PALAEOBOTANICAL AND SEDIMENTOLOGICAL STUDIES ON THE LOWER BAJOCIAN (MIDDLE JURASSIC) FLORA OF YORKSHIRE

by

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ABSTRACT

Results are presented from studies on fossil plant beds of Middle Jurassic (Lower Bajocian) age exposed at Hasty Bank in North East Yorkshire. The abundances of the fossils are described quantitatively and the sedimentology of the beds examined in detail.

The upper part of the main plant bed was deposited by a stream channel, the margins of which supported a dense swamp of Equisetum columnare. There is evidence for a belt of vegetation which grew near to salt water and which was characterised by Hirmerella crucis and Pachypteris papillosa. This probably gave way further inland to a flora characterised by Pterophyllum thomasii, Ptilophyllum hirsutum, Marskea thomasiana and many other species.

During deposition the formerly whole plants became fragmented and their organs detached. Associations between these organs were detected repeatedly in the quantitative data, and when considered together with evidence from cuticular studies partial reconstructions of the plants could be deduced from them. These reconstructions agree with those proposed previously by other workers and add the following new ones which are discussed.

Androstrobus major + Pseudoctenis oleosa (Cycadales)

Alvinia florinii + Pseudoctenis lanei/Paracycas cteis (Cycadales)

Palissya harrisii, female cones + foliage shoots (conifer)

Brachyphyllum crucis + Hirmerella crucis (conifer)

The following new taxa are described.

Mariestopesia blackii (van Cittert) gen.et comb. nov. (Marattiales)

Alvinia florinii gen. et sp. nov. (Cycadales)

Zamites johannae sp. nov. (Bennettitales)

Pterophyllum pruinosum sp. nov. (Bennettitales)

Hirmerella crucis (Kendall) comb. nov. (conifer)

Palissya harrisii sp. nov. (conifer)

Mariestopesia is regarded here as somewhat intermediate in morphology between living *Angiopteris* and Palaeozoic-Triassic forms such as *Asterotheca*. The resemblance of *Alvinia* to the megasporophyll of living *Cycas* is remarkably close.

ACKNOWLEDGMENTS

Many colleagues and friends have given invaluable advice and encouragement. In particular I thank the following: Mr. A. Wesley, Professor T.M. Harris, Dr. K.L. Alvin, Dr. R. Knox, Mr. H. Sharp, Dr. H.W. Ball, Dr. J.D. Lovis.

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Finally I thank Morag Jones and my parents for their invaluable help in many ways and Mrs. Ann Walsh for typing the manuscript.

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This thesis investigates three approaches to the Yorkshire Jurassic Flora. These are palaeobotany, sedimentology and "palaeoecology." Previous work on each is here summarised and the aims of the thesis thus introduced.

PALAEOBOTANY

The main aim of palaeobotanical work on the Yorkshire Jurassic Flora has been to understand the morphology and phylogeny (evolution) of the fossil plants. Early pioneering studies by Young and Bird in 1822 were succeeded by a number of increasingly sophisticated ones of which the most recent is an exhaustive series of monographs by T.M. Harris, 1961, 1964, 1969, and in preparation. Summaries of the important advances in ideas and techniques are given by Harris (1961:1-2) and of the early literature by Seward (1900:2-14).

The flora itself is typical of the Middle Jurassic. It is chiefly represented by Equisetales, Filicales, Cycadales, pteridosperms, Bennettitales/Ginkgoales and conifers. A few Algae, lycopods and bryophytes are also known. Although it has sometimes been claimed that Angiosperms were in existence in the Jurassic there is no convincing evidence for this. Indeed the first appearance of convincing fossil Angiosperms occurs during the succeeding Cretaceous period.

Study of the morphology of the Yorkshire Jurassic fossil plants has not been straightforward. During deposition in muddy rivers the formerly whole plants became broken up into their constituent organs, such as leaves and cones, and because of this the organs are rarely found in attachment. The palaeobotanist is thus faced with fragmentary fossilised plant debris which is distinctly unimpressive compared to

living material. Morphology and phylogeny nevertheless involve the whole plants and therefore a good deal of effort has gone into attempts to reconstruct the plants from their detached organs.

Direct evidence for reconstruction is from the rare discoveries of organs in attachment, but besides this there are two important kinds of indirect evidence. Firstly it has long been recognised that consistent associations between detached organs occur in the plant beds. These are often seen both at several horizons within a single locality and also repeated in different localities. Secondly it was later found that the associated organs often agree remarkably well with one another in cuticle structure, as do the different parts of many living plants. When these lines of evidence for reconstruction are taken together they are widely regarded as a powerful tool. Standard examples of their use are studies by Thomas & Harris (1960) and Harris (1941) on fossil cycads.

A general criticism of this indirect evidence for reconstruction is that the associations have not previously been described in detail. Thus some of them may have been imagined rather than real and certain less obvious ones may have been overlooked. Indeed sometimes they may merely represent the effects of sorting during deposition, so that organs of similar size or density rather than of natural affinity have become buried together (Black, 1929:417-418; Krasilov, 1969). In view of these criticisms an aim of this thesis is to consider the validity of associations as a basis for reconstruction.

Sedimentology and "Palaeoecology"

Early work on sedimentology of the plant-bearing rocks was summarised by Fox-Strangways (1892) whose conclusions were later extended chiefly by Black (1928, 1929, 1934)

and more recently by Knox (1969 unpublished).

The majority of the plant fossils occur in fresh-water sediments. At first it was thought that these were deposited from river estuaries separated by islands and they were thus named the Estuarine Series (Fox-Strangways 1892). However it later became clear that the rivers were actually separated by swampy flood-plains characteristic of a delta rather than an estuary (Kendall in Kendall & Wroot 1924: 308-310). This had in fact been recognised much earlier by Simpson in 1868. The beds were therefore eventually re-named the Deltaic Series (Hemingway 1949).

Studies on the sedimentology of individual plant beds showed that deposition of the fossils reflected physical processes and possibly also the geographical distribution of the whole plants in life ("palaeoecology"). The following selected examples illustrate the kinds of observation and thinking involved.

Distribution of the plants in life in relation to their debris found as fossils in the sediments

Black (1928) described plant beds deposited in former stream channels of the delta. These channels are incised discordantly into earlier sediments and must therefore have been erosional. As continuity with neighbouring sediments is confined to their extreme top they must each represent a single cycle of erosion and subsequent infilling. Such channels, eroded and filled in a single cycle rather than in several, are called "washouts".

The shape of these channels and the upward decrease in grain size of the sediment filling them are characteristic general features of deposits from streams (Selley, 1970). They are lens shaped in cross section and have a basal layer

of boulders and or logs, succeeded above by a great mass of coarse sandstone. This is replaced near the top by finer grained sediments in which delicate plant debris often occurs abundantly enough to form a plant bed.

Black's conclusion was that certain plant beds were formed in the final phases of washout channels, presumably when the stream was sluggish. Large amounts of plant debris would thus sink compared to sediment and become concentrated. Harris (1953) and in discussion points out that plant remains would also sink in the earlier more active phases of the stream channels but here they would be much diluted by the rapid sedimentation. In the coarse sand they would also be preserved less effectively than in the finer grained sediments of the sluggish phases.

Black later extended his observations to other kinds of Yorkshire Jurassic plant bed, chiefly those exposed in the cliffs at Scalby and Burniston (Black 1929). He concluded that there are two main kinds of plant bed, as follows:

Drifted ("allochthonous") plant beds

The plant material is distinctly sorted and is dominated by robust forms such as Ginkgoales. These beds commonly occur in washouts and also in more extensive level-bedded deposits such as the Scalby Wyke drifted plant bed.The sediment is typically fairly coarse-grained though not always.

In situ ("autochthonous") plant beds

The plant material is not much sorted and both robust and delicate forms occur together. These beds occur in fine-grained sediments deposited in lakes and swamps.

He gives a detailed comparison of a typical drifted flora, the Scalby Wyke drifted plant bed, with a typical "in situ" one, the Gristhorpe plant bed (summarised in

"IN SITU" (Gristhorpe plant bed)	DRIFTED (Scalby Wyke drifted plant bed)
The plant fossil fragments are distributed erratically on the bedding planes. A species abundant at one point may thus be lacking a few metres away.	The fragments are spread out uniformly on the bedding planes.
The fragments are large and often complete fronds are preserved.	The fragments are small
Size of the fragments is very variable.	Size of fragments more or less uniform
Both robust and delicate remains occur side by side	Robust remains dominate
Vertical roots are often seen	Vertical roots are never seen
Associations of leaves and reproductive organs are well marked	No such associations.

Table 1. Summary of comparison given by Black (1929: 413) of an "in situ" plant bed v. a drifted one. Vertical roots do not in fact occur in the Gristhorpe bed.

table 1). He suggests that the plants of "in situ" beds grew near to where they were deposited: "more or less on the spot", and thus give information about the flora of the delta swamps. In contrast the more highly sorted plants of drifted beds were probably washed in from some distance. This idea based on sedimentological work was a major advance in plant "palaeoecology" and is further discussed below(p.9).

The classification of plant beds into two kinds was later refined by Harris (1952) and extended by him to include every Yorkshire Jurassic plant bed then known. He points out that the term autochthonous had been used in too wide a sense by Black and should be restricted to beds where the plants are strictly in position of growth. He defines the following five kinds of plant bed.

1. Beds with plants preserved in position of growth. These are beds of upright stems and roots, chiefly of Equisetum columnare Brongniart, for example the Equisetum bed at the foot of Beast Cliff near Hayburn Wyke.
2. Lagoon and sluggish river channel beds, the prevailing sediment being fine mud. The flora shows features of Black's "in situ" beds (table 1.) but includes some water-worn material. Harris puts the Gristhorpe bed in this category and I would also include Hasty Bank.
3. Distributary channel beds, the prevailing sediment being fine sand, for example the Whitby Long Bight plant bed. A higher proportion of water-worn plants occurs than in category 2 but their floras are otherwise similar.
4. Drifted plant beds, the prevailing sediment being sand, for example Black's Scalby Wyke drifted plant bed. All

but the smallest plant fossils are severely water-worn. Water-worn wood (occurring mainly as fusain pebbles) is common.

I would add many of the marine plant beds to this category, for example the Millepore bed.

Though drifted floras are typically associated with sandy beds it is a fact that the sediment of Black's Scalby Wyke drifted plant bed is mostly fine-grained. This is commonly also the case in marine drifted plant beds.

5. Redeposited plant beds. The floras of these are almost entirely lacking in uncutinised plant remains and consist chiefly of tough cuticles. Characteristically the cuticles were oxidised before final deposition and are therefore brown rather than the normal black colour. Example: Bilsdale Tripsdale Todd Intake.

I would add to this category certain plant beds such as Westerdale Stockdale Beck waterfall bed where the plant remains occur in pebbles of claystone re-worked into sandstone. In these pebbles the cuticles are either brown or black.

Redeposited plant beds may be regarded as an extreme kind of drifted flora.

I think Harris uses the term water-worn to encompass three processes of deposition:

a. Wear in the usual sense of the geologist, i.e. rounding.

b. Extent of fragmentation.

c. Sorting of fragments by size and density.

He points out that plant beds of categories 2, 3 and 4 intergrade.

Harris (1966) made a general observation on redeposited plant beds found within the uppermost division of the Deltaic Series, in beds known as the Moor Grit. The plant beds are thin and occur in great thicknesses of otherwise barren and coarse sandstone. Instead of the usual flora there are numerous fragmentary remains of conifers and presumed taxads which were described by Florin (1958). Harris suggests that this unusual flora is from the higher reaches of the delta and in other localities is normally concealed by the overwhelming abundance of different species which grew nearer the site of deposition.

Mangrove species

Harris (1964: 129-133) put forward a hypothesis to explain certain facts about the pteridosperm Pachypteris papillosa (Thomas & Bose) Harris. This plant is peculiar in both its morphology and distribution:

MORPHOLOGY : Pachypteris papillosa is strongly xeromorphic in that its leaves were succulent and have an extremely thick cuticle

DISTRIBUTION : This is almost unique amongst Yorkshire Jurassic plants. The 22 localities are almost entirely confined to the very base of the Deltaic Series and in these P. papillosa is always the most abundant species. It is

associated with microfossils of marine origin in all of them.

Harris points out that bona fide P. papillosa is also known from the younger Stonesfield Slates of southern England and of Bathonian age. Thus its odd distribution in Yorkshire could not have been the result of evolutionary extinction. He suggests that its presence with abundance or complete absence must point to an ecological factor of overwhelming importance. Of these factors burning is a possibility but there is no special correlation with fusain to support it. From the association with marine microfossils and xeromorphy of the leaves he thus concludes that flooding by seawater is the most likely explanation. His hypothesis is that P. papillosa was a mangrove (Rhizophora)-like plant which grew in the tidal part of the delta. He explains the distribution of the constant and also xeromorphic associate Brachyphyllum crucis Kendall (wrongly called B. expansum) by suggesting that it shared the same habitat.

