAD	–	–	–	2	–	–	–	–	–	–	2	–	–	2	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
10 CYCAD	–	–	–	–	2	–	–	–	–	–	–	–	–	2	–	–	–	3	–	–	–	–	–	–	–	–	–	2	2
11 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	2	2
13 BENN	–	–	–	–	3	–	–	–	–	–	–	–	–	3	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
14 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2	4	–	–	–	–	–	–	–	–	–	–	–	–	–
15 BENN	–	–	–	2	3	–	–	2	–	–	–	–	–	4	4	–	–	3	–	–	–	–	–	–	–	–	–	–	–
16 BENN	–	–	–	2	3	–	–	–	–	–	2	–	2	3	3	–	–	3	2	–	–	–	–	–	–	2	–	–	–
17 BENN	–	–	–	3	4	–	–	–	–	–	2	–	2	3	3	–	–	3	–	–	–	2	–	–	3	3	–	3	3
18 BENN	–	2	–	3	3	–	–	–	–	2	–	–	–	3	3	–	–	–	–	–	2	–	–	2	–	–	–	–	–
19 BENN	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20 BENN	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
21 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	2	–	–	–	3	2	2	–	–	–	–	–	–	–	–	2
22 BENN	–	–	–	3	–	–	–	–	–	–	–	–	3	3	3	–	–	3	–	–	–	–	–	–	–	–	–	–	–
23 BENN	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
24 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25 GINK	–	–	–	–	3	–	–	–	–	–	–	3	–	3	2	–	–	3	–	–	–	–	2	–	–	–	–	–	–
27 GINK	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	4	–	–	–	–	–	–	–	–	–	–	2
28 GINK	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–
30 CHEIR	2	2	2	–	2	–	–	–	–	2	2	–	2	2	–	–	–	5	–	–	3	–	–	–	4	4	2	3	4
31 TAXOD	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
32 TAXOD	–	–	–	2	–	–	–	2	–	–	–	–	–	–	–	–	5	–	–	–	–	–	2	3	–	–	–	–	–
34 CONIF	4	4	4	4	4	4	3	–	4	3	3	–	3	3	3	2	2	–	–	–	3	–	–	–	2	–	–	–	–
35 CONIF	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
36 CONIF	3	3	4	4	3	4	3	4	4	4	4	3	–	4	2	4	2	4	3	3	3	3	–	–	4	3	4	4	4
38 GYMN	–	–	–	2	2	–	–	–	–	–	–	–	–	3	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
39 GYMN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40 GYMN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
WOOD Bl	1	4	3	3	3	4	3	4	3	4	3	2	1	2	2	3	4	2	3	3	2	5	4	5	3	3	3	4	3
WOOD Br	2	3	3	2	3	3	4	3	3	4	3	4	1	2	–	–	–	1	4	3	–	2	2	3	2	3	2	3	3
MEGASPR	–	3	1	2	–	1	3	1	1	2	2	2	1	1	–	1	1	–	4	3	5	4	3	4	2	3	4	3	3
SEEDS	2	3	2	2	1	2	2	1	2	2	2	2	1	2	2	2	2	1	2	3	2	1	1	2	2	2	2	2	2

EXPLANATION OF PLATE 71

Figs. 1, 3, and 5. 27 GINK GkA. 1, × 500, SEM., surface 2, outside, ridges and stomatal apertures; B39. 3, × 150, LM., surface 1, epidermal cells and hypodermis; P49: 10/2.1. 5, × 500, SEM., surface 1, inside, epidermal cells and hypodermis; B39.

Figs. 2, 4, 6–8. 28 GINK GkB. 2, × 50, LM., surface 2, general view; P121: 2/1.1. 4, × 150, LM., surface 1, epidermal cells; P121: 2/1.1. 6, × 500, SEM., surface 2, inside, epidermal cells; B25. 7, × 500, SEM., surface 2, outside, stomatal apertures; B25. 8, × 1000, SEM., inside, stoma; B25.



OLDHAM, 27 GINK GkA and 28 GINK GkB

masked any trend. Indeed, the lack of sites from which good cuticular material can be obtained in the English Wealden is a serious drawback to any quantitative study.

This aside, certain significant groupings were shown by the clustering procedure:

1. The samples from the Isle of Wight and the very top of the Dorset Wealden succession clustered together. (Samples 50AIOW, 50BIOW, 50CIOW, 50DIOW, 50EIOW, 48AIOW, 48CIOW, 48DIOW, 44AIOW, 2AD, 5D, 10D.) This is as expected considering the close stratigraphic proximity of the samples and their isolation from most of the rest of the samples that come from the lower part of the succession. A few samples that are close to this group stratigraphically did not cluster with them because of their lack of species diversity.
2. The samples from the lower to middle part of the Dorset succession clustered together in many cases. (Samples 7DD, 7BD, 8D, 18BD, 18DD, 20AD, 20BD.) The absence of samples from the south-eastern area from this group is perhaps best explained in terms of geographical differences in the flora and in the nature of the plant beds.
3. Another group of samples from the Dorset succession, but more wide-ranging than the previous group. (Samples 7AD, 11AD, 11BD, 13D, 27AD, 27BD, 27CD, 27DD, 17D, 18AD, 18BD, 18CD, 18DD, 22D.) This group encompasses the species-poor samples and those very rich in 30 CHEIR.
4. A group of species-rich samples from the Fairlight Clay of Sussex. (Samples 51BH, 41H, 13H, 18AH, 22H.) Several cuticle species are exclusive to this group.

It became clear from the study that although samples that were closely related stratigraphically tended to cluster together and show high similarity coefficients this was not always the case. The coefficient of similarity between two samples only separated by a few metres of sediment can be very low indeed. There is also a tendency for species to be of similar abundance in samples closely related stratigraphically and if a species is absent from one such sample it is unlikely to be more than occasional in another.

The variation that occurred within a single band of a plant debris bed complex was determined by collecting samples at intervals along the exposed length of two bands. It was difficult to follow any band for more than four metres and more usually they petered out or merged with other bands within a metre. The two bands selected were from the south-eastern area and neither was used in the main analysis. An analysis of these two bands is presented in Table 4. Similarity coefficients were calculated for the samples from each band. Most samples showed high coefficients, but in some cases the coefficients were so low the particular samples could have been

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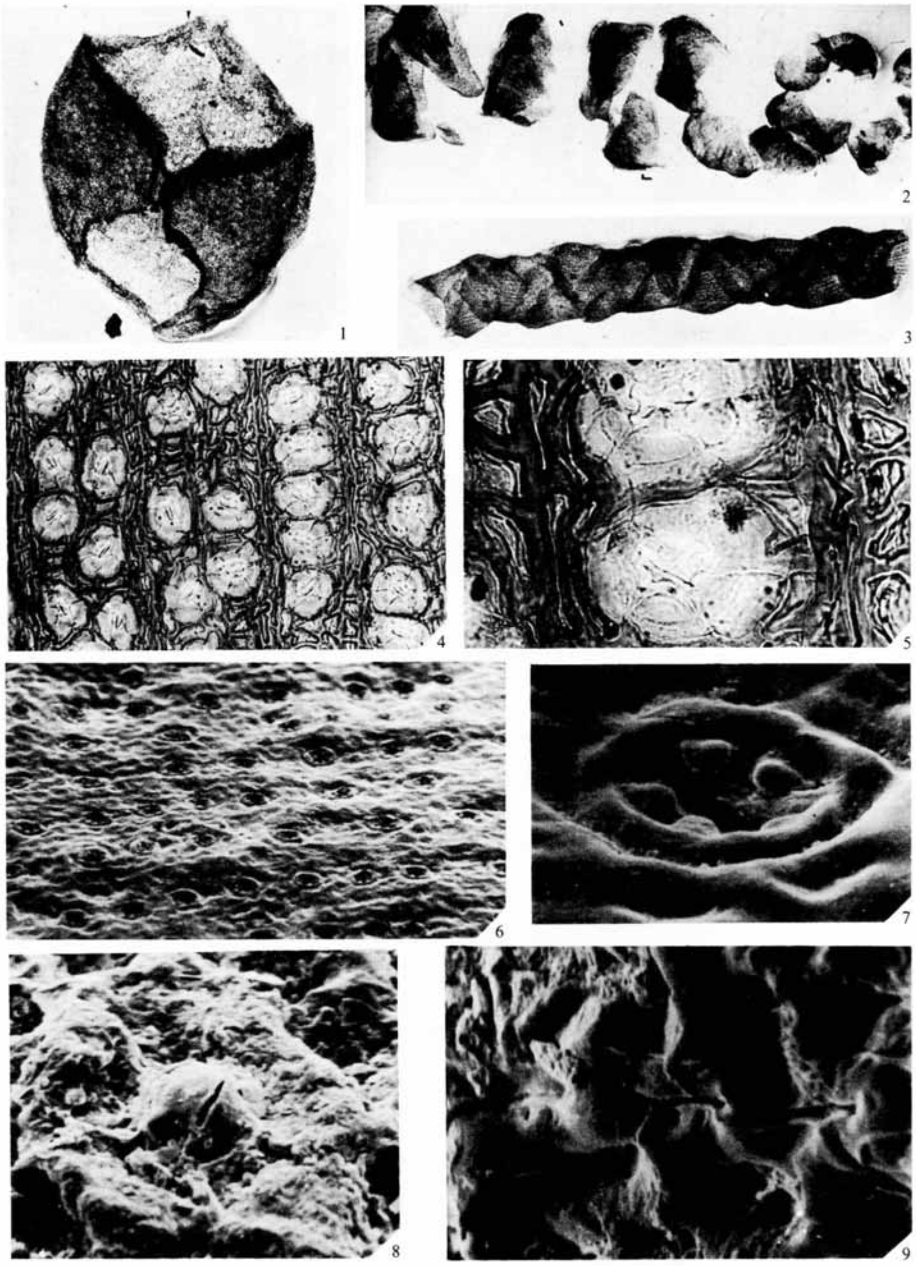
EXPLANATION OF PLATE 72

Figs. 1, 4–9. 30 CHEIR MaA. 1, ×20, LM., leaf; P49: 3/2.1. 4, ×150, LM., abaxial surface, stomata; P49: 6/1.1. 5, ×500, LM., abaxial surface, stomata; P49: 6/1.1. 6, ×100, SEM., abaxial surface, outside, stomatal apertures; B7. 7, ×1000, SEM., abaxial surface, outside, stomatal aperture; B7. 8, ×1000, SEM., abaxial surface, inside, stoma; B12. 9, ×1000, SEM., abaxial surface, inside, hypodermis; B12.

Figs. 2, 3. Cf. 30 CHEIR MaA. 2, ×5, LM., shoot, 'exploded'; P110: 2/1. 3, ×5, LM., shoot; P130: 7/1.1.



OLDHAM, 30 CHEIR MaA and cf. CHEIR MaA

TABLE 4. Analysis of the content of two selected bands.

	BAND 1								BAND 2						
	I	H	G	F	D	C	B	A	G	F	E	D	C	B	A
2 CYCAD	–	–	–	–	–	–	–	–	3	3	3	3	3	3	3
4 CYCAD	2	–	–	–	–	–	–	–	–	–	–	–	–	1	–
6 CYCAD	2	–	–	–	–	–	–	–	–	–	–	–	–	1	1
8 CYCAD	3	2	–	2	–	2	2	–	2	2	–	–	–	2	2
10 CYCAD	–	–	–	–	–	–	–	–	2	2	2	2	3	3	3
11 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
13 BENN	–	2	2	2	2	2	2	2	–	–	–	–	–	–	2
15 BENN	2	4	3	3	3	3	3	3	–	2	1	–	3	2	3
16 BENN	2	2	3	2	2	2	2	2	2	2	2	2	3	3	3
17 BENN	–	–	2	–	–	–	2	–	2	3	2	2	3	3	3
18 BENN	3	3	3	2	3	3	3	3	–	–	–	–	–	–	–
21 BENN	2	2	–	–	2	–	2	2	–	–	–	–	–	–	2
22 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
25 GINK	2	2	3	3	2	3	3	2	2	3	2	2	3	3	3
26 GINK	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–
27 GINK	–	2	2	2	1	2	1	–	3	3	3	3	3	3	3
29 GINK	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
30 CHEIR	2	3	2	2	1	2	3	3	5	5	5	5	5	5	5
34 CONIF	2	2	3	3	2	2	2	3	2	2	2	2	2	3	3
35 CONIF	–	–	–	–	–	–	–	–	3	3	2	3	3	2	2
36 CONIF	4	4	3	3	3	3	3	3	3	3	3	4	4	4	3
38 GYMN	–	–	3	3	3	–	–	–	2	2	2	2	2	3	3
40 GYMN	–	–	2	–	–	–	–	2	–	–	–	–	2	–	2
WOOD Bl	3	3	5	5	2	2	2	2	3	4	3	3	2	2	2
WOOD Br	3	3	3	3	2	2	2	3	4	5	4	4	3	3	3
MEGASPR	2	2	2	2	2	2	2	2	2	2	2	2	–	–	1
SEEDS	–	1	2	1	2	2	2	2	2	2	2	2	2	2	2

Samples I–A from Band 1 collected at 0·3-m intervals along the length of the band. Samples G–A from Band 2 collected at 0·6-m intervals along the length of the band. See Table 1 for key to abundance scale.

suspected of being widely separated in both space and time. The range of abundance of the species present was not great within a single band. If a species was absent from one sample it was only rarely more than occasional in the other samples.

ASSOCIATION ANALYSIS

The association of each taxon with every other was calculated using the Chi square value for each pair. A probability of 1% or less was considered significant and of

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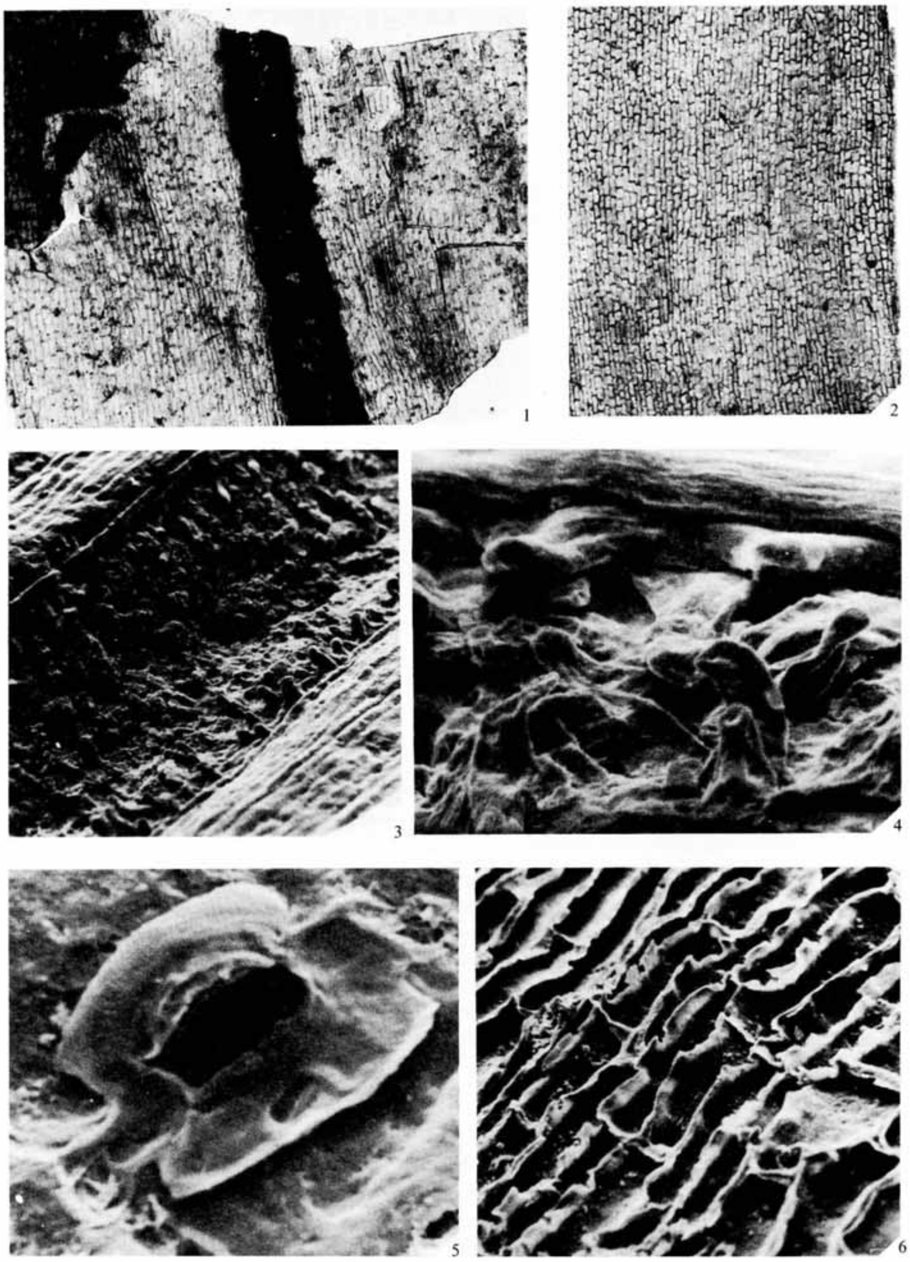
EXPLANATION OF PLATE 73

Figs. 1–6. 31 TAXOD ScA. 1, ×50, LM., surface 2, general view; P49: 40/1.1. 2, ×50, LM., surface 1, general view; P49: 40/1.1. 3, ×200, SEM., surface 2, outside, groove; B24. 4, ×1000, SEM., surface 2, outside, groove; B24. 5, ×1000, SEM., surface 2, inside, stoma; B64. 6, ×500, SEM., surface 2, inside, epidermal cells; B64.



OLDHAM, 31 TAXOD ScA

TABLE 5. Taxa showing positive associations at or below the 1% probability level.

	40 GYMN	39 GYMN	38 GYMN	37 TAXAC	35 CONIF	32 TAXOD	31 TAXOD	29 GINK	28 GINK	27 GINK	26 GINK	25 GINK	24 GINK	23 BENN	22 BENN	21 BENN	19 BENN	18 BENN	17 BENN	16 BENN	15 BENN	14 BENN	13 BENN	11 CYCAD	10 CYCAD	9 CYCAD
1 CAYT	–	3	2	–	–	–	3	–	–	2	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
2 CYCAD	–	–	3	–	–	–	–	–	–	3	–	3	–	–	–	–	–	–	–	–	–	–	2	3	3	–
4 CYCAD	–	–	–	1	–	–	2	–	–	–	–	1	–	–	–	3	2	1	2	–	–	–	2	–	–	–
5 CYCAD	2	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
6 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	2	–	3	–	3	3	–	–	–
7 CYCAD	–	–	3	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	3	2	2	–	3	–
8 CYCAD	–	–	–	–	–	–	–	–	–	2	2	–	–	3	–	–	3	–	3	–	–	–	2	–	–	–
9 CYCAD	2	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
10 CYCAD	–	–	3	–	–	–	3	–	–	3	–	2	3	–	–	–	–	–	–	–	3	–	3	3		
11 CYCAD	–	–	3	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–			
12 CYCAD	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
13 BENN	–	2	3	–	–	–	3	–	–	3	–	3	3	–	–	–	–	3	–	3	3	2				
14 BENN	–	2	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–					
15 BENN	–	–	–	–	–	1	3	–	–	–	–	3	3	–	3	3	–	2	–	3						
16 BENN	–	–	–	–	–	–	–	–	–	–	–	1	3	–	3	–	–	2	3							
17 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–								
18 BENN	–	–	1	–	–	–	–	–	–	–	–	–	3	–	2	–	–									
19 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–										
21 BENN	–	–	2	–	1	–	3	2	–	2	–	–	–	–	1											
22 BENN	–	–	3	–	–	–	–	–	–	2	–	2	1	–												
23 BENN	–	–	–	1	–	–	–	–	–	–	–	–	–													
24 GINK	–	3	3	–	–	–	3	–	–	3	–	3														
25 GINK	–	3	3	–	–	–	3	–	–	3	–															
26 GINK	–	–	–	–	–	–	3	–	–	–																
27 GINK	–	3	3	–	–	–	–	–	–																	
29 GINK	–	–	–	–	2	–	–	–																		
30 CHEIR	–	–	–	–	2	–	–																			
31 TAXOD	2	3	–	–	–	–																				
34 CONIF	–	–	2	–	–																					

1 = 1·0% level
2 = 0·5% level
3 = 0·1% level

the 819 possible associations only 112 satisfied this requirement. These are shown in Table 5.