DISCUSSION

The idea of Black (1929)

Black's idea and its later application by others is essentially that plant fossils behave like sedimentary particles. Because drifted floras are more highly sorted and fragmented than "in situ" ones it is assumed that they have been transported further and therefore represent an inland flora.

A more refined view of Black's idea arises from the fact that the drifted floras of the Deltaic stream channels nearly always occur in predominantly coarse grained sediments whereas the "in situ" floras occur in fine-grained sediments.

This shows that the sedimentary environment in which drifted floras were deposited was a highly energetic one, for example the actively erosional washout channels. In modern streams it happens that the sediment of coarsest grain size is typically deposited closer to the inland source where the energy is high, and the finer sediment lower down where the river is tranquil. Sorting and fragmentation of plant debris are generally greater in an energetic environment of deposition. It is reasonable to assume that the stream channels of the Yorkshire Jurassic delta behaved in a broadly similar way. The plant fossils in the more energetic (coarse-grained) sediments of the stream channels are more likely to have been derived from an inland source than those in the fine-grained deposits. By the time the fine-grained deposits in the tranquil lower parts of the streams were deposited the inland flora would have been comminuted beyond recognition and the plants growing nearby would be deposited to give "in situ" floras.

Similar arguments apply if the river suddenly increases in energy, in which case coarser sediments and the inland plants would be carried further downstream.

I should stress that where drifted floras occur in fine-grained sediments the evidence for an inland source is solely their greater sorting and fragmentation compared with "in situ" floras.

As a further refinement one may also reasonably assume that the more energetic coarse-grained deposits were produced during relatively rapid sinking of the delta. The usual "in situ" deltaic flora would thus be drowned by the sea and the inland flora preferentially represented in the deltaic sediments. This view was first put forward by Chaloner (1958) and was used by Harris (1966) to interpret the Moor Grit

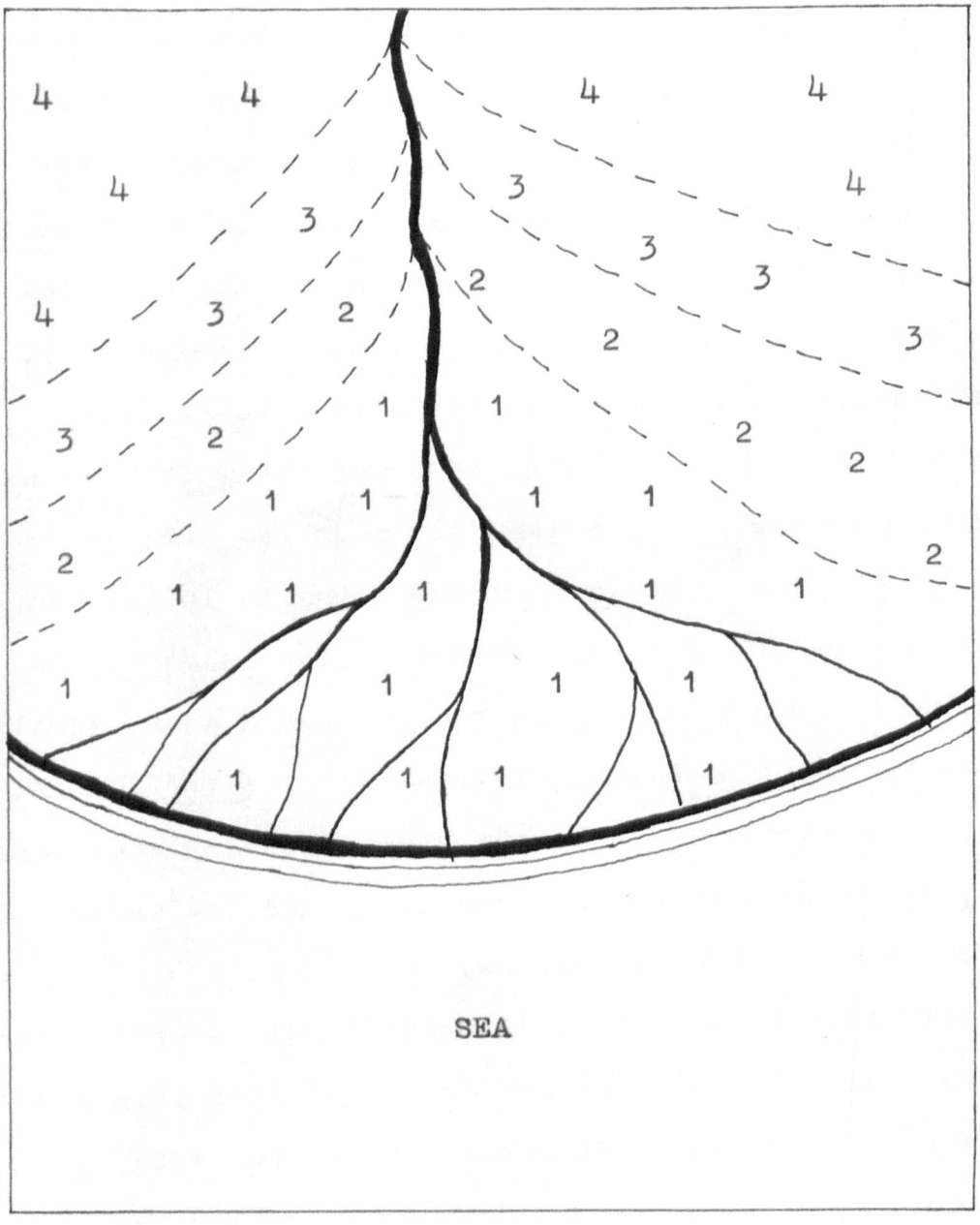


Fig. 1. Zonation of vegetation postulated for a fossil delta. 1: mangroves, 2: "in situ" floras, 3: drifted floras, 4: inland floras.

conifers.

Whilst Black's idea and its refinements are rational they are nevertheless open to several criticisms, as follows.

1. A general criticism is that a simple shift in grain size of the sediment at source would lead to a difference in grain size of sediment deposited by the streams. Thus there need not have been a change in the energy of deposition and the coarser sediments might not have been transported further or be nearer to source than the finer ones. If this was so the drifted floras would merely be a sorted version of the more robust species from the normal delta vegetation.

Clearly this criticism should always be borne in mind when interpreting drifted floras. It does not apply for example to the Yorkshire Jurassic example discussed by Harris (1966). The Moor Grit conifers are quite unknown from "in situ" beds yet conifers with equally thick cuticles from these latter beds are unknown in the Moor Grit.

2. I believe the conventional interpretation in terms of an inland flora v. a delta one is too simple. It gives the impression of a uniform delta flora succeeded inland by a completely different one. Popularly it has been suggested that the drifted flora grew on upland hills but there is no evidence for this.

Modern deltas show several zones of vegetation and I therefore suggest the Yorkshire Jurassic delta was similar (Fig. 1). I postulate that the drifted v. "in situ" floras may merely represent two zones of normal delta vegetation. It is statistically likely that representation of the real upland and inland floras would be overwhelmingly dominated and thus obscured by deposition of debris from

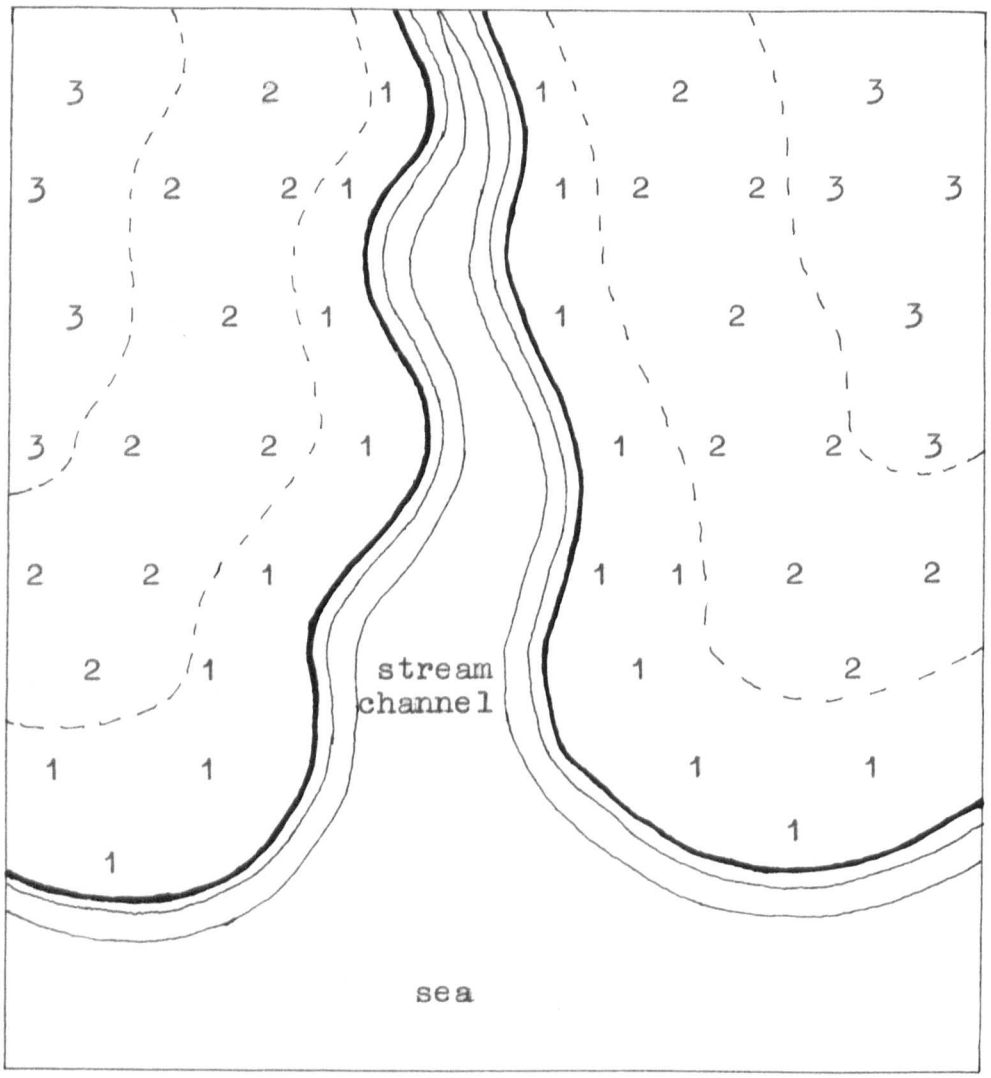


Fig. 2. Postulated distribution of drifted v. "in situ" vegetation according to criticisms 2 and 3 of Black's 1929 idea. 1: mangroves; 2: "in situ" floras of the swamps; 3: drifted floras of the higher ground.

the delta floras themselves. The inland flora would probably show up clearly only in marine miospore assemblages (Makhin Sein 1961 unpublished, see Chaloner 1968; Muir 1964) and as those macrofossils scattered fairly uniformly through the Deltaic rocks such as Phlebopteris woodwardii Leckenby (Harris 1961).

If this view of the delta vegetation is right then both drifted and "in situ" floras may have grown relatively close to each other. The "in situ" floras may have grown on low swampy ground whilst the drifted ones grew on drier ground which need only have been a metre or so higher (Fig. 2). I imagine that during normal delta growth the drifted plants may have grown as a stable flora between the delta channels. As the meandering channels slowly shifted this stable flora would also shift because of ecological control. The overwhelming abundance of debris deposited in the channels would therefore be from the "in situ" vegetation growing along their swampy margins. The drifted flora would only be deposited when the delta sank and erosional channels bulldozed their way through the formerly stable ground. As these channels would be highly energetic it follows that the flora would quickly become sorted over short distances.

In view of the limited facts this hypothesis may seem unnecessarily complicated compared with the conventional view. It is however merely a refinement: though the stable flora is imagined as interfingering with the swamp flora its overall distribution would relatively speaking be "inland" (Fig. 2).

3. This is the chief criticism as it is based on observation of fact. It arises from re-examination of Black's "in situ" and drifted plant beds.

Harris (1952) has pointed out that Black's "in situ"

flora at Gristhorpe was not growing on the spot. Roots and stems in position of growth are unknown in the Gristhorpe bed and the flora must therefore have been drifted if only for a short distance. He has suggested to me in conversation that the well marked associations and erratic distributions seen in the bed may merely reflect the way in which it was deposited. He suggests the bed may have been built up from a complex of small shifting channels and need not have been the lagoon it is usually thought to represent. The sources of the channels may have been at some distance and have exploited different communities of vegetation at different times. Nevertheless he agrees with Black's reasoning that the plants were probably not carried quite so far as the Scalby drifted ones.