The following picture emerges:

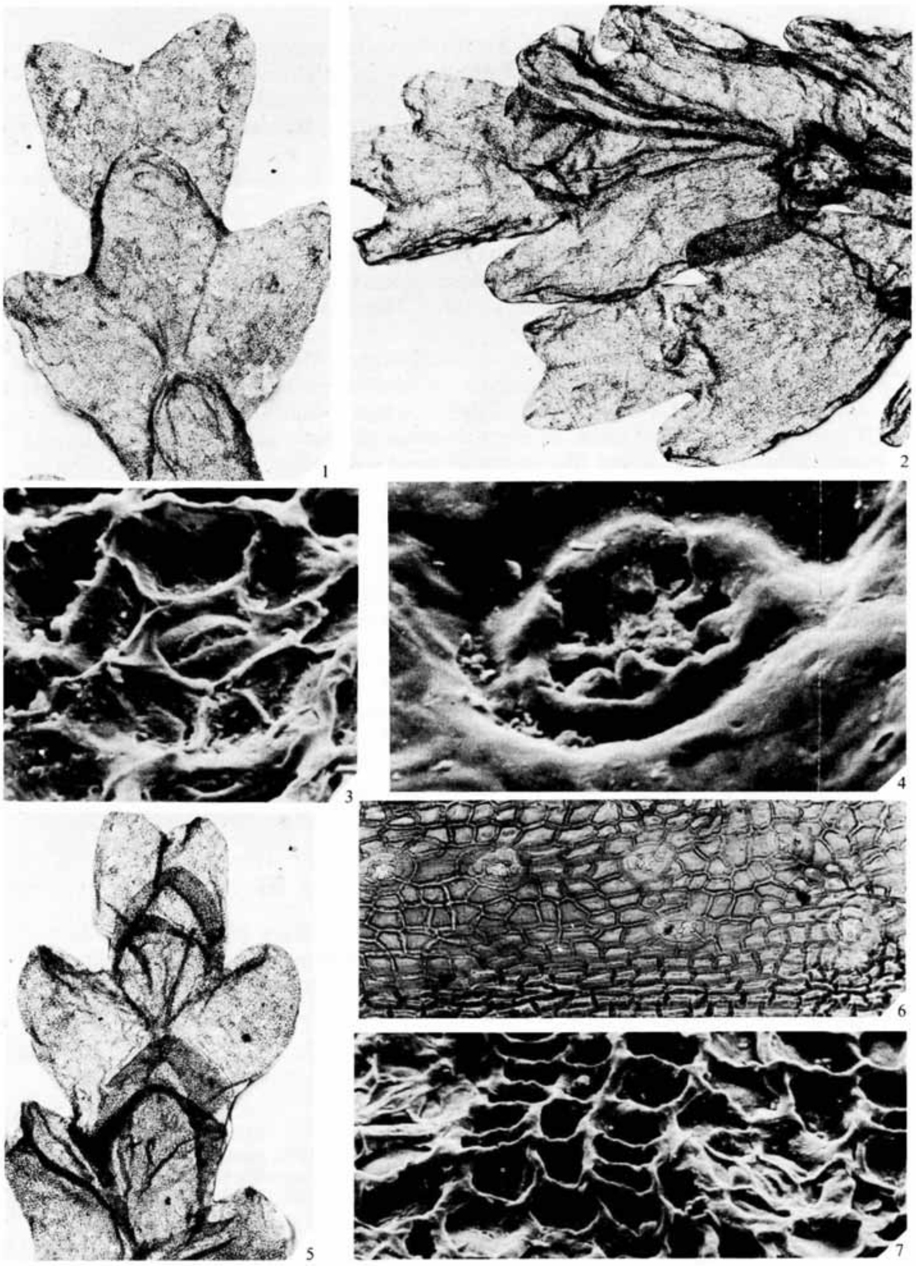
1. Those taxa that are not significantly associated with any other. This includes 3 CYCAD, 20 BENN, 33 CUPR, and 41 GYMN.

2. Those that are significantly associated with other taxa but do not form part of any mutual association group of three or more taxa. This includes 12 CYCAD, 26 GINK, 30 CHEIR, 32 TAXOD, 34 CONIF, and 37 TAXAC.

3. Those taxa that form mutual association groups of three or more taxa. There are nine of such groups, some probably representing real associations in nature, others not so.

EXPLANATION OF PLATE 74

Figs. 1–7. 33 CUPR CuA. 1, ×20, LM., shoot; P93: 3/4.2. 2, ×20, LM., shoot; P93: 3/3.2. 3, ×500, SEM., abaxial surface, inside, stoma; B21. 4, ×1250, SEM., abaxial surface, outside, stomatal aperture; B21. 5, ×20, LM., shoot; P93: 3/3.1. 6, ×150, LM., abaxial surface, stomata; P93: 5/2.1. 7, ×500, SEM., abaxial surface, inside, stoma; B21.



OLDHAM, 33 CUPR CuA

Group A. 8 CYCAD, 19 BENN, and 23 BENN. These three taxa are all found in moderately species-rich samples especially from the Isle of Wight.

Group B. 1 CAYT, 27 GINK, 31 TAXOD, and 39 GYMN. Also often associated are 25 GINK and 38 GYMN. This is unlikely to be of significance as several samples rich in 1 CAYT do not fit in here.

Group C. 21 BENN, 29 GINK, and 35 GYMN. Again a group that is not likely to be of significance.

Group D. 9 CYCAD, 28 GINK, and 40 GYMN. Also often associated are 5 CYCAD and 31 TAXOD. This may well reflect the restriction of the taxa to the lower strata of the Dorset succession rather than any close association in nature.

Group E. 4 CYCAD, 21 BENN, and 31 TAXOD. This group is of doubtful significance as two of the taxa are wide-ranging.

Group F. 7 CYCAD, 13 BENN, 14 BENN, and 24 GINK. Also 39 GYMN is often associated with this group. This is a group from the species-rich beds of the Fairlight Clay.

Group G. 16 BENN, 17 BENN, and 22 BENN. A bennettitalean group.

Group H. 6 CYCAD, 13 BENN, 15 BENN, 16 BENN, 18 BENN, and 22 BENN. The largest bennettitalean group which like group G may well reflect a close association in nature.

Group I. 10 CYCAD, 13 BENN, 15 BENN, 24 GINK, 25 GINK, 27 GINK, and 38 GYMN. Also often associated are 2 CYCAD, 7 CYCAD, 11 CYCAD, 21 BENN, 22 BENN, 31 TAXOD, and 39 GYMN. This is a group of taxa from the Fairlight Clay of Sussex, many of the species being confined to this area. It may reflect a close association in nature or may simply reflect the nature of the beds involved.

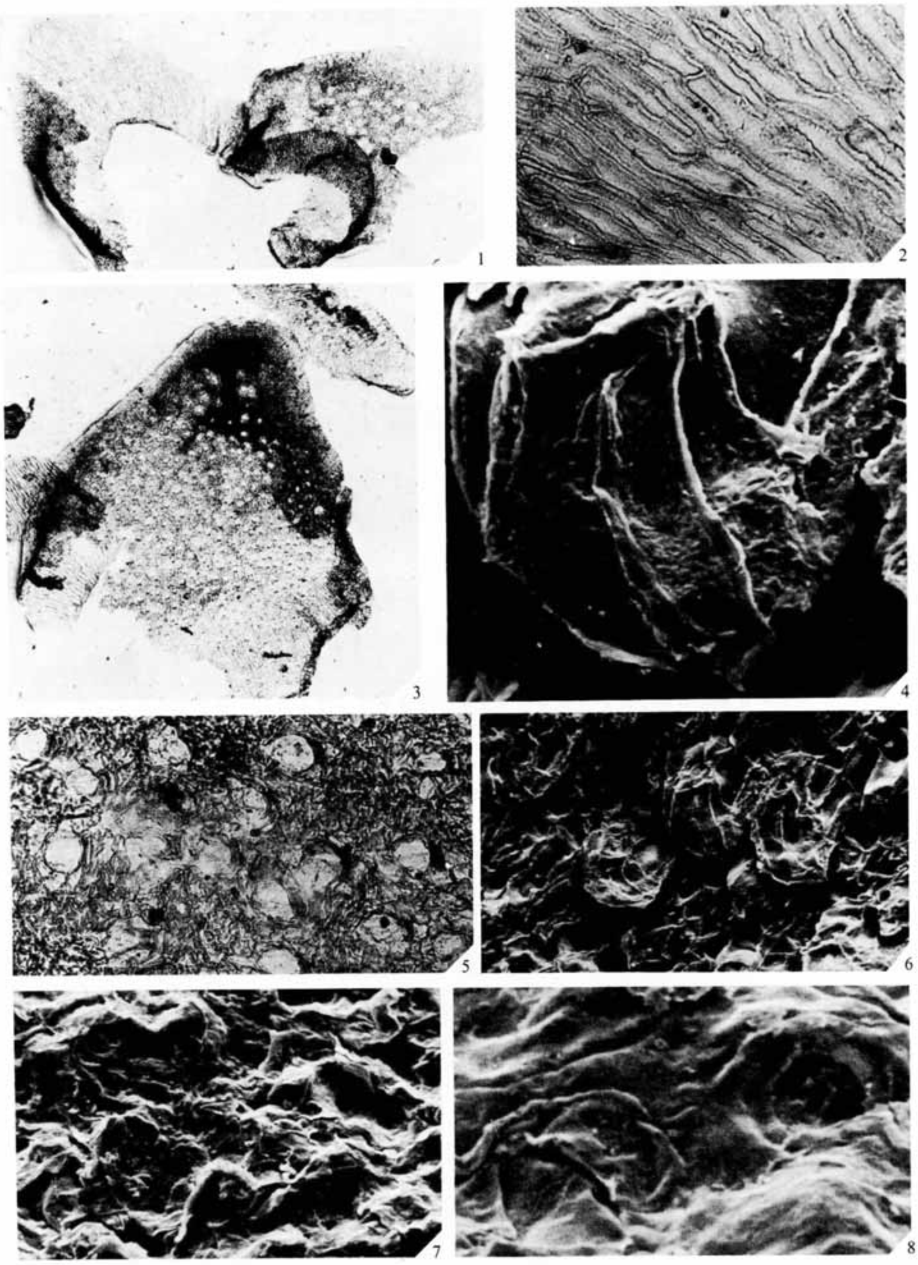
The association of other types of plant material with the samples was also examined. Seeds and brown wood showed no significant association with any factor. Black wood (*sensu* Batten 1973*a*) tended to be more abundant in the species-poor samples and especially those with poorly preserved cuticle remains. Megaspores were more abundant in those samples where the cuticle matter was of small bulk and of low species diversity. If these megaspores are from aquatic plants with correspondingly poorly cutinized parts such a result is to be expected.

LOCALITY FREQUENCY AND ABUNDANCE OF THE TAXA

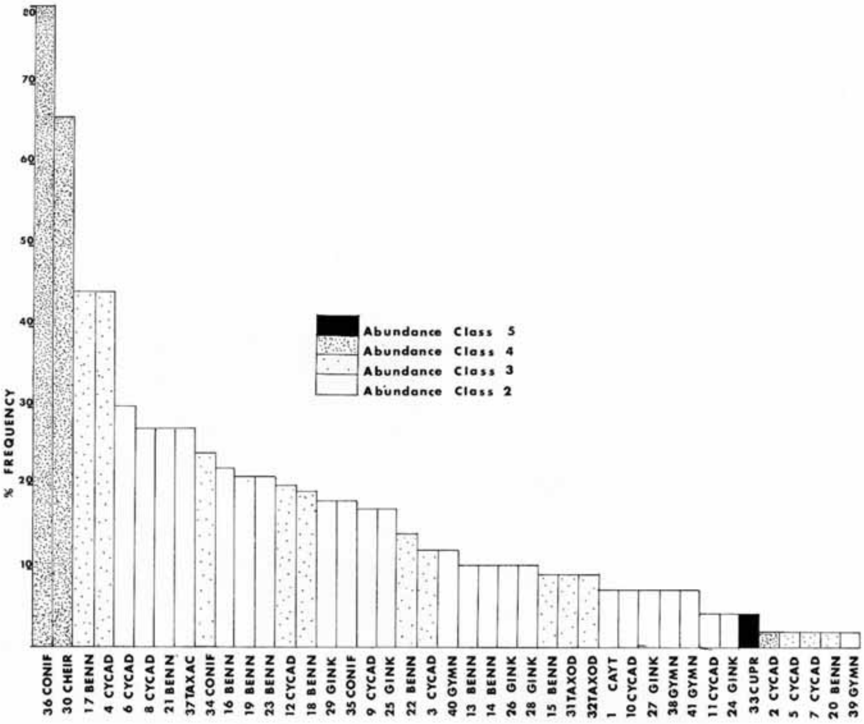
The importance of the various taxa within the context of the plant debris beds can be considered in terms of presence or absence, Couper's (1958, p. 88) locality frequency, or in terms of relative abundance within each sample. These values are displayed in text-fig. 2.