It also happens that redeposited (drifted) leaves of Bilsdalea and Ginkgo occur in the Gristhorpe bed, though it is true that most of the other species occurring there were not redeposited.

There is confusion in Black's 1929 paper between the Scalby Ness plant bed and other plant beds of the Upper Deltaic. Black lists the Scalby Ness bed as a drifted one whereas in fact it shows all the essential features of an "in situ" plant bed (though like the Gristhorpe bed vertical roots are lacking). Indeed as the Scalby Ness plant bed shares Gingko huttonii (Sternberg) with the drifted floras of the other washouts there is little evidence to consider Ginkgo a plant drifted from far inland. Similarly Haiburnia blackii Harris is shared by the Scalby Ness plant bed and the Scalby Wyke drifted plant bed.

These considerations lead me to doubt the validity of classifying whole plant beds in the ways suggested by Black

(1929) and Harris (1952); and I believe they support my hypothesis that drifted and "in situ" floras probably occurred fairly close together on the delta.

The Mangroves of Harris 1964

1. The marine microplankton may have been redeposited as a result of active erosion of the underlying marine beds by the earliest deltaic streams. Harris gives no figures for relative abundance of the plankton from the basal deltaic beds compared with the underlying marine beds yet up to about 20% redeposition is known to occur in such environments of deposition (Williams and Sarjeant 1967).

2. Because of its exceptionally thick cuticle Pachypteris papillosa may have been carried out into marine rocks preferentially compared with other species. Its association with marine plankton would thus have no direct palaeoecological significance.

It is a fact that many of Harris's Pachypteris localities occur in marine rocks of the Yorkshire Dogger (work in progress). Nevertheless Pachypteris also occurs in association with marine microfossils in a few localities of characteristically deltaic sedimentology such as Hasty Bank, and the association in these localities is especially strong evidence in support of Harris's hypothesis.

3. Dr. Knox has pointed out in conversation that if P. papillosa was a mangrove it might be expected to recur immediately above the marine transgressions over the delta. Though P. papillosa does not recur in this way Brachyphyllum crucis does so (in the Millepore bed). This perhaps indicates that the primary ecological control over Pachypteris was some other factor than directly salt, possibly openness of

Fig. 3.

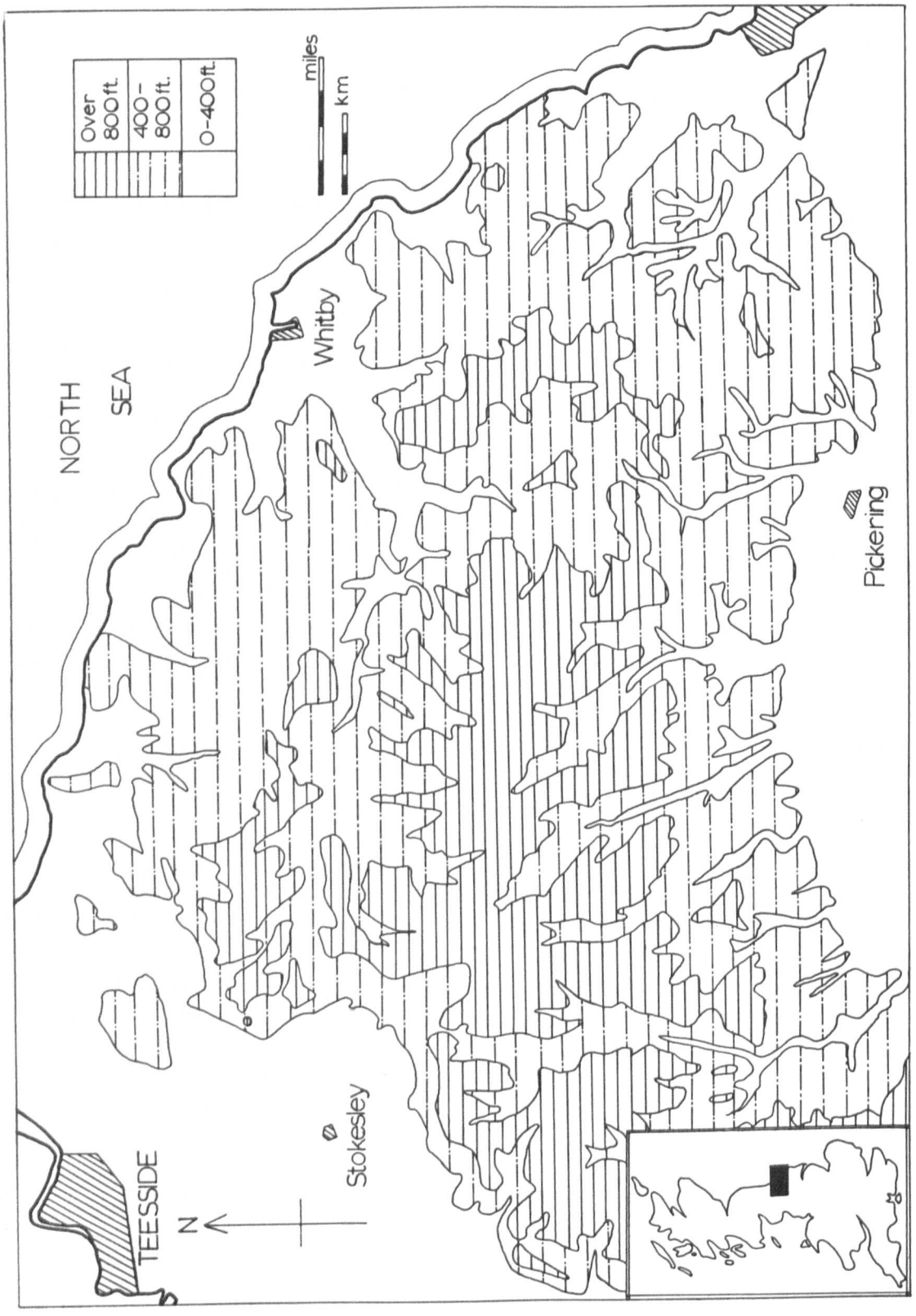


Fig. 3. Topography of the Cleveland and North Yorkshire Moors region.

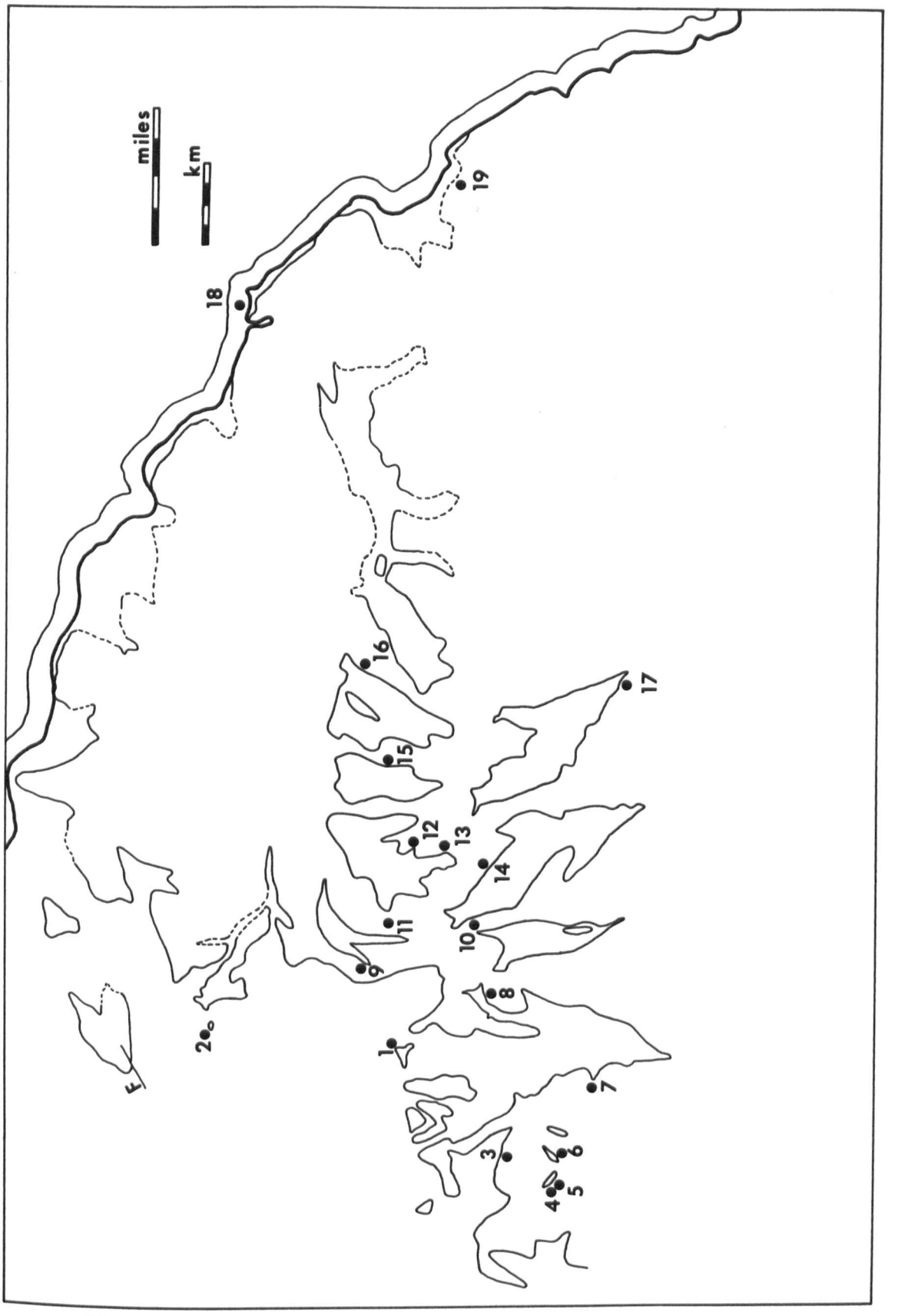


Fig. 4. For explanation see overleaf

Fig. 4. Outcrop of the Yorkshire Dogger and the base of the Saltwick Formation. F : fault, ----------: drift covered. Localities mentioned in the text are numbered as follows:

1. Hasty Bank plant beds
2. Roseberry Topping plant beds
8. Bilsdale, Tripsdale, Todd Intake
11. Westerdale, Stockdale Beck waterfall bed
16. Fryupdale, Finkel House ironstone adit
18. Whitby, Long Bight plant bed