EXPLANATION OF PLATE 75

Figs. 1–8. 34 CONIF BrA. 1, ×20, LM., leaf; P59: 31/1.2. 2, ×150, LM., adaxial surface; P59: 31/2.1. 3, ×20, LM., leaf; P59: 31/2.1. 4, ×1000, SEM., abaxial surface, inside, stoma; B15. 5, ×150, LM., abaxial surface, stomata; P59: 31/2.1. 6, ×200, SEM., abaxial surface, inside, stomata; B15. 7, ×500, SEM., abaxial surface, outside, general view; B65. 8, ×1000, SEM., abaxial surface, outside, stomatal apertures; B65.



OLDHAM, 34 CONIF BrA



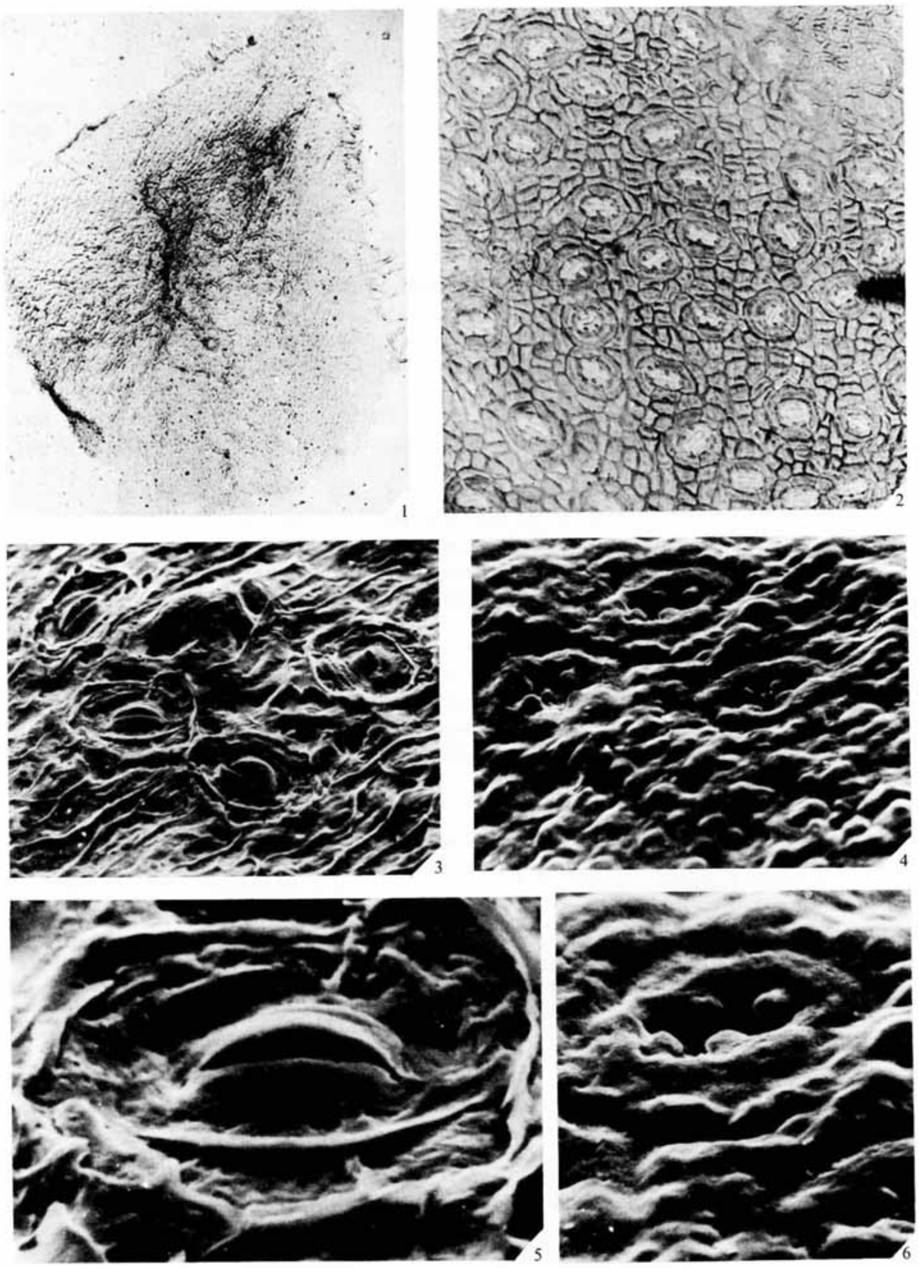
TEXT-FIG. 2. Histogram to show the locality frequency and abundance of the plant taxa.

Only 10% of the taxa have a locality frequency of greater than 30%. 30 CHEIR and 36 CONIF stand out as the two most frequent taxa, followed by 17 BENN and 4 CYCAD.

In terms of relative abundance within each sample, most taxa are only occasional. The two most frequent taxa in terms of locality frequency are also the most abundant taxa in terms of quantity of preserved material. Others, that are of low locality frequency are sometimes abundant when they do occur, for example, 33 CUPR.

EXPLANATION OF PLATE 76

Figs. 1–6. 35 CONIF BrB. 1, ×50, LM., leaf; P107: 5/3.2. 2, ×150, LM., abaxial surface, stomata; P107: 5/3.1. 3, ×500, SEM., abaxial surface, inside, stomata; B20. 4, ×500, SEM., abaxial surface, outside, stomatal apertures; B20. 5, ×2000, SEM., abaxial surface, inside, stoma; B20. 6, ×1000, SEM., abaxial surface, outside, stomatal aperture; B20.



OLDHAM, 35 CONIF BrB

PALYNOLOGICAL DATA

Thirty of the seventy-one samples were examined for their palynological content. The results are presented in Table 6. These data were examined to see what they revealed regarding the plant debris beds, and also to see how well they agreed with Batten's (1973*a*) assemblage types for the English Wealden, see Table 7.

Samples varied between those with only twelve genera represented to those with thirty. All of Batten's diversity classes were therefore encountered. The distribution being: small diversity 7%, average diversity 30%, and large diversity 63%. There was no marked relationship between diversity of cuticle taxa and diversity of spore genera.

Only one sample showed poorly preserved miospores but this did not show any relation to the preservation of the cuticle remains. Those with good miospore preservation also show high spore diversity and the cuticle remains of such samples are also usually well preserved. This follows Batten's (1973*a*) findings but it does not follow that if a sample contains well-preserved plant remains the miospores will be well preserved.

The picture of the brown wood, black wood, and cuticle content of the palynological preparations reflects the picture obtained from the cuticle preparations.

The distribution of *Classopollis* is of particular interest considering its probable relationship to 30 CHEIR, one of the most frequent and abundant cuticle species. *Classopollis* is present in all but two samples and frequent in nine. In all samples where 30 CHEIR is very abundant and the miospore content has been analysed *Classopollis* is frequent. The converse is true in nearly all cases.

It can be concluded that the miospore content of a sample is to some degree independent of the diversity and preservation state of the cuticular material. The factors affecting the distribution of miospores not being those necessarily affecting the distribution of cuticular material. There is, however, some relationship as is shown by *Classopollis* and 30 CHEIR.

STRATIGRAPHIC CORRELATION

The work of Hughes *et al.* (1958, 1967*a*, 1969, 1973) gives an indication of the sort of picture that could be expected when correlating the samples from the four areas studied.

The majority of the samples from the south-eastern area are from the Fairlight Clay and Ashdown Sand formations. These are considered to be Berriasian to Valanginian (Hughes 1958) and samples from them should only correlate with

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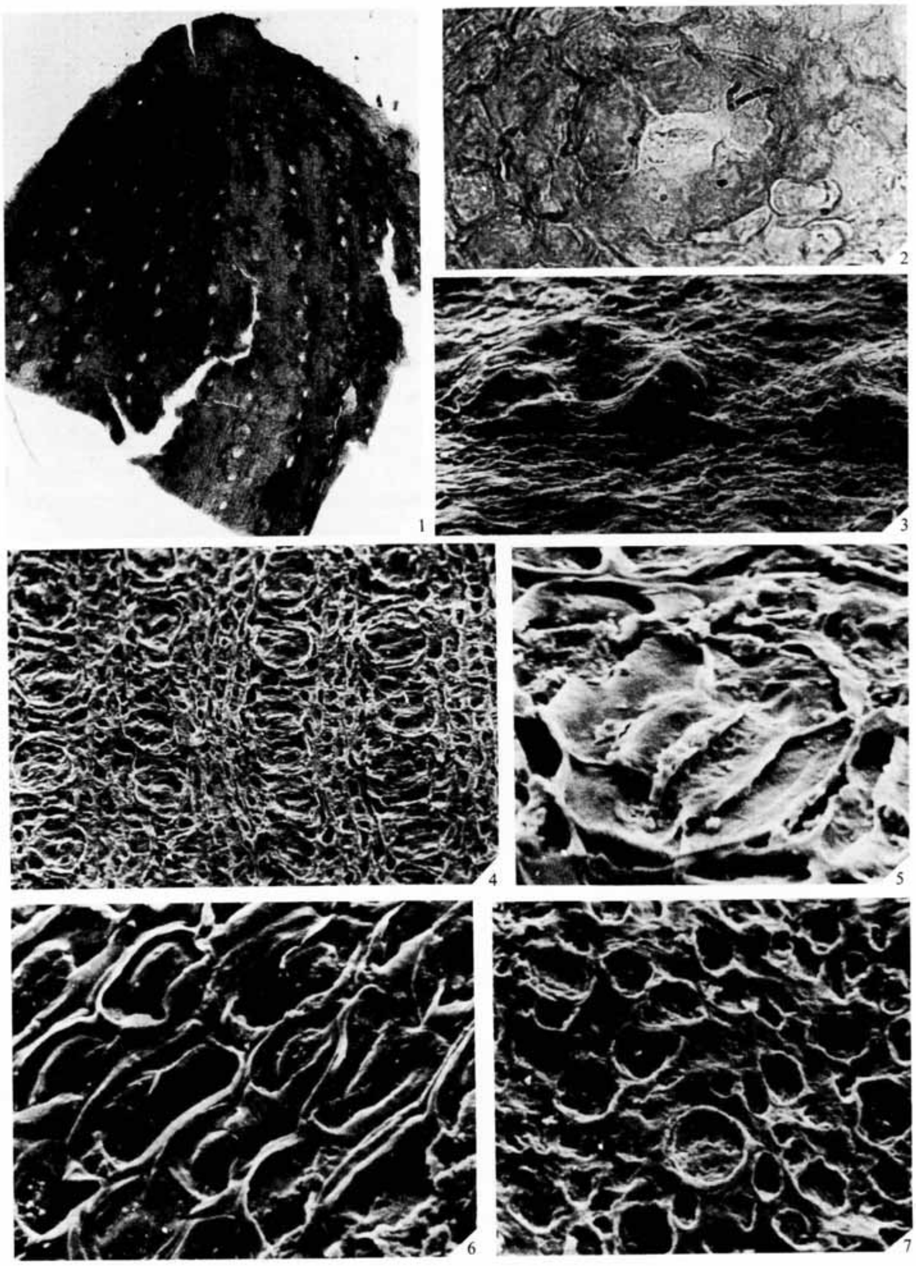
EXPLANATION OF PLATE 77

Figs. 1–7. 36 CONIF BrC. 1, ×50, LM., leaf; P98: 18/3.2. 2, ×500, LM., abaxial surface, stoma; P98: 18/2.1. 3, ×500, SEM., abaxial surface, outside, stomatal aperture; B29. 4, ×200, SEM., abaxial surface, inside, stomatal; B29. 5, ×1000, SEM., abaxial surface, inside, stoma; B29. 6, ×1000, SEM., abaxial surface, inside, hypodermis; B29. 7, ×1000, SEM., abaxial surface, outside, 'crater'; B29.