Fig. 5

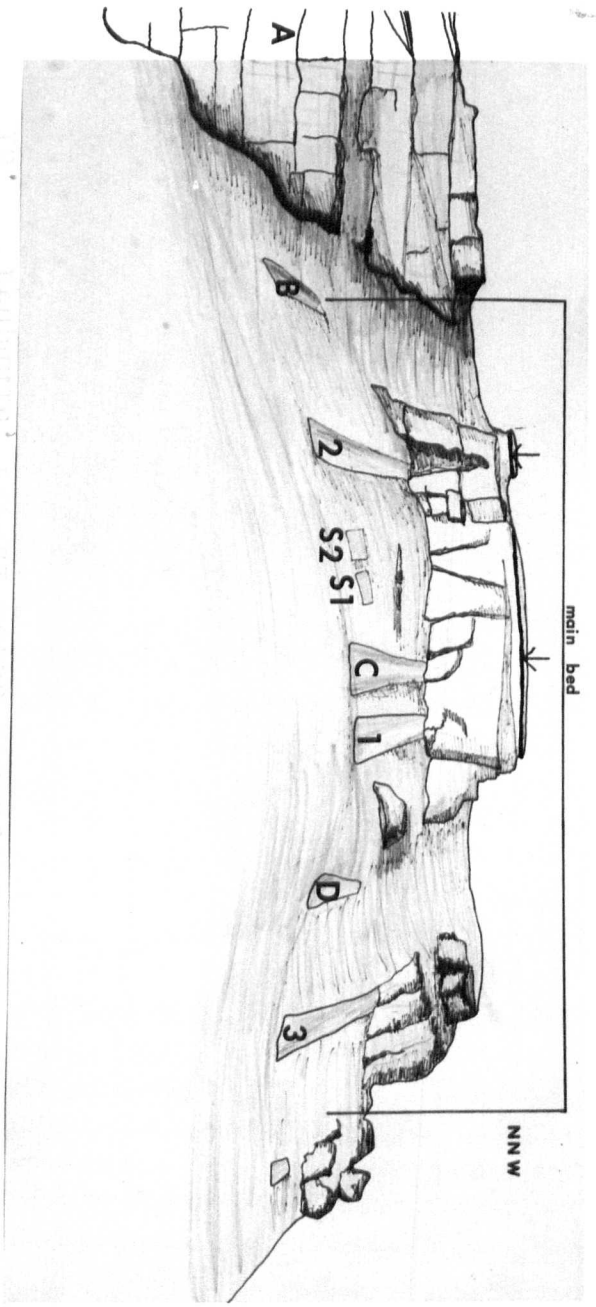


Fig. 5. For explanation see opposite

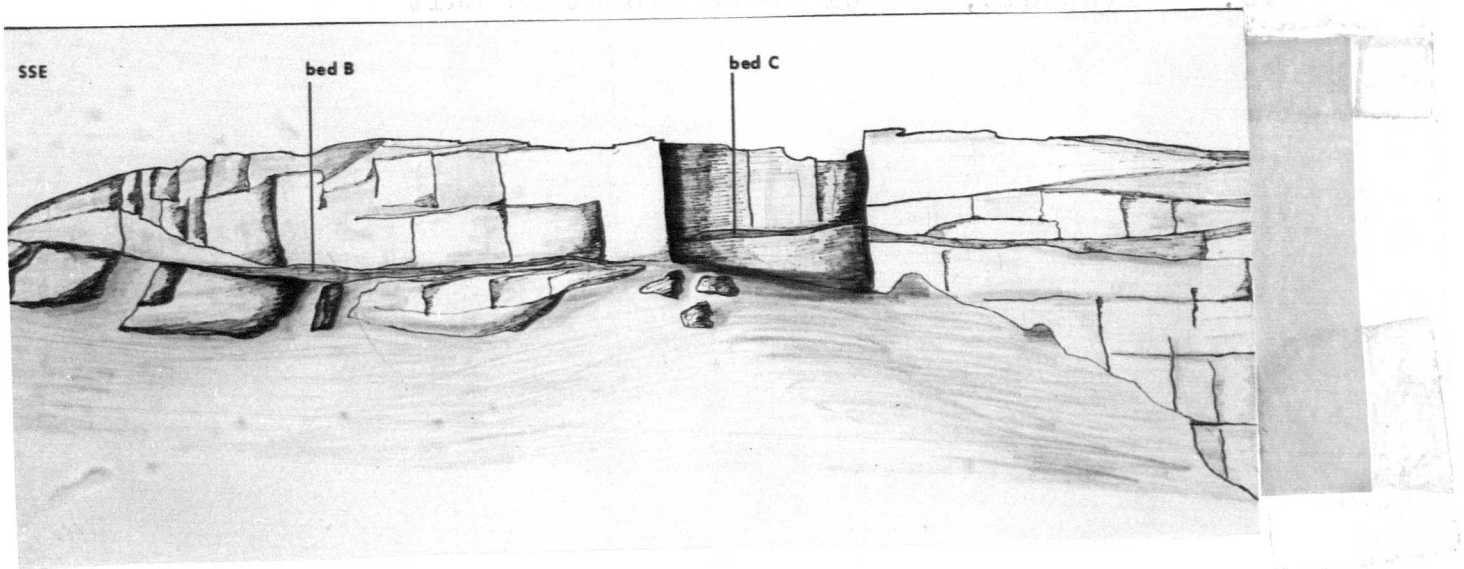

SSE
bed B
bed C

Fig. 5 Sketch of the Saltwick Formation sandstones at the top of the East-facing slope of Hasty Bank. Length of the outcrop 0.4 Km.
Geological sections through the main plant bed are shown on the slope beneath the sandstones (B, 2, S1, S2, C, 1, D, 3); section A is also shown. These sections form the basis of Fig. 6.

The outcrop of the Hasty Bank main leaf coal is indicated by arrows.

habitat near to saltwater or availability of bases in the soil.

I believe the discussions given above show that there is scope for reconsideration of previous sedimentological work on the Yorkshire Jurassic Flora. Much of this previous work was based on general comparison of locality to locality. My conviction is that detailed re-examination of deposition of individual species in the individual localities is needed, and this forms an aim of my thesis.

A single locality was chosen for study, the Hasty Bank plant beds. The location of the beds is shown in Fig. 4 and their outcrop at Hasty Bank in Fig. 5. These plant beds are richly fossiliferous and of both considerable thickness and lateral extent. Several kinds of rock occur in them. They should therefore be suitable for detailed studies on the flora and for detection of any correlations with different environments of deposition.

I am grateful to Mr. Wesley for originally suggesting this choice of locality.

	Fox-Strangways 1892	Hemingway 1949	Hemingway & Knox 1973
Upper Jurassic	C O R N B R A S H		
Middle Jurassic	Upper Estuarine Series	Upper Deltaic Series	Scalby Formation
	Grey Limestone Series	Grey Lime-Stone Series	Scarborough Formation
	Middle Estuarine Series	Middle Deltaic	Cloughton Formation
	Millepore Series		
	Lower Estuarine Series		
		Eller Beck Bed	Eller Beck Formation
		Lower Deltaic Series	Saltwick Formation
	Dogger	Dogger	Dogger Formation
Lower Jurassic	L I A S		

Table 2. Comparison of stratigraphic terms used for the Yorkshire Jurassic Flora. From Hemingway & Knox 1973: 529.
In this work the Dogger is termed the Yorkshire Dogger in an attempt to remove confusion with the term Dogger as used differently by European geologists for the whole of the Middle Jurassic.

Stratigraphy of the Yorkshire Jurassic Flora

The deltaic rocks are divided by marine transgressions into four units. They are succeeded above by marine rocks of the Cornbrash and preceded by those of the Yorkshire Dogger and the Lias. In table 2 the familiar terminologies of Fox-Strangways (1892) and Hemingway (1949) are contrasted with a new terminology recently proposed and discussed by Hemingway & Knox (1973). Details of the new terms are given in table 3 and these terms are adopted subsequently in this work.

The outcrop of the base of the Saltwick Formation is shown in Fig. 4 p.18 and topography of the Yorkshire Jurassic outcrop on the same scale in Fig. 3 p.17 The Hasty Bank plant beds occur right at the base of the Saltwick Formation.

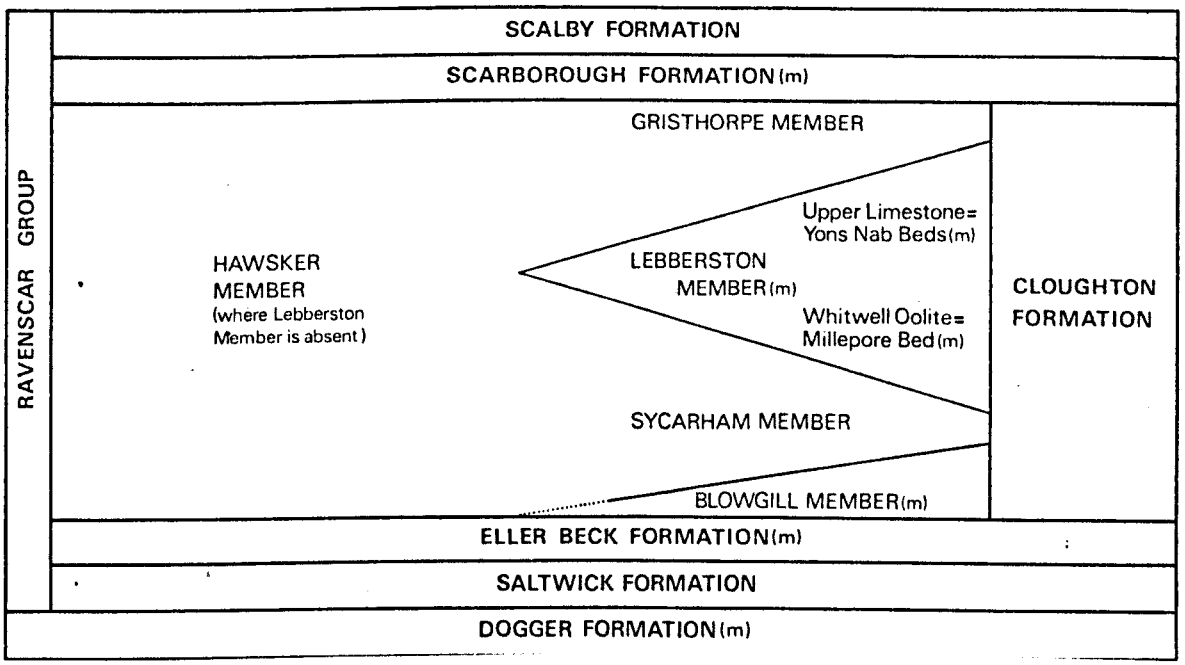


Table 3. Details of the stratigraphic terminology recently proposed for the Yorkshire Middle Jurassic. (m) = marine beds.
From Hemingway & Knox 1973: 530.

Fig. 6.

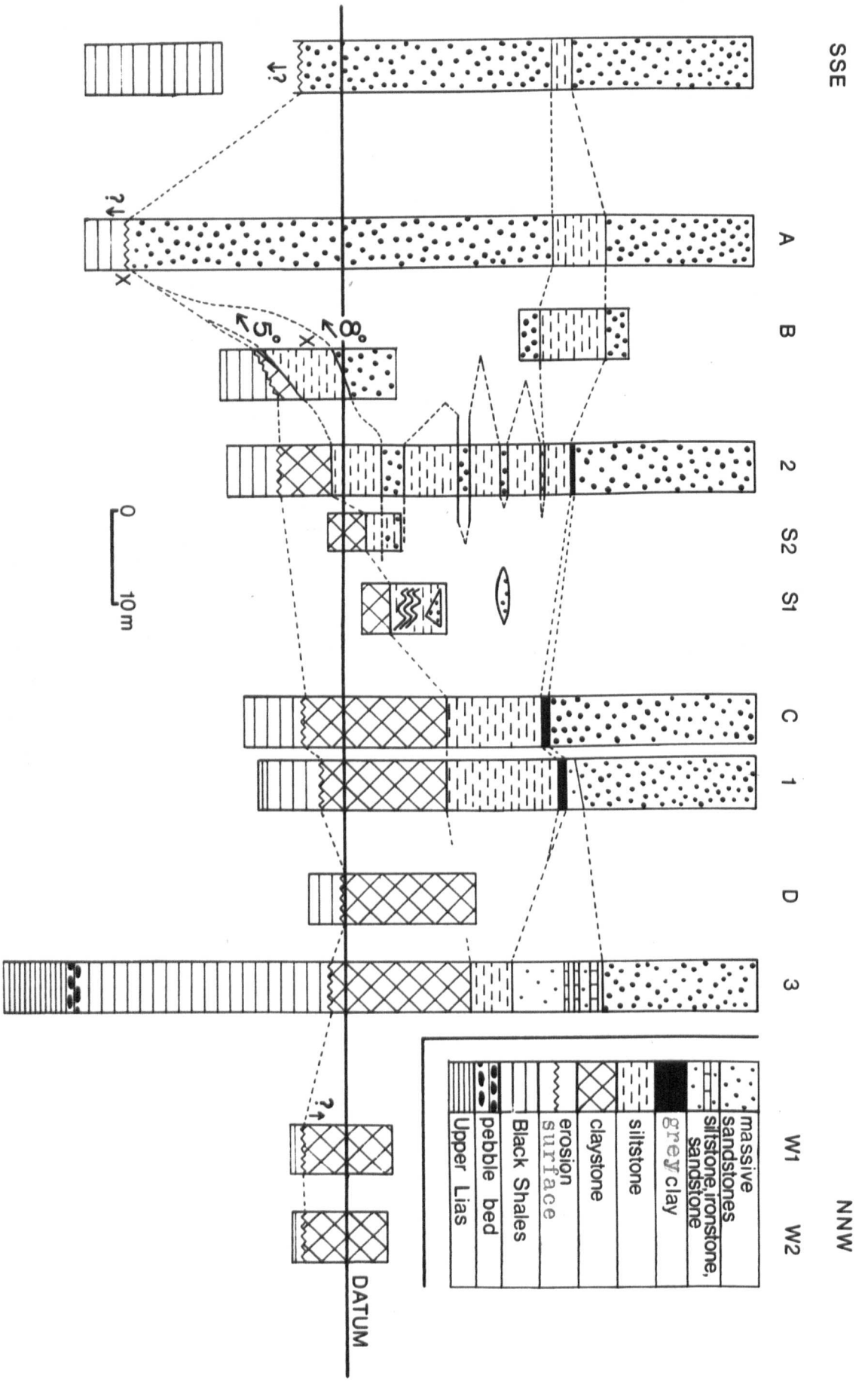


Fig. 6.

For explanation please turn to p. 27

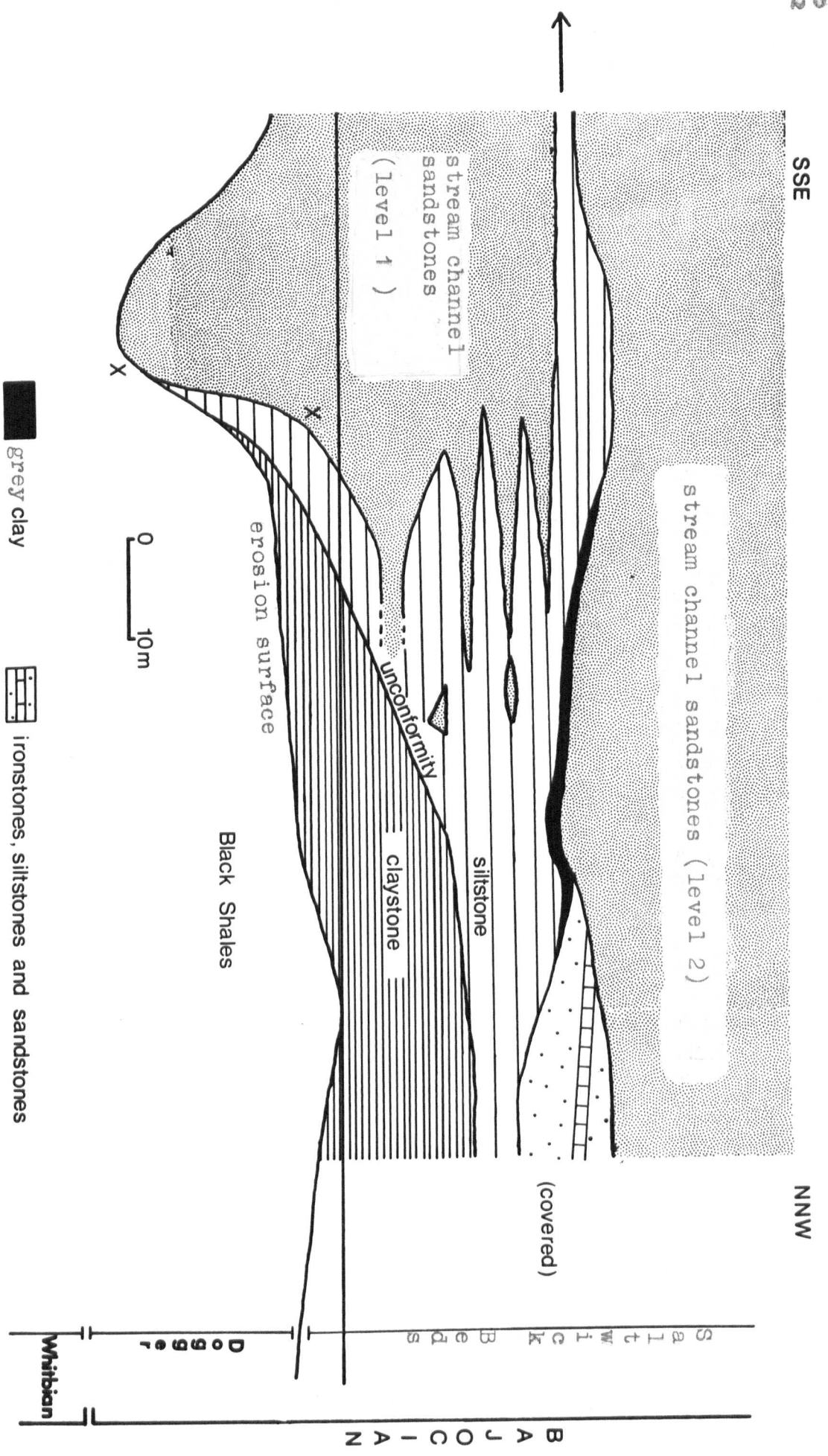


Fig. 7.
For explanation please turn to p.27.

Fig. 7.

Figs. 6,7. Geology of the Hasty Bank main plant bed (NZ 568 038).
Vertical scale 4 x horizontal.

Fig. 6. Measured sections. The datum level is marked by a steel stake which was hammered into the unconformity between the claystone and the Black Shales at the base of section D.

Fig. 7. Generalised section inferred from data given in Fig. 6. The main plant bed is composed of three lithological units: claystone, siltstone and grey clay. The uppermost part of the siltstone continues southwards (arrowed) for some 200 m and thickens to form plant beds B and C at the two points shown in Fig. 5 p.20

Stream channel sandstones dominate the outcrop at Hasty Bank (Fig. 5) and occur at two levels. The lower (level 1) occurs at about the same horizon as the main plant bed and is succeeded upwards by level 2. The level 2 sandstones are a persistent feature of the Saltwick Formation for many miles.

2: STRATIGRAPHY AND SEDIMENTOLOGY OF THE HASTY BANK PLANT BEDS.

Age of the plant beds.

The Hasty Bank plant beds outcrop at the base of the freshwater deltaic rocks and are preceded by marine rocks of the Lias and Yorkshire Dogger. Like the similar beds at Roseberry Topping their age was once regarded as Liassic, chiefly because Pachypteris papillosa was mistakenly identified with the Lower Liassic fossil Thinnfeldia rhomboidalis Ettingshausen and also because the plant beds were thought to intergrade with the Lias. It was later shown that the main plant bed in fact lies on the eroded top of the underlying marine shales and the mistaken identity of Pachypteris was corrected (Harris 1964, 1964a, Muir 1964, Thomas & Bose 1959). For these reasons Harris suggests that the plant beds are of Saltwick Formation (Lower Deltaic) age.

Muir (1964), however, reported that microplankton of marine origin occurs in the main plant bed and this revived the old idea that it may have been deposited in marine or brackish conditions. On the basis of this plankton and also the miospore assemblages she suggested that the main plant bed belongs to the Yorkshire Dogger, although its sedimentology is typical of the Saltwick Formation. Van Konijnenburg (1971) accepts Muir's view and points out that the distinctive assemblage of plant fossils at Hasty Bank tends to support it.

As the possibility that the plankton of Muir was redeposited from underlying marine beds has not yet been excluded I provisionally accept in this thesis the Saltwick

Formation age suggested by Harris.

Details of the Hasty Bank exposure (NZ 568038)

The outcrop is sketched in Fig. 5 (p.20) and the individual geological sections studied are shown in Fig. 6 (p.25) A generalised section through the main plant bed is shown in Fig. 7 (p.26).

Passing upwards from earlier to younger rocks the major sedimentological change is an increase in grain size, from claystones through siltstones to stream channel sandstones. Such a change is characteristic of the beginning of deltaic sedimentation in general (Selley 1970).

The main lithologies exposed at Hasty Bank and their environments of deposition are as follows:

Lower Jurassic (Toarcian stage)

The Lias

Liassic shales are exposed on the slope beneath the plant beds. In the uppermost layers they are brittle brownish-grey claystones named the Alum Shales which elsewhere in Yorkshire yield ammonites of the bifrons and communis zones (Fox-Strangways 1892). They also yield abundant marine microplankton, chiefly acritarchs, but plant macrofossils of terrestrial origin are almost entirely lacking. These facts indicate that the Alum Shales were deposited from a sea and it is known that this sea was of considerable geographical extent, stretching for example to Dorset in the South of England (Fox-Strangways 1892).

Middle Jurassic (Bajocian stage)

The Yorkshire Dogger

This is a lithologically variable formation though characteristically pebbly (Hemingway 1963). It is

represented at Hasty Bank by the Black Shales facies, of murchisonae age (Black 1934; Rastall & Hemingway 1943 and 1949). These shales were assigned to the Aalenian stage by Black but as this term has since become obsolete they are now incorporated in the Lower Bajocian (Hemingway 1963).

Although the Black Shales look very similar to the underlying Alum Shales the junction between the two lithologies is an unconformity, marked by a pebble bed. The pebbles probably represent removal of several earlier ammonite zones by erosion.

Other than rare ammonites the characteristic fossils of the Black Shales are small lamellibranchs (Posidonia). A few fragmentary plant macrofossils of terrestrial origin, chiefly wood and Phlebopteris woodwardii, occur in them, and marine acritarchs are abundant. These shales are therefore marine rocks but the terrestrial plants indicate that they were probably deposited nearer to land than the Lias.

The Black Shales probably represent prodelta deposits and thus heralded the advance of the delta proper (Selley 1970).

The erosion surface of Harris 1964a (Muir 1964)

Harris showed that the top of the Black Shales was weathered to a yellow colour. Because of this he inferred that the weathering represented ancient erosion of the Black Shales and thus their unconformity with the succeeding main plant bed. The Shales form an angular contact with the plant bed, shown in Fig. 7, p.86 and as both of these lithologies are more or less level-bedded this angularity is consistent with unconformity. The angle of contact however is small (5°) and may well have been caused by Recent slumping

which is often severe at Hasty Bank. I think an erosion surface representing a non-sequence in deposition is therefore indicated rather than an unconformity.

In 1972 Dr. Knox discovered Diplocraterion burrows which penetrate the topmost 5cm of the Black Shales and open into the erosion surface (Farrow 1966). The burrows are filled with sand and cuticle fragments such as Equisetum columnare. The limitation of sand to these burrows within lithologies which are dominantly composed of claystone is further evidence for a non-sequence representing removal, by erosion, of sandy layers which must at one time have been deposited above them. Nevertheless, sand of similar appearance occurs in the basal 3 cm of the plant bed. For this reason I do not suggest that the non sequence represents any great gap in time and it may indeed be a very minor one. These burrows and the occurrence in them of cuticles derived from land plants suggests an inshore marine or brackish regime of deposition, possibly for the basal layers of the plant beds and certainly for the period represented by the non-sequence.

The Saltwick beds.

These are Bajocian in age and probably Lower Bajocian. Though their precise ammonite zonation is uncertain the age is probably younger than murchisonae and earlier than discites (Bate 1967: 134).

The stratigraphy and sedimentology of the Saltwick beds at Hasty Bank reflect that of the formation as a whole (Knox 1969). Typically the earliest sediments of the formation are horizontally bedded shaley claystones or siltstones and erosional channelling was delayed until a

few feet of fine-grained sediments had been laid down. The channels are filled with sandstone and occur at three levels of which the lower two are exposed at Hasty Bank. I call these level 1 (the earlier one) and level 2 (the younger one).

Hasty Bank is atypical of the formation as a whole only in that some of the beds are rich in terrestrial plant fossils and in the occurrence of marine microplankton.

The main plant bed

1. The Claystone component

This is almost entirely composed of a micaceous claystone which is light brownish-grey to brownish-black in colour. It corresponds to a layer of comparable lithology and stratigraphic horizon at Roseberry Topping which has been termed the "basal black layer" by Harris.

The basal 15-30 cm of the claystone is composed of an exceptionally hard, very micaceous and massive matrix which shows steeply inclined cross bedding planes. The plant fossils in it are sparse and occur dominantly as tiny fragments. In the basal 3 cm of sections 2 and D impersistent lenses of a sandy leaf coal, less than 0.5 cm thick, were seen. Here the plant fragments again are tiny although abundant. The intimate association of plant fragments with coarse-grained sediment defines a drifted flora (Harris 1952). It is the only occurrence of sand in the claystone component and presumably represents a phase of energetic deposition, most of the sand and associated coal having been removed later by erosion. Such thin impersistent sandy layers are a general feature of the Saltwick Formation near its base. Knox (1969) suggests that

this sand was sometimes probably reworked from the Yorkshire Dogger though it also looks like sand found in the Saltwick Formation and its derivation is therefore uncertain.

In other parts of the claystone the fragment size of the plant fossils is typically large enough to give good hand specimens. Fracture of the matrix is dominantly conchoidal, the size of the resulting blocks varying from horizon to horizon and rarely exceeding about 10 cm in width. Parting planes are chiefly formed by the fossil leaves: where leaves are abundant the parting is good and where sparse it is poor. Trough cross-bedding is developed throughout. At places lenses of rock of varying size, up to a metre or more in breadth and about 10 or 20 cm thick occur in which the bedding is horizontal. The occurrence of these lenses suggests that deposition may have occurred in a complex of shifting small channels or pools though details of the bedding require further study.

Pyrite spheres are abundant in the claystone and rarely larger nodules up to 1 cm in width are seen. The spheres are $<$ 1 mm in diameter and are usually weathered to form tiny white-coloured flecks. Each is composed of numerous spherules.

The junction with the succeeding siltstone component is marked by an angular unconformity the sloping surface of which was smoothed by compactional slipping and scoured irregularly by erosion.