PLATE 77



OLDHAM, 36 CONIF BrC

TABLE 6. Miospore content of thirty selected samples.

	57H	53H	19H	22H	18AH	25H	28H	13H	41H	34AH	51BH	15AH	7AH	54H	8D	7AD	6D	5D	3AD	2AD	22D	20AD	18DD	27DD	13D	43AIOW	47IOW	48CIOW	49AIOW	50DIOW
Smooth *Triletes*	P	C	V	V	V	V	F	C	V	V	C	F	F	F	C	C	C	V	V	V	V	V	C	C	C	V	C	V	C	C
Acanthotriletes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–
Apiculatisporis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–
Baculatisporites	P	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	P	P	–	–	–	–	–	–
Ceratosporites	–	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	–	–	P	–	–	P	P	–	–	–	P
Concavissimisporites	–	–	P	P	P	P	P	P	P	P	–	P	P	C	P	P	–	–	–	–	–	–	–	P	–	–	P	P	–	P
Converrucosisporites	–	P	P	–	–	P	P	P	P	–	–	P	P	–	P	P	–	–	–	–	–	–	–	P	–	–	–	–	–	P
Kuylisporites	–	–	–	–	–	–	P	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptolepidites	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	P	–	–	–	–
Neoraistrickia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	P
Osmundacidites	–	–	–	P	P	–	–	P	–	P	C	P	P	–	P	P	P	P	P	–	–	P	P	P	P	P	P	P	P	P
Pilosisporites	–	–	P	–	P	P	–	P	–	P	C	P	P	–	C	–	P	–	P	C	–	P	–	–	P	C	–	P	P	C
Verrucosisporites	–	–	–	–	–	P	P	–	P	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	P	–	–	–	–
Cicatricosisporites	P	P	C	C	C	C	C	C	C	C	C	C	C	C	C	C	P	P	P	V	P	C	C	C	C	P	P	C	C	V
Foveosporites group	–	–	–	–	–	–	P	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–
Klukisporites	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lycopodiumsporites	–	–	P	P	P	–	P	P	P	P	–	C	P	–	P	–	P	P	–	–	C	P	P	P	–	–	–	P	P	P
Staplinisporites	P	P	–	–	–	P	P	P	–	P	–	–	–	–	–	–	P	–	–	P	P	–	–	P	P	–	P	–	–	P
Tripartina	–	–	–	–	–	P	–	P	–	P	P	P	–	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–
Perotrilites	–	–	P	–	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ischyosporites	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Matonisporites	–	P	P	–	P	P	–	–	P	P	P	P	P	P	P	–	P	P	P	P	P	P	P	–	P	P	P	–	–	P
Trilobosporites	–	P	C	P	C	C	P	P	P	P	C	P	P	P	P	–	P	P	P	–	–	P	P	P	P	–	–	P	P	–
Gleicheniidites	P	P	C	C	C	C	C	P	P	C	–	P	C	C	P	–	P	P	P	–	–	P	P	P	P	P	C	P	–	P
Contignisporites	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Densoisporites	–	P	–	–	P	–	P	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Patellasporites	–	–	–	–	–	–	–	P	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aequitriradites	P	–	–	P	–	P	P	P	P	–	–	–	P	P	P	–	–	–	P	P	–	–	–	–	P	–	–	–	–	–
Coptospora	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	P	–	–	P	–	–	–	–	–	–	–	–	–	–
Rouseisporites	–	–	P	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	P	–	–
Total *Triletes*	C	C	F	V	F	F	F	V	F	F	F	F	F	F	F	V	V	V	V	F	F	F	V	V	V	V	V	F	V	F
Monolites	P	–	P	P	P	P	P	C	C	P	–	C	C	P	C	–	P	P	P	P	P	P	–	P	P	P	P	P	P	C
Marattisporites	–	–	P	–	P	–	P	P	P	–	–	P	P	–	P	–	–	–	–	–	–	P	–	–	P	P	–	P	–	P
Peromonolites	–	–	P	–	–	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	P	P	C	–
Araucariacites	P	–	C	P	P	–	P	C	P	P	–	P	P	–	C	C	C	C	P	P	C	C	C	C	C	P	P	P	–	P
Inapertisporites	–	–	C	P	C	C	C	C	C	C	C	P	C	P	C	C	P	C	–	–	C	P	P	P	C	P	–	C	C	C
Inaperturopollenites	C	P	C	V	C	C	C	V	V	C	C	C	V	C	C	V	C	C	P	V	C	C	C	C	C	V	C	C	C	C

Pilasporites	F	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Reticulatasporites	P	–	P	–	–	P	P	P	P	–	–	–	P	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–
Cerebropollenites	P	P	P	–	–	P	P	–	–	–	–	–	–	P	P	–	–	–	P	–	P	–	–	P	–	–	–	–	–	–
Tsugaepollenites	C	P	C	–	P	P	P	C	P	P	P	P	–	P	P	C	C	P	P	P	C	C	P	C	P	C	P	C	P	P
Bisaccates	C	F	V	F	F	V	V	F	V	F	C	V	V	V	V	V	C	V	C	F	C	V	V	V	V	F	F	V	C	V
Eucommiidites	–	C	P	P	P	P	P	C	P	C	–	P	P	–	P	P	P	C	P	–	–	P	–	P	–	P	P	P	–	P
Cycadopites	P	C	P	–	P	C	C	C	C	P	V	C	C	P	C	C	P	C	–	P	–	P	C	P	C	C	C	C	C	P
Clavatipollenites	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	V	–
Classopollis	P	F	P	C	P	–	P	C	P	C	F	P	P	P	C	C	F	C	F	P	F	V	F	F	F	–	C	C	F	P
Exesipollenites	–	–	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	P	–	–	–	–
Perinopollenites	P	–	P	C	–	–	–	P	P	P	–	–	P	–	P	–	P	C	–	–	–	C	P	P	–	–	C	C	P	–
Schizosporis	–	P	P	P	–	–	–	–	–	–	–	–	C	P	C	P	–	P	–	–	–	P	P	–	P	–	–	P	P	C
Indeter. miospores	C	C	C	C	P	P	P	P	P	P	P	C	C	P	P	P	P	P	P	P	P	C	P	P	P	P	P	P	P	C
Black Wood	V	C	C	C	C	C	C	C	C	C	C	C	C	F	C	C	C	C	C	F	P	C	C	F	P	C	F	V	V	F
Brown Wood	C	C	F	V	F	F	F	F	F	V	F	C	C	C	V	V	V	C	C	C	F	F	V	F	F	V	C	V	C	C
Megaspores	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	P
Cuticle	V	F	F	F	F	F	F	F	F	F	F	F	F	C	F	F	F	F	F	C	F	F	F	F	F	C	C	F	F	F
Miospore diversity	A	A	L	A	L	L	L	L	L	L	A	L	L	L	L	S	L	L	L	A	S	A	L	A	L	A	A	L	A	L
Preservation state	M	M	G	P	M	M	M	M	M	M	M	G	M	G	G	M	G	M	G	M	M	G	G	G	M	M	M	G	G	G
Density of miospores	5	5	4	1	2	2	3	2	3	3	1	4	4	5	3	1	3	3	3	2	1	3	3	4	2	2	2	2	2	4

Key to symbols in Table 6

P = less than 3% of total miospores. Present.
C = 3% to 14% of the total miospores. Common.
V = 15% to 29% of the total miospores. Very common.
F = 30% or more of the total miospores. Frequent.

Miospore diversity:

S = little diversity. 13 or fewer taxa.
A = average diversity. 14–19 taxa.
L = large diversity. 20 or more taxa.

Preservation state:

B = poor.
M = fair.
G = good.

Density of miospores:

1 = 1–19 spores per traverse.
2 = 20–49 spores per traverse.
3 = 50–99 spores per traverse.
4 = 100–199 spores per traverse.
5 = 200 + spores per traverse.

samples from well below the 'Coarse Quartz Grit' bed in Dorset. Hughes and Croxton (1973) consider this bed to be probably late Valanginian to early Hauterivian and on this basis only samples 18AD, 18BD, 18CD, 18DD, 20AD, 20BD, and 22D from Worbarrow fall into the required category. Samples from Swanage Bay are all from above the 'Coarse Quartz Grit' except for 8D and this is only just below it. If Arkell's (1947) tracing of this bed is not altogether correct, and the botanical evidence goes some way to suggesting this, a different picture would emerge. This evidence suggests that samples 7AD, 7BD, 7DD, and 8D from Swanage Bay correlate with samples from well below the Coarse Quartz Grit bed as developed at Worbarrow Bay. If this is correct then the bed in question is not contemporaneous in the two areas.