2. The Siltstone component

This is micaceous and light brownish-grey to dark brownish-grey in colour. The range of grain size is

considerable, from clay to fine sand. To the North, at section 3, it is fine-grained and supports a root bed. Southwards the grain size gradually increases towards the neighbouring level 1 stream channel sandstones, and the upper part of the siltstone becomes interbedded with sandy extensions from them (Figs. 6 p.25 and 7 p.26). In sections 1 and 2 the silt is laminated, the laminae occurring at a concentration of about three per cm though this is variable. The laminae are composed of white sandstone about 1 mm thick and become strongly marked nearer to the stream channel sandstones. They expand occasionally to form small, irregular pockets or lenses of sand a few mm thick, especially near the channel. Predominantly they run horizontally though in section S1 they dip northwards towards the claystone at about 5^{o} and there show small folds owing to slumping prior to final solidification (Fig. 6). Isolated wedges and lenses of sandstone also occur in the siltstone near to the stream channel (Fig. 7).

Plant fossils are abundant throughout the siltstone though less so than in the claystone. The largest fragments and in the least abundance occur near the neighbouring stream channel sandstones.

These facts suggest overwhelmingly that the deposition of the siltstone and the plant fossils in it was intimately related to that of the neighbouring stream channel sandstones. The lamination also shows that this deposition was rhythmic, probably occurring in floods. The manner of deposition of the siltstone is considered below (p.37).

Parting of the siltstone is variable and is generally similar to that of the claystone though near the stream channel the better developed parting planes are often

micaceous and only sparsely covered by plant fossils. Here the mica rather than the plants must determine the parting. Trough cross bedding occurs but on a larger scale than in the claystone. Fracturing is irregular and often gives large blocks exceeding 10 cm in width. Pyrite spheres about 1 mm wide are common but I did not see any larger nodules like those seen in the claystone.

Recent weathering of both claystone and siltstone is commonly strongly marked, giving rise to colours in various shades of olive, pink, yellow, orange and brown. Occasionally leaves swirled as in a whirlpool and crossing the prevailing bedding obliquely or sometimes even vertically are seen. This indicates that currents were involved in their deposition.

In both lithologies some of the massive layers have a distinctly earthy texture. The mica flakes and the fossils in them show no preferred orientation and this is unusual (there is no evidence of bioturbation).

3. The grey clay

This is variable in thickness and its exposure runs along the contour at the base of the succeeding level 2 sandstones. Its structure is massive but in the lower part grades down into the siltstone component. Though usually medium-grey in colour the clay is almost black in section 2.

The dominant plant fossils of the grey clay are fusain and dispersed cuticles and this is different from the siltstones which are dominated by good hand specimens of leaves and reproductive organs. The clay may have been deposited in very shallow turbulent water such as may sometimes be seen at the present day in a marshy environment.

The ironstone, siltstone, sandstone unit (Figs.6,7) p.25-26

The lens-shaped exposure suggests a stream channel or lagoon, the beds are more or less horizontal and the sandstones flaggy. Plant fossils occur chiefly as small fragments of cuticles and a few poorly developed upright roots which are smaller than those of Equisetum columnare. As bedded ironstones and abundant Botryococcus occur in this unit I imagine the water flow was intermittent and sometimes almost stagnant. The cuticle fragments are associated with the sandy layers, thus indicating that they form a drifted flora. Many of them are redeposited in the sense of Harris (1952).

The level 2 sandstone (Figs. 5 p.20 and 7)

This is composed of several lens-shaped masses of cross-bedded sandstone. The lenses are discrete although intimately interbedded with neighbouring ones. Each is virtually devoid of plant fossils except for a basal layer of logs and fusain.

These features are typical of ancient stream channels, each lens representing a single infilled channel. They probably indicate a phase of deposition involving a complex of moderately erosional shifting or braided streams (Selley 1970).

The main leaf coal (Fig. 5)

This occurs at about 20 m above the base of the level 2 sandstones and was described briefly by Hill (1974). At the northern end of its outcrop the section is:

	metres
(Quaternary peat)	0.5
flaggy sandstones	1.0

	metres
friable grey-brown to dark grey claystone, speckled with fusain	1·0
The Hasty Bank main leaf coal. This is sandy and the plant fossils fragmentary (drifted)	0·05
Orange-brown sandstone irregularly interbedded with thin layers of grey clay. The clay contains plant fossil fragments, notably detached leaves of Marskea thomasiana	0·1
(overgrown)	4·0
level 2 sandstone	21·0
main plant bed (section D)	7·0

Deposition of the main plant bed siltstone

There can be little doubt that the siltstone of the main plant bed was deposited in direct relation to the sandstones of the stream channel which is seen exposed in cross section immediately to the South of it in the level 1 sandstone. This channel is infilled with laminated cross-bedded sandstones which are almost devoid of plant fossils in the parts seen (the base is covered by fallen blocks).

The lower half of this stream channel has almost every characteristic described by Black (1928) for erosional channels, including a pronounced discontinuity with the downwarped siltstone (X-X on Figs. 6 and 7, p. 25-26). Had only this lower part of the channel been preserved the single cycle of erosion and deposition represented would indicate that it

was a washout (Black 1928; Hill & van Konijnenburg 1973). However Figs. 6 and 7 show that the upper half is not only interbedded with the siltstone but the extensions of the sandstone must represent several flow cycles of high energy. Thus although the stream which deposited the sand had an actively erosive first cycle it then settled down to become a more ordinary stream. The sandy extensions from the channel and isolated lenses and wedges of sandstone are typical of point bar deposits produced today on the concave side of meanders in streams of low velocity (Selley 1970).

A possible interpretation of the mode of deposition of the siltstones is that they represent levee deposits which flanked the sandy stream channel. The lamination of the silts, decreasing in intensity and also dipping away from the channel sandstones, is consistent with this interpretation. Knox (1969) regarded similar channel deposits seen elsewhere in the Saltwick Formation, as levees.

However, the absence of root growth near the channel is unlike levee deposits of modern deltas and there is no evidence to suggest that roots which once grew there were later removed by erosion. Furthermore the dip of the laminations is steeper than is usual in modern levees (Moore 1966). In discussion Dr. Knox has suggested to me that his levee interpretation is no longer sufficient to explain these anomalies. He tells me that on the basis of continued fieldwork these siltstones are in every case piled up against a palaeoslope like the one formed at Hasty Bank by the top of the claystone component.

These palaeoslopes dip towards the related sandstones.

This shows that deposition of the siltstones was limited to a restricted hollow, formed at Hasty Bank by erosion of the claystone, and like the associated sandstones this hollow is of the lens-shaped form of a stream channel in cross section.

The most plausible explanation of the siltstones thus seems to be that they were deposited within essentially the same channel as the neighbouring sandstones during phases of sluggish flow, rather than as overbank deposits such as levees or floodplains. I imagine sluggish flow was perhaps initiated as a result of impedence and alteration in direction of the main channel flow, initiated by the growth of point bars in the meandering stream.

It is interesting that no single kind of modern depositional environment is known which combines the sedimentological features seen in these Saltwick Formation siltstones (Dr. Knox).

The sandstone of the stream channel gives way upwards to the extensive layer of laminated siltstones which forms plant beds B and C. This siltstone probably represents the final sluggish phase of infilling of the channel after it was eventually abandoned (Selley 1970).

There is no evidence that the stream channels at Hasty Bank were part of a deltaic system of branching distributary channels. Furthermore, meandering streams of the kind seen at Hasty Bank are unusual in modern deltas. This raises the possibility that some of the earliest sediments of the Saltwick Formation may have been fluvial rather than deltaic. If Muir's claim that the Hasty Bank main plant bed is marine is right then it is tempting to speculate that a fluvio-marine environment of deposition may have obtained there,

thus partially reviving the old idea of "estuarine" deposition.

Further aspects of deposition of the fossil plants are discussed below, in chapters 4 and 5.

3: COLLECTING METHODS

Qualitative v. quantitative collecting

Though I did a good deal of qualitative (general) collecting an aim of my work at Hasty Bank was to detect associations of botanical significance between detached organs. A second aim was to detect any correlations which might be of depositional or "palaeoecological" significance.

It occurred to me that qualitative collecting was ill-suited to these aims. Considering for example the association of detached bennettitalean flowers Weltrichia whitbiensis (Nathorst) Harris and Williamsonia hildae Harris with their leaf Ptilophyllum pectinoides (Phillips) Phillips. Harris (1969) stated that he had recognised this association repeatedly from qualitative collecting but gave no numerical data to support it. Was he possibly imagining the association? Clearly if he was right these associations should show up strongly in quantitative data and from analogy to living plants one might also expect the leaf of the fossil to be more abundant than its flowers.

The presumed mangrove Pachypteris papillosa exemplifies the trend of my reasoning in relation to deposition and "palaeoecology". We know from qualitative collecting that this species occurs at the top of the plant bed as well as at the bottom. It would be interesting, however, to know if the plant perhaps decreases in abundance upwards in the bed, maybe implying a decrease in salinity. If such a trend occurs then quantitative work should be able to detect it.

In considering the potential merits of quantification Ager reminds us (1963:186-188) that the bias of qualitative collecting towards the larger or otherwise more conspicuous specimens is likely to be considerable.

In view of these potential advantages I decided to use a quantitative approach to collecting besides the conventional qualitative one.

A potential disadvantage of quantifying is of course that it is time-consuming compared with qualitative methods. It is also currently fashionable and I believe for this reason often becomes an end to itself without any clear vision of purpose. In appendix 1 I therefore consider the question of whether quantifying the flora at Hasty Bank was worthwhile in relation to the results obtained.

Sampling

Basically there is a vast wealth of information in a plant bed which could all be quantified, though to do this would involve an enormous effort and a great deal of intellectually superfluous repetition of data. Statisticians call this total information the target population or target. Sampling is meant to ensure that every "individual" of the target population has a chance of being represented in a restricted portion of it, termed the sample population or sample. In this way the minimum of effort is expended yet generalisations about the target can reasonably be inferred from the samples.

Difficulties arise when samples are unrepresentative, as generalisations about the target are then likely to be wrong, or at best, limited.

Sampling methods used by palaeobotanists for broadly similar purposes to the present study have been described occasionally (Davies, 1921; Chaney, 1924; Thomas, 1925), though none was considered sufficiently detailed to be useful at Hasty Bank. Detailed methods of similar scope

have however been used by Watts & Winter (1966) on Quaternary deposits.

The sampling methods used at Hasty Bank

A systematic method using very short channel-samples was adopted (Krumbein 1965). The term systematic means that the samples were taken according to a rigid pattern rather than randomly, and in this case geological sections were used. A channel-sample is essentially a trench of fixed dimensions, excavated perpendicular to the bedding.

Three sections were sampled, chosen because they are widely and evenly spaced along the exposure (sections 1, 2 and 3 of Figs. 5/, 6/, 7/). Section 1, located in the middle of the exposure, was studied in the greatest detail and the others in less detail for reasons given in appendix 1.

Before sampling could be attempted the sections had first to be cleared of a good deal of loose and heavily weathered surface debris, between 0·5 and 2·0m deep, to expose the solid relatively unweathered rock beneath. Each section was then excavated from the top downwards, to give a continuous series of short channel-samples (some 30 tons of sample material was examined in this way).

The area of each sample, plane to the bedding, was 50 x 50 cm square except in the claystone of section 1 where 25 x 25 cm^2 was used. Depths, perpendicular to the bedding, were either 10 or 20 cm depending on whether or not obvious vertical changes in the flora were detected.

Volumes of the channel-samples were thus 50 x 50 cm^2 in area x 10 or 20 cm deep, restricted to 25 x 25, x 10 or 20 cm in the claystone of section 1. The smaller volumes

Table 4.

Point on scale	Description of abundance and dominance	Numerical equivalent
10	Abundant. Easily the most abundant species in the sample	300 fragments
9	Abundant. Occurring with other species of similar abundance	300 fragments
8	Very common. The only species of this abundance in the sample	100-300 fragments
7	Very common. With other species of similar abundance	100-300 fragments
6	Common. The only species of this abundance in the sample	50-100 fragments
5	Common. With other species of similar abundance	50-100 fragments
4	Rare or localised	20-50 fragments
3	Rare	5-20 fragments
2	Very rare	about 5 fragments
1	one or two specimens	1-5 fragments

Table 4. Dominance-abundance scale of ten points used for quantitative work at Hasty Bank.

were used for the section 1 claystone in view of the great abundance of fossils there and the overwhelming tedium of making detailed counts on them.