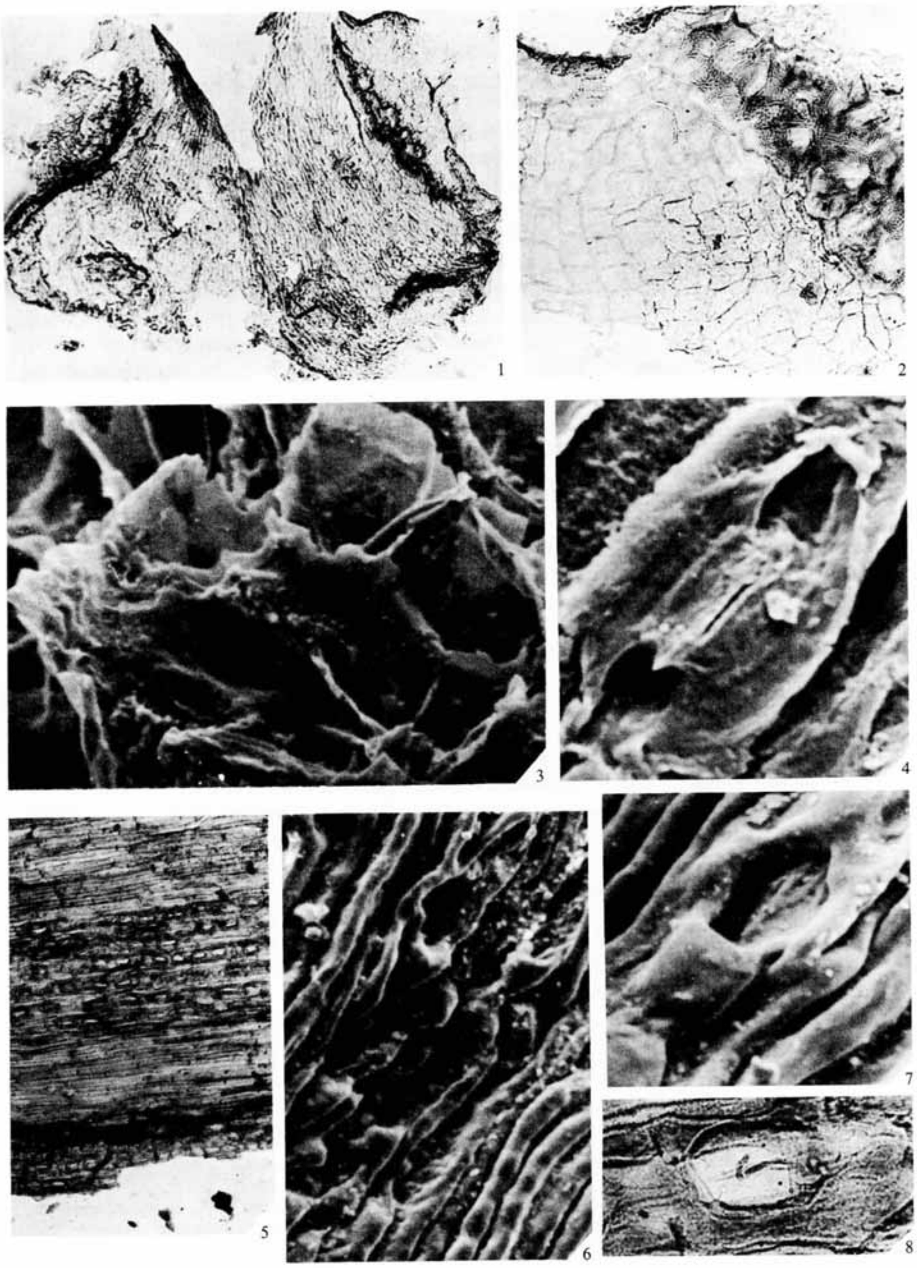
TABLE 7. Relationship of samples to Batten's (1973) assemblage-types.

	AT1	AT2	AT3	AT6	AT7	AT8	AT10	AT11	AT12	AT13	AT14	AT15	AT17
50DIOW	–	×	×	–	–	–	–	–	×	×	–	–	–
49AIOW	–	×	–	–	–	–	×	–	–	–	–	–	–
48CIOW	–	×	×	–	–	–	–	–	–	–	–	–	–
47IOW	–	–	–	–	–	–	–	–	–	–	–	–	×
43AIOW	–	–	–	–	×	–	–	–	–	×	–	–	–
13D	–	–	×		–	–	×	–	–	–	–	–	–
27DD	–	×	–	×	–	–	×	–	–	–	–	–	–
18DD	–	×	×	–	–	–	×	–	–	–	–	–	–
20AD	–	×	–	×	–	–	–	–	–	–	–	–	–
22D	–	–	–	×	–	–	×	–	–	–	–	–	–
2AD	–	–	–	–	×	–	–	–	×	×	–	–	–
3AD	–	×	×	–	–	–	×	–	–	–	–	–	–
5D	–	–	×	–	–	–	–	×	–	–	–	–	–
6D	–	×	×	–	–	–	×	–	–	–	–	–	–
7AD	–	–	–	–	×	–	–	–	–	–	–	–	–
8D	–	×	×	–	–	–	–	–	–	×	–	–	–
54H	–	×	×	–	–	–	–	–	–	–	–	×	–
7AH	–	–	×	–	×	–	–	–	–	–	–	–	–
15AH	–	×	×	–	–	–	–	–	–	–	–	–	–
51BH	–	–	–	×	–	–	×	–	–	×	×	–	–
34AH	–	–	×	–	–	–	–	×	–	–	–	–	–
41H	–	–	×	×	×	–	–	–	–	–	–	–	–
13H	–	–	×	×	×	–	–	×	–	–	–	–	–
28H	–	–	×	×	–	–	–	–	–	–	–	–	–
25H	–	–	×	×	–	–	–	–	–	–	×	–	–
18AH	–	–	×	×	–	–	–	–	–	–	×	–	–
22H	×	–	–	–	×	–	–	–	–	–	–	–	–
19H	–	×	×	×	–	–	–	–	–	–	×	–	–
53H	–	–	–	–	–	–	×	×	–	–	–	–	–
57H	–	–	–	–	–	×	–	–	–	–	–	–	–

EXPLANATION OF PLATE 78

Figs. 1–3. 32 TAXOD SpA. 1, ×50, LM., leaf; P55: 7/1.2. 2, ×150, LM., stomatal band; P55: 5/4.1. 3, ×1000, SEM., inside, stoma; B59.

Figs. 4–8. 37 TAXAC ThA. 4, ×1000, SEM., surface 2, inside, stoma; B47. 5, ×50, LM., surface 2, general view; P99: 9/2.1. 6, ×500, SEM., surface 2, outside, groove; B47. 7, ×1000, SEM., surface 2, outside, stomatal aperture; B47. 8, ×500, LM., surface 2, stoma; P99: 9/2.1.



OLDHAM, 32 TAXOD SpA and 37 TAXAC ThA

The samples from the Isle of Wight are probably Barremian to Aptian (Hughes 1958) and are well separated from all the other samples except those from the very top of the Dorset succession such as 2AD and 10D.

The majority of the samples from Swanage Bay are probably late Valanginian to early Barremian as are those from Worbarrow Bay. They should be expected to correlate well with each other but not with samples from the other areas except the few from the Tunbridge Wells Sand.

This expected picture is seen in the findings of the study. The samples from the Fairlight Clay and Ashdown Sand are well delimited by the presence of such taxa as 2 CYCAD, 7 CYCAD, 10 CYCAD, 11 CYCAD, and many bennettites including especially 13 BENN, 15 BENN, 24 GINK, 25 GINK, 27 GINK, 34 CONIF, 38 GYMN, and 39 GYMN. The absence of certain other taxa is also significant. These samples were seen to cluster out in the analysis. Their association with samples from the base of the Worbarrow succession is seen on the basis of such taxa as 28 GINK, 31 TAXOD, and 49 GYMN. That this link is not as clear as might have been hoped is probably due to the masking effect of the different sorts of debris beds in the two areas.

The samples from the Isle of Wight are delimited by the presence of 12 CYCAD, 26 GINK, and 37 TAXAC and also by the constancy of occurrence of the more wide-ranging taxa 8 CYCAD, 19 BENN, and 23 BENN. Most of the taxa of the lower strata are absent. Samples 2AD and 10D as expected fit in with this group. This grouping was also brought out in the cluster analysis.

The expected clustering of samples from Dorset was brought out in the cluster analysis. They are characterized by a high bulk of 30 CHEIR and the occurrence of 33 CUPR and 35 CONIF, both more or less confined to Dorset.

ORIGIN OF THE DEBRIS BEDS

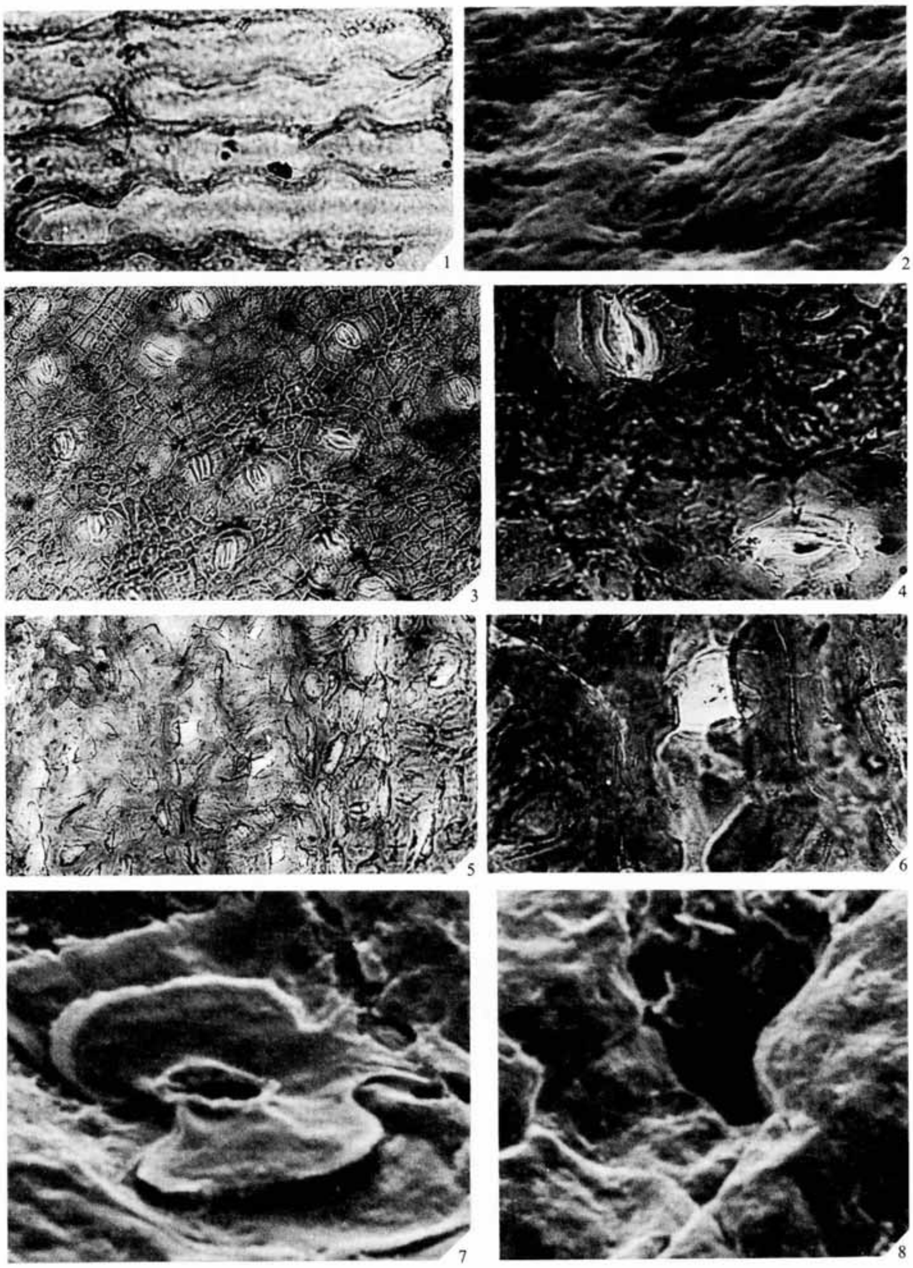
The absence of a known environmental framework within the Wessex basin and an ambiguous one in the south-eastern area make any attempt to determine the origin of the debris beds somewhat speculative. The paper by Spackman *et al.* (1969) discussing sedimentation in southern Florida is of relevance. They describe how degraded plant material is carried out into the Gulf of Mexico usually to be decomposed but occasionally to be carried by longshore currents and cast on beaches. This is normally a temporary resting place but if it becomes covered with a layer of inorganic sediment it will remain to form a lens of carbonaceous material. These deposits were examined by the author and their resemblance to those developed in the Fairlight Clay and Ashdown Sand is marked.