Each sample volume was marked out with metal skewers and the rock then excavated. The blocks of rock thus obtained were split to the thinnest units of bedding practicable. The number (abundance) of determinable plant fragments in each volume was recorded under species headings on data sheets designed for the purpose. In section 1 the numbers were counted but in sections 2 and 3 they were estimated on an essentially logarithmic dominance-abundance scale of ten points shown in table 4 (opposite).

Unfortunately my choice of this scale was ill considered. The concept of dominance in points 5 to 10 is misleading and unnecessarily complicated. Though dominance is sometimes useful when applied to living communities in a plant-sociological sense, it has no other meaning than straightforward abundance when applied to fossil assemblages (see Kershaw 1973:12 for pertinent discussion).

For future work I would therefore adopt a scale defined simply against numerical equivalents, for example the following.

Point on scale	Estimated numerical equivalent (fragments)
10	500
9	300-500
8	200-300
7	100-200
6	75-100
5	50-75
4	20-50
3	5-20
2	about 5
1	1-5

The merits of estimating abundance on a scale of ten points rather than counting are discussed in appendix 1.

Information on other variables besides abundance was also recorded for each sample, for example sediment colour and lamination, fragment size of the plant fossils, kind of fracturing of the matrix, oxidation of cuticles.

At horizons listed below (table 5) the size of most of the plant fragments was too small for satisfactory determination in the field. From these about 300g of the rock was macerated in bulk and the number of cuticle fragments was estimated on an abundance scale of 1-5 described by Hill & van Konijnenburg (1973).

Section 1 (cm)	Section 2 (cm)	Section 3 (cm)
130-140	0-6	(0-10)+(25-40)
140-150	715-725	40-65
685-700	725-745	65-87
		92-122
		122-170
		170-225
		235-255
		255-280
		680-710

Table 5. Horizons examined by bulk maceration.

The main leaf coal was also investigated by bulk maceration.

Presentation of the data Figs. 9 p.56, 10 p.57, 11 p.58, 14 p.70, 22 p.111, 23 p.113, 26 p.147, 28 p.164.

The data on abundance is presented in the form of bar histograms essentially similar in construction to those of Watts & Winter (1966). Owing to difficulties in presentation the data on fragment size was omitted except in Fig. 14 p.70 and data on other variables was also omitted from all the

diagrams.

In each diagram the stratigraphy and sample horizon are shown vertically at the left and the species are arranged horizontally in the sequence of Hill & van Konijnenburg (1973). Each horizontal row of bars thus represents a single channel-sample and each vertical one a single species.

Accuracy of determinations

The majority of the determinations were made in the field. Whenever there was considerable doubt, however, a selection of specimens representing the observed range of gross form was collected and taken to the laboratory for further study. This was usually of the cuticles or spores and in all some 700 cuticle preparations were made. When the doubtfully determined species were rare (less than 5 specimens per sample) every specimen was examined in the laboratory. When abundant at least one specimen and usually about 5 or more were examined and appropriate adjustments of the field determinations were then made.

The accuracy of my determinations probably varies widely from species to species. I would regard the determinations of Pachypteris papillosa and Brachyphyllum crucis for example as almost 100% correct and this is my judgement for many species. At the other extreme however are two species which often look very similar to each other in gross form. These are Nilssonia tenuinervis Seward and Nilssoniopteris vittata (Brong.) Florin. Their cuticles are different but that of Nilssonia tenuinervis can scarcely ever be satisfactorily prepared and that of Nilssoniopteris vittata though more satisfactory as a rule is often poorly preserved at Hasty Bank.

The following species are normally easy to determine

though as they sometimes approach others I may well have sometimes determined them wrongly.

Equisetum columnare	small fragments of internode may mimic a wide range of other species
Dictyophyllum rugosum v. *Clathropteris obovata*	gross form looks similar when in small fragments
Sagenopteris colpodes v. *Ctenis kaneharai*	gross form looks similar when in small fragments
Pseudoctenis herriesii v. *Nilssonia kendalliae* v. *N. compta* v. *N. syllis*	extremes of the ranges of gross form overlap
Pseudoctenis oleosa v. *P. lanei*	extremes of the ranges of gross form overlap and the cuticles may also sometimes be very similar
Paracycas cteis v. *Pterophyllum spp.*	when the venation is poorly preserved the gross form looks similar
Ptilophyllum pectinoides v. *Otozamites penna*	extremes of the ranges of gross form overlap

Eretmophyllum whitbiense v. Sphenobaiera gyron	the form of small fragments may look similar
Marskea thomasiana v. Bilsdalea dura	the gross form of detached leaves looks similar
Elatides thomasii v. Haiburnia setosa v. Sewardiodendron laxum	small pieces of sterile shoots occasionally look similar in gross form and the cuticles can scarcely ever be satisfactorily prepared.

Clearly any limitation in the accuracy of determinations leads to a corresponding limitation in reliability of quantitative data on the species concerned.

4: ASSOCIATIONS OF BOTANICAL SIGNIFICANCE

A main aim of this thesis was to find out if quantitative collecting is a useful basis for detecting associations between organs which became detached from whole plants before their final burial. The considerations of individual species given in Part 7 show that every association previously recognised at Hasty Bank by other workers is indeed supported by the quantitative data. These associations are:

Marattia anglica + axes

Sagenopteris colpodes + Caytonia kendalliae

Nilssonia tenuinervis + Androstrobus wonnacottii

N. kendalliae + Beania cf. gracilis

Pseudoctenis lanei + Androstrobus prisma

Pachypteris papillosa + Pteroma thomasii

+ axis showing berets

Ptilophyllum pectinoides + Williamsonia hildae

+ Weltrichia whitbiensis + Cycadolepis hypene + Bucklandia pustulosa

Brachyphyllum mamillare + Araucarites phillipsii

+ male cone

Elatides thomasii + male and female cones.

The following associations recognised from the quantitative data are new:

Pseudoctenis oleosa + Androstrobus major (cycad)

Pseudoctenis lanei + Alvinia florinii (cycad)

Brachyphyllum crucis + Hirmerella crucis (conifer).

The association of Palissya harrisii cones with their shoots, also new, was recognised from qualitative collecting.

The following are general observations on the associations at Hasty Bank.

1. The leaves are nearly always much more abundant than the associated reproductive organs, and I believe this is generally true of living plants except for small organs such as seeds and pollen. Only very rarely does a determinable fructification occur in the absence of the leaf with which it normally occurs in association.
2. The fructification attributed to a particular species of leaf is usually at its most abundant where the leaf is abundant, and often (though by no means always) this is where the leaf occurs at its greatest abundance encountered in the locality. Whilst this is true, and also the general relationship that leaves are commoner than the associated fructifications, the exact ratio varies from sample to sample. For example the ratio of the counted abundance of Ptilophyllum pectinoides to Cycadolepis hypene Harris varies in the section 1 claystone from about 5:1 to 50:1.
3. The leaf is often abundant where the fructification which probably belonged to it is lacking (or else so rare that it was overlooked). This may reflect production and deposition of fructifications during a limited season compared with the leaves, though it may simply have been caused by taphonomic factors such as sorting of leaves from fructifications owing to density or size differences. Thefact that fructifications are scarcely ever found on their own (1. above) tends, however, to support the idea of seasonal production, though as fructifications are rare this view

may be statistically ill-founded.

4. In any one sample the associations are usually confusedly mixed up with other, unrelated, ones. However, as the mixture varies with the horizon the individual associations can normally be separated easily, by noting their fidelity at several horizons in relation to the others. Ideally the fidelity would be assessed in several localities.

5. When the leaves and fructifications of a plant are abundant the stems attributed to it sometimes also occur in association. This applies to stems of Brachyphyllum, Elatides, Pachypteris papillosa, Marattia anglica, and also those of Ptilophyllum pectinoides named Bucklandia pustulosa Harris. This is discussed on p.74-76.

6. About twenty of the reasonably common leaves and fern fronds have now been linked with at least one of their fructifications or with fertile fronds. For most of these reconstructions the evidence seems to me strong though I think further study is needed on Alvinia + Pseudoctenis lanei (or Paracycas cteis) and also on Beania cf. gracilis + Nilssonia kendalliae.
The following are the outstanding moderately common leaves occurring at Hasty Bank and for which the fructification indicated is at present unknown:

Species	Unknown fructification
Cladophlebis harrisii	fertile fronds
Nilssonia syllis	male and female
N. kendalliae	male
Ctenozamites cycadea	male and female
Ctenis kaneharai	male and female

Pachypteris papillosa	female
Eretmophyllum whitbiense	male and female
Sphenobaiera gyron	male and female
Palissya harrisii	male
Sewardiodendron laxum	male and female

Of the determinable reproductive structures known from Hasty Bank the following five have not yet been linked with a leaf:

Triletes areolatus

Osmundopsis sp. (fertile pinnae are known only)

Amphorispermum pullum

Androstrobus sp. A

Hastystrobus muirii

There is thus plenty of scope for further work on associations.

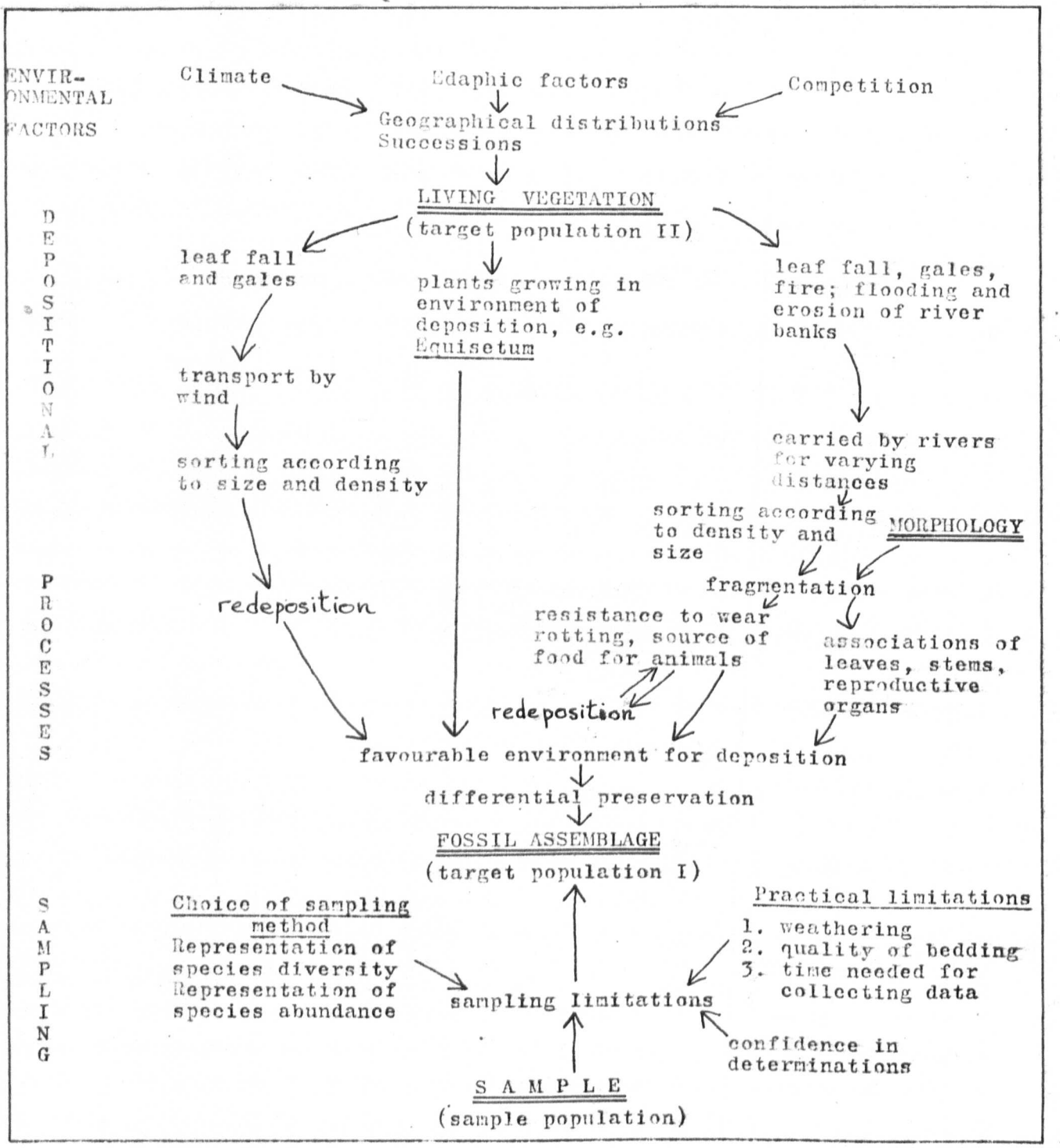


Fig.8. Diagram illustrating some of the many depositional processes which may act on living vegetation (target II) before it becomes a river-deposited fossil assemblage (target I). Limitations of sampling aimed at the targets and discussed in appendix 1 are also shown.