EXPLANATION OF PLATE 79

Fig. 1. 37 TAXAC ThA. 1, ×500, LM., surface 2, epidermal cells; P99: 9/2.1.

Figs. 2–4. 38 GYMN GyQ. 2, ×200, SEM., surface 2, outside, stomatal aperture; B52. 3, ×150, LM., surface 2, stomata; P49: 27/3. 4, ×500, LM., surface 2, stomata; P49: 27/3.

Figs. 5–8. 39 GYMN GyI. 5, ×150, LM., general view; P59: 7/4.2. 6, ×500, LM., stomatal aperture; P59: 7/4.2. 7, ×1000, SEM., inside, stoma; B43. 8, ×1000, SEM., outside, stomatal aperture; B43.



OLDHAM, 37 TAXAC ThA, 38 GYMN GyQ, and 39 GYMN GyI

If a delta environment is invoked, as seems most probable, evidence from the debris beds suggests that they were formed on the delta top and/or shore face and delta front environments. The evidence for this is six-fold.

1. The concentration of plant material into bed complexes, each consisting of many individual beds that are short-lived and irregular in formation.
2. The thickness of some of the laminae and the composition of the material. In some cases almost pure cuticular material makes up laminae over 20 mm thick.
3. The high quality of preservation of the material, little evidence of attrition or decay, delicate structures such as hairs being intact, structure of the epidermal cell traces being clear.
4. The occurrence of beds composed almost exclusively of a single species and the implied lack of mixing of material.
5. The restriction of the beds in Sussex to the Fairlight Clay, Ashdown Sand, and Tunbridge Wells Sand. The last two of these formations are considered to have been formed in delta-front and shore-face environments by Allen (1959). He considers the Fairlight Clay to be pro-deltaic but the large numbers of megafossil and debris beds in this formation throw some doubt upon this. The absence of plant remains from the Wadhurst Clay and the Grinstead Clay, apart from equisetalean ones, which Allen also considers to be pro-deltaic also implies a different environment of origin for the Fairlight Clay.
6. The similarity of the debris beds to the plant lenses formed in the shore-face environment of southern Florida.

The plant material has obviously been transported and the main problem in accounting for the origin of the beds is the concentration of this material into thick laminae. The lagoons, active and sluggish river channels invoked by Harris (1953, 1963) to explain many of the plant beds of the Yorkshire Jurassic, are no doubt responsible in some part for the formation of the Wealden plant debris beds. The shore-face environment can be suggested as another possibility.

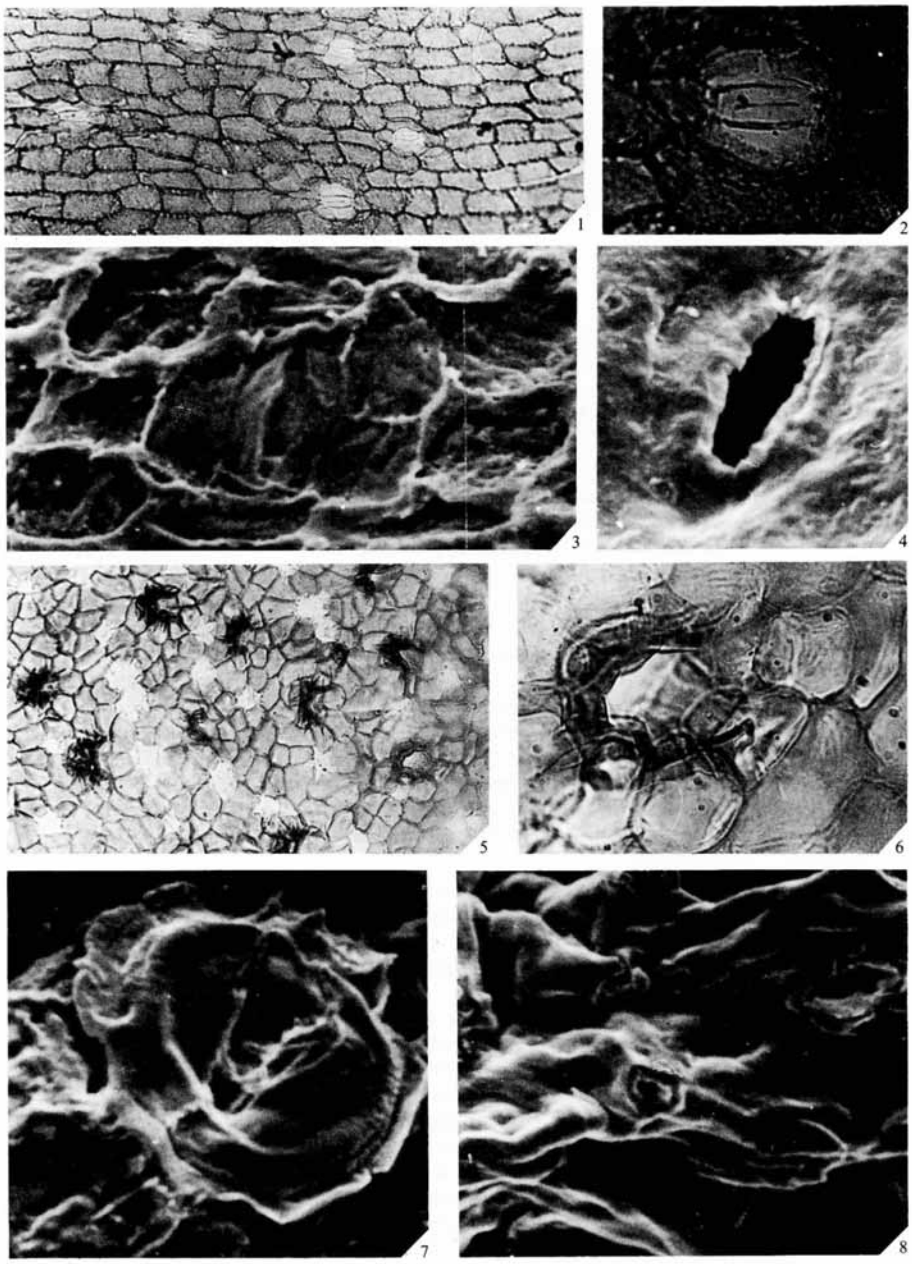
The source of material for the beds could be either fresh or reworked. Both sources may have been involved but the lack of megafossil beds with the Wealden suggests that much of the material must have been fresh.

The debris beds as indicators of the Wealden flora. No one type of bed in isolation can give a balanced picture of both the specific content and the relative importance of any one group within the flora. Beds rich in miospores give the most information with regard to the specific content of the flora, but as pollen from plants of bennettitalean, cycadalean, and ginkgoalean affinity tends to be under represented the

EXPLANATION OF PLATE 80

Figs. 1–4. 41 GYMN GyD. 1, ×150, LM., surface 2, general view; P98: 6/4.2. 2, ×500, LM., surface 2, stoma; P98: 6/4.2. 3, ×1000, SEM., surface 2, inside, stoma; B54. 4, ×1000, SEM., surface 2, outside, stomatal aperture; B54.

Figs. 5–8. 40 GYMN GyH. 5, ×150, LM., general view; P120: 1/3.1. 6, ×500, LM., stoma; P120: 1/3.1. 7, ×1000, SEM., inside, stoma; B56. 8, ×500, SEM., outside, stomatal apertures; B56.



OLDHAM, 41 GYMN GyD and 40 GYMN GhH

picture is not balanced. Megafossil beds only give an indication of a small part of the flora with waterside plants being over represented. Generalizations based upon them, especially in the Wealden where they are so scarce are suspect.

The plant debris beds fall between the two extremes. Waterside plants are again over represented and ferns are not recorded. Generalizations based upon them must be qualified, but by taking into account information from other sources a reliable picture of the flora and the relative importance of some of its members can be achieved.

THE WEALDEN GYMNOSPERMS

The Calytoniales are represented by three leaf species and the pollen grain *Vitreisporites*. Apart from the pollen grain, representatives of this group are of local occurrence only and are not found later than the Ashdown Sand in Sussex and the lower part of the Wealden Marls in Dorset. These records are some of the latest for this order.

Other plants of a possibly pteridospermous affinity have been grouped with the Cycadales in this paper. The two cuticle species relating to *Ctenozamites* are possibly pteridospermous and are found throughout the Wealden succession.

The Cycadales are not well represented in the miospore or megafossil record. The evidence from the debris beds, however, suggests that this group was of some importance, cuticle of cycadalean affinity occurring in nearly every sample studied.

The Bennettitales are second only to the Coniferae in importance and show no signs of the decline they were to undergo later in the Cretaceous. Eleven species have been described from the debris beds and several more are known only as megafossils. The large number of bennettites recorded by Daber (1960) and Benda (1961, 1962*a*, 1962*b*) from the German Wealden reinforces their importance. They tend to be associated together in samples.

The Ginkgoales are poorly represented in the miospore record but six cuticle species probably belonging to this group have been described. The group tends to favour northerly latitudes and so their presence in only a limited manner is to be expected.

The Coniferae are the major group within the flora. They are well represented in the megafossil record, are abundantly preserved as miospores, and they form by far the greatest proportion of the plant material in the debris beds. A few species may well have dominated large areas as the total number of species is low compared to the bulk of material.

The Cheirolepidiaceae as represented by 30 CHEIR and some of the *Brachyphyllum* species could be regarded as the most important Wealden family.

The Araucariaceae is only known from the Wealden as miospores and other reproductive structures. The lack of material suggests only a minor role for this family or a source at some distance from the major distributaries.

The Cupressaceae only became important in the Tertiary. Their occurrence in the Wealden is spasmodic but they are of some abundance when they do occur. This suggests a specialized habitat requirement.

The Taxodiaceae are prominent in the mid Tertiary and were only beginning their development in the Cretaceous. The appearance of a few species of local occurrence is to be expected and is found.

The Pinaceae, like the Cupressaceae, are not an important Mesozoic group and are only known from pollen grains and other reproductive structures.

The gross form of all these conifers is unknown but present-day species suggest they were likely to have been trees. The large bulk of wood present in the sediments goes some way to support this view. Wooded scenery may well have been developed over much of the delta top. Hughes and Moody-Stuart (1967*a*) invoke a mangrove type of vegetation to explain the distribution of *Classopollis* in Wealden sediments. This is of special interest considering the association of this pollen grain with

30 CHEIR.

The only representative of the Taxales is one cuticle species. In view of Florin's (1958) paper showing the importance of this group within the Mesozoic their virtual absence in the Wealden is surprising.

POSSIBLE FORM OF THE WEALDEN VEGETATION

In attempting to visualize the form and composition of the plant communities that were developed in the Wealden the botanist is faced with several problems. The sort of environment that was found in the Wealden would nowadays be dominated by angiospermous plants, many of them of a herbaceous nature. The gymnosperms that must have filled these niches in Mesozoic times are now extinct and their living relatives confined, for the most part, to high altitudes and high latitudes.

In southern Florida a combination of features occur that bear a resemblance to certain features that were probably developed in the English Wealden. This area was visited to see what light it could throw upon the problem of Wealden vegetation.

It is a low-lying area, generally wet, and supporting several gymnosperm-dominated communities. Extensive areas of arborescent angiosperms in semi-aquatic conditions also occur.

The most obviously comparable community is the cypress swamp. Pure stands of the gymnosperm *Taxodium distichum* and the exclusion of angiosperms except for a few epiphytes and creepers and the luxuriant growth of ferns, comprise a community that could well have been present in the Wealden. The ability of *T. distichum* to flourish whilst being constantly innundated by water points to a way of life that could have been of value in the wet, low-lying Wealden delta.

The succession within the cypress swamp and the gradual build up of plant material that allows other species to come in gives an example of how several different niches can be brought about solely through the agency of the vegetation from a previously flat plain. Indeed, the tree hammocks that rise above the sawgrass marsh, and are such a feature of Florida, suggest an explanation of where many of the non-water tolerant gymnosperms could have lived. Previous ideas place such plants at a distance from the delta on high ground. The considerable quantity of well-preserved plant remains at a considerable distance from any high ground could not be explained by such ideas, but by invoking tree hammocks the problem is solved.

The large variation in vegetation brought about by the slightest changes in elevation suggests that a variety of communities could have been developed on the Wealden

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delta. Of interest here are the pine flatwood developed on well-drained sandy soil, only 5 m above sea level. The gymnosperm *Pinus elliotti* forms an open stand with the saw palmetto *Serenoa repens* forming the main ground cover. This plant could be likened to the habit of the Mesozoic cycads and bennettites. The living cycad *Zamia integrifolia* also forms part of the ground cover in this community.

The possibility previously mentioned concerning the mangrove habit of 30 CHEIR is strengthened by an observation of the mangrove swamps of Florida. The trees line the distributaries and form a belt along the shore. Species diversity is extremely low, the vegetation being very monotonous. 30 CHEIR could well fit into this niche and its occurrence as almost the only species in several samples could be so explained.

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APPENDIX

LOCATION OF SAMPLES MENTIONED IN THE TEXT

1. *Samples from the cliff sections in the Hastings area*

Ashdown Sand

7AH Medium grey, fine siltstone, plant material concentrated in laminae; 0·3 m above beach, Haddock's Rough, TQ 881122.

14H Medium light grey, coarse siltstone, plant material dispersed in irregular laminae; 3 m above beach, Cliff End, TQ 885125.

15AH Medium light grey, coarse siltstone, plant material dispersed irregularly through the matrix; Haddock's Rough, TQ 882123.

47H Light grey, fine siltstone; plant material dispersed irregularly through the matrix; 3 m above beach, Little Galley Hill, TQ 767069.

Fairlight Clay

13H Medium light grey, fine siltstone, plant material concentrated in laminae; 3 m above beach, Ecclesbourne Glen, TQ 837099.

18AH Medium dark-grey siltstone, plant material concentrated in laminae; 2·5 m above beach, Haddock's Rough, TQ 878116.

19H Medium light grey, fine siltstone, plant material dispersed irregularly through the matrix; 1 m above beach, Haddock's Rough, TQ 877116.

21BH Light-grey siltstone, plant material concentrated in laminae; 4·5 m above beach, Lee Ness, TQ 870112.

22H Light medium grey, fine siltstone, plant material dispersed in fine laminae; 15 m above beach, Lee Ness, TQ 868112.

23H Light-grey siltstone, plant material concentrated in laminae; 15 m above beach, Lee Ness, TQ 866111.

25H Medium light-grey siltstone, plant material dispersed irregularly through matrix; 6 m above beach, Warren Glen, TQ 863109.

26H Light grey, fine siltstone, plant material dispersed irregularly through the matrix; 6 m above beach, Warren Glen, TQ 861108.

27H Light medium-grey siltstone, plant material dispersed irregularly through matrix; 1 m above beach, Warren Glen, TQ 857108.

28H Light grey, fine siltstone, plant material dispersed irregularly through the matrix; 4·5 m above beach, as 27H.

30H Light-grey siltstone, plant material dispersed irregularly through the matrix; 1 m above beach, Warren Glen, TQ 856107.

32H Light grey, fine siltstone, plant material in laminae; 0·3 m above beach, Warren Glen, TQ 855107.

33H Light medium-grey siltstone, plant material dispersed irregularly through the matrix; 9 m above beach, Fairlight Glen, TQ 853106.

34AH Light medium-grey siltstone, plant material in laminae; 4·5 m above beach, East Cliff, TQ 835097.

41H Light-grey siltstone, plant material dispersed in irregular laminae; 2·5 m above beach, Ecclesbourne Glen, TQ 837099.

44H Medium-grey siltstone, plant material concentrated in thick laminae; 5·5 m above beach, Ecclesbourne Glen, TQ 842107.

51BH Medium grey, fine siltstone, plant material concentrated in very thick laminae; 5·5 m above beach, Galley Hill, TQ 761077.

2. *Samples from the South-east of England apart from the Hastings area*

Wadhurst Clay

54H Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 11 m below top of the Wadhurst Clay, High Brooms Brickyard, Southborough, TQ 593418.

Purbeck

53H Medium-grey claystone, plant material in irregular laminae; River Line, Netherfield, TQ 715192.

57H Medium-grey siltstone, plant material dispersed irregularly through the matrix; Darwell Stream, Crackle Street, TQ 696200.

3. *Samples from the Cuckfield No. 1 Borehole, Sussex* (TQ 29612731)

(Sample numbers indicate depth to the nearest foot)

CUC431 Light-grey siltstone, plant material concentrated in thin laminae.

CUC434 Light-grey siltstone, plant material concentrated in thin laminae.

CUC443 Medium light-grey siltstone, plant material in laminae.

CUC634 Medium-grey siltstone, plant material concentrated in laminae.

CUC635 Light-grey siltstone, plant material concentrated in laminae.

CUC931 Medium light-grey siltstone, plant material in laminae.

4. *Samples from Swanage Bay*

Wealden Marls

2AD Light-grey siltstone, plant material dispersed in irregular laminae; 18 m above beach, SZ 037807.

3AD Light grey, coarse siltstone, plant material concentrated in laminae; 6 m above beach, SZ 036806.

3BD Light grey, coarse siltstone, plant material in irregular laminae; 0·1 m below 3AD.

5D Light-grey siltstone, plant material concentrated in laminae; 9 m above beach, SZ 035805.

6D Light-grey siltstone, plant material irregularly dispersed through the matrix; 6 m above beach, SZ 035805.

7AD Medium light-grey siltstone, plant material concentrated in laminae; 5 m above beach, SZ 033799.

7BD Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 0·3 m above 7AD.

7DD Medium light-grey siltstone, plant material dispersed irregularly through matrix; 3 m above 7AD

8D Medium light-grey siltstone, plant material concentrated in laminae; 9m above beach, SZ 033798.

5. *Samples from Worbarrow Bay*

Wealden Marls

10D Medium light-grey claystone, plant material dispersed irregularly through the matrix; Bed 26, SY 865803.

11AD Light grey, coarse siltstone, plant material concentrated in laminae; Bed 23, SY 866803.

11BD Medium light-grey siltstone, plant material in irregular laminae; 0·5 m below 11AD.

13D Medium light-grey siltstone, plant material dispersed irregularly through the matrix; Bed 16, SY 867802.

17D Light-grey claystone, plant material irregularly dispersed through the matrix; Bed 3, SY 869799.

18AD Medium light-grey claystone, plant material irregularly dispersed through the matrix; Bed 3, SY 869799.

18BD Light-grey claystone, plant material irregularly dispersed through the matrix; 0·6 m below 18AD.

18CD Light-grey siltstone, plant material concentrated in laminae; 3 m below 18AD.

18DD Medium light-grey claystone, plant material irregularly dispersed through the matrix; 4 m below 18AD.

20AD Light grey, fine siltstone, plant material in irregular laminae; 5 m below 18AD.

20BD Light grey, fine siltstone, plant material in irregular laminae; 5·5 m below 18AD.

22D Light-grey siltstone, plant material concentrated in laminae; Bed 2, SY 870798.

27AD Light-grey siltstone, plant material in irregular laminae; Bed 12, SY 868801.

27BD Light grey, fine siltstone, plant material concentrated in irregular laminae; 0·2 m below 27AD.

27CD Light-grey siltstone, plant material in irregular laminae; 0·3 m below 27AD.

27DD Light-grey claystone, plant material in irregular laminae; 0·5 m below 27AD.

(The Bed numbers are those used in Arkell 1947.)

6. *Samples from the Isle of Wight* (all from the south-west coast)

Wealden Shales

47IOW Medium light-grey claystone, plant material irregularly dispersed through the matrix; 3 m above beach, Shepherd's Chine, SZ 446798.

Wealden Marls

39IOW Medium-grey siltstone, plant material dispersed irregularly through the matrix; 14 m above beach, Chilton Chine, SZ 404824.

40IOW Medium-grey claystone, plant material dispersed irregularly through the matrix; 0·6 m below 39IOW.

41IOW Medium-grey claystone, plant material in irregular laminae; 5 m above beach, Chilton Chine, SZ 409822.

42BIOW Light-grey siltstone, plant material in fine laminae; 10 m above beach, Chilton Chine, SZ 409822.

43IOW Medium-grey siltstone, plant material in irregular laminae; 6 m above beach, Grange Chine, SZ 418818.

44IOW Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 14 m above beach, Grange Chine, SZ 421817.

48AIOW Medium light-grey siltstone, plant material concentrated in thick laminae; 6 m above beach, Brook Chine, SZ 383837.

48CIOW Medium light grey, fine siltstone, plant material in fine laminae; 0·5 m below 48AIOW.

48DIOW Medium grey, fine siltstone, plant material in irregular laminae; 0·7 m below 48AIOW.

49AIOW Light-grey siltstone, plant material in irregular laminae; 1 m above beach, Compton Grange Chine, SZ 378837.

49BIOW Light-grey siltstone, plant material in irregular laminae; 1 m above 49AIOW.

50AIOW Medium light-grey siltstone, plant material in fine laminae; 3 m above beach, Compton Grange Chine, SZ 373847.

50BIOW Medium light-grey siltstone, plant material in fine laminae; 0·2 m below 50AIOW.

50CIOW Medium light-grey siltstone, plant material in fine laminae; 0·7 m below 50AIOW.

50DIOW Medium-grey siltstone, plant material in irregular laminae; 1·7 m below 50AIOW.

50EIOW Medium light-grey siltstone, plant material in irregular laminae; 3 m below 50AIOW.