5: DEPOSITION OF THE FOSSIL PLANTS AT HASTY BANK AND THEIR "PALAEOECOLOGY"

Interpretation of the quantitative data

Interpretation of the quantitative data from the points of view of deposition and palaeoecology is difficult. In theory any correlations other than associations of botanical significance between detached organs should reflect depositional or palaeoecological factors, and if those of depositional significance can be extracted from the data any remaining correlations ought to be palaeoecological. However, a number of variable factors were probably involved in deposition of fossil plants in streams, and I believe any reasoned attempt at interpretations on "palaeoecology" should take these into account as fully as possible (Krasilov 1969b). Some of the factors are shown in Fig.8 and I will try to illustrate their complexity by discussing just one of them: fragmentation.

The extent of fragmentation of the fossil leaves at Hasty Bank varies tremendously from sample to sample, and for this reason abundance counts can scarcely be expected to reflect directly the real proportions of whole leaves deposited in the plant bed. Even less can they be expected to reflect the proportions produced by the different species when they were alive. Theoretically, however, the problem could be overcome by determining "cover" of the leaves on the bedding planes. This would at least give the relationship in terms of whole leaves as deposited in the bed. In a Quaternary or Recent deposit this value for cover might be related to that of leaves in leaf-litter produced by a st and

of living vegetation, and in turn related to cover in the stricter sense of that of the (known) whole plants. This kind of reasoning was used by Chaney (1924)in his study of the Bridge Creek fossil flora of Tertiary age.

A major difficulty, however, seems likely to be the proximity of the plants to the site of deposition, as one would expect plants growing nearby to be over-represented. Chaney's reasoning is further questionable because there is evidence that many Tertiary species are now extinct (Dilcher 1973). We can therefore only guess at the stature of the fossil plants and in consequence the average size and production of leaves by them.

Problems of this kind as a rule increase with the age of the deposit. In the Yorkshire Jurassic very few of the species are referable to living genera, and only one to a living species. Clearly living vegetation can hardly be used as a secure model for direct species comparisons. It also happens that whole leaves, as opposed to fragments, are rare in the Yorkshire Jurassic, and I think those seen tend to be the smaller ones of the original range of size. The average area of the whole leaves as produced by the living plants is often therefore unknown.

Because so many variables of this kind of complexity are involved in deposition it seems to me that the problem of fossil plant palaeoecology is an enormously difficult one, demanding study of as many different lines of available evidence as possible. The following discussion of Hasty Bank is for these reasons preliminary and I believe the validity of my conclusions needs testing not only against other evidence such as microplankton but also in other localities of the Saltwick Formation. Comparison with deposition in modern deltas might well be instructive.

Figs. 9 - 11.

Abundances and distributions of plant fossils at Hasty Bank, in sections 1, 2 and 3 through the main plant bed. The construction of the diagrams is explained on p. 46.

To facilitate comparison between the sections the counts from section 1 (Fig. 9) were calculated to their equivalent points on a 1-lo scale, using table 4, p.44. For the same reason the estimates in each diagram have been referred to a sample volume of 50x50x20 cm^3, using the following multiplication factors:

Volume of sample studied (cm^3)	Factor for conversion to 50x50 x 20 cm^3
50 x 50 x 10	x2
25 x 25 x 20	x4
25 x 25 x 10	x8

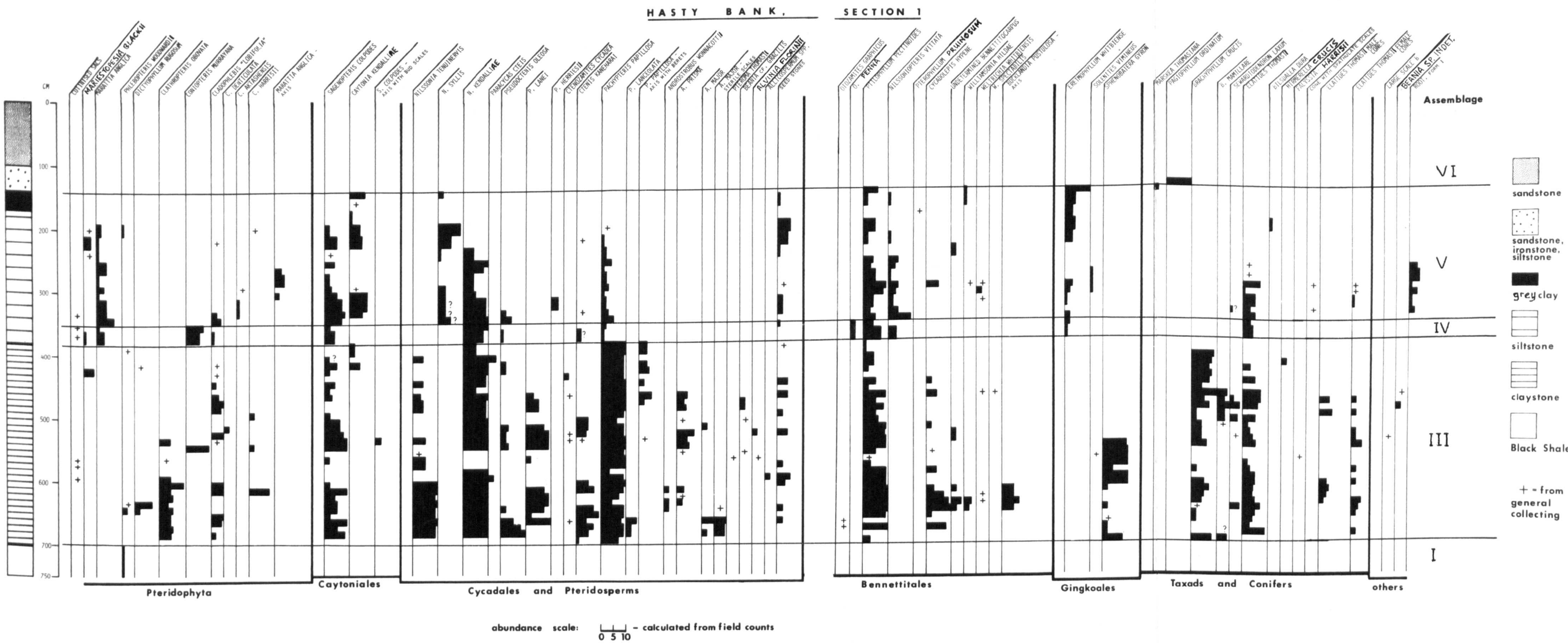

HASTY BANK, SECTION 1
Assemblage
VI
V
IV
III
I
sandstone
sandstone, ironstone, siltstone
grey clay
siltstone
claystone
Black Shales
+ = from general collecting
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Taxads and Conifers
others
abundance scale: 0 5 10 - calculated from field counts

Fig. 9.


HASTY BANK, SECTION 2.
CM
0
100
200
300
400
500
600
700
750
Assemblage
V
IV
III
II
grey clay
sandstone
siltstone
claystone
Black Shales
+ = from general collecting
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Conifers
other
abundance scale: 0 5 10 -estimated

Fig. 10.

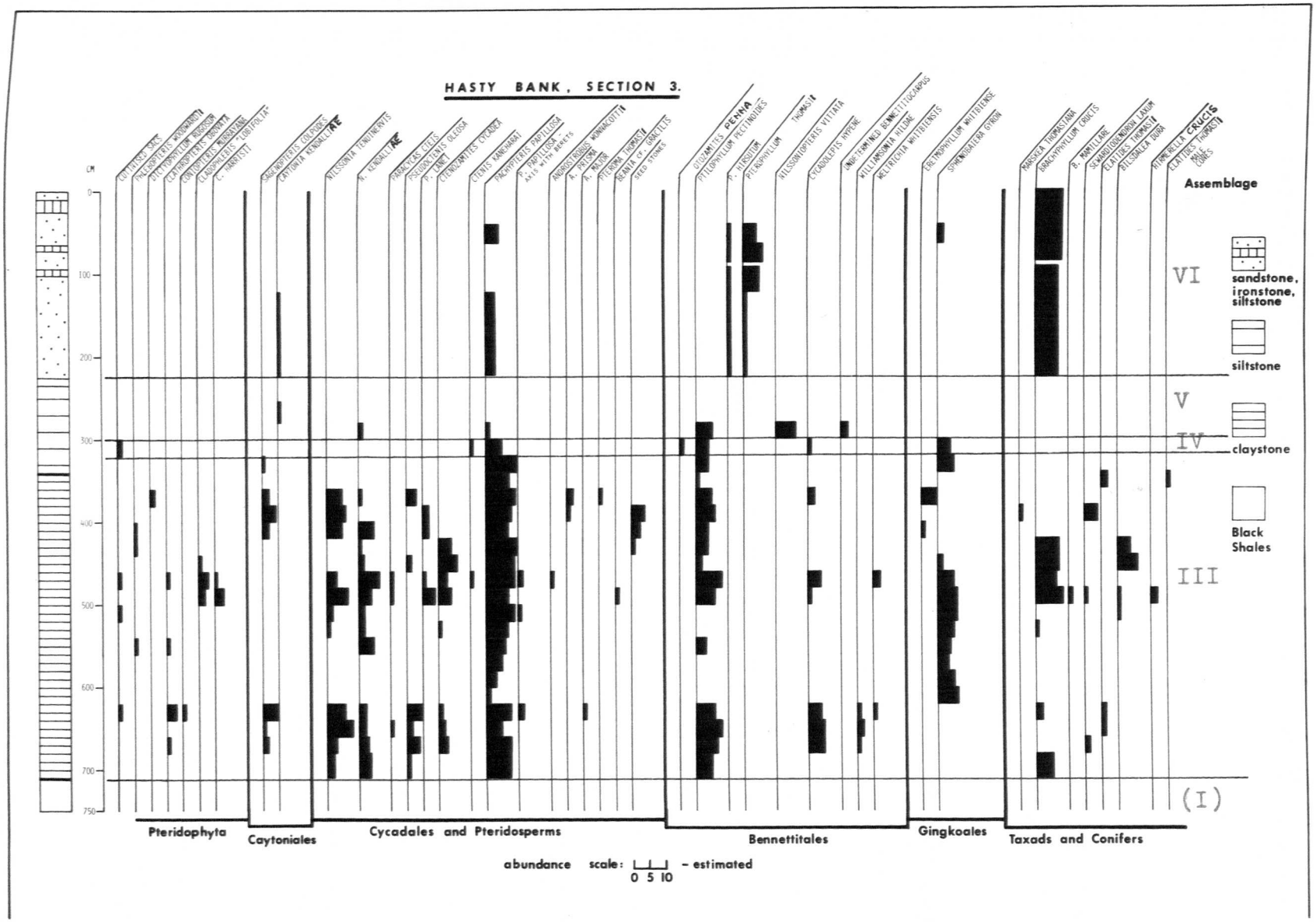

HASTY BANK, SECTION 3.
CM
0
100
200
300
400
500
600
700
750
Assemblage
VI
V
IV
III
(I)
sandstone, ironstone, siltstone
siltstone
claystone
Black Shales
Pteridophyta
Caytoniales
Cycadales and Pteridosperms
Bennettitales
Gingkoales
Taxads and Conifers
abundance scale: 0 5 10 – estimated

Fig. 11.

Vertical changes in the assemblages at Hasty Bank (Figs. 9-11, pp. 56-58.

These changes occurred in the Hasty Bank flora during the early growth of the delta. Seven groups of species, which I will call assemblages, may be defined. Starting with the oldest these are as follows.

Assemblage I occupies the Black Shales of the Yorkshire Dogger and except in worm burrows only one determinable species occurs in it, Phlebopteris woodwardii.

Assemblage II is restricted to section 2. It occurs at the base of the claystone of the main plant bed and a component of it is the sandy leaf coal mentioned on page 32. Its flora resembles assemblages III, IV and V but differs in having Ptilophyllum hirsutum and Pterophyllum thomasii.

Assemblage III is characteristic of the claystone of the main bed but also extends into the lowermost parts of the siltstone. Species diversity, especially of Filicales, is higher than in the other assemblages. Characteristic species are: Cladophlebis harrisii, Clathropteris obovata, Nilssonia tenuinervis, Pseudoctenis lanei, Ctenozamites cycadea, Sphenobaiera gyron, Hirmerella crucis, Brachyphyllum crucis, Brachyphyllum mamillare. Whilst the occurrences of these species at Hasty Bank are limited almost entirely to assemblage III the following are almost entirely absent from it: Marattia anglica, Nilssonia syllis,

Table 6. Abundances of species in the Hasty Bank main leaf coal, estimated on a scale of 1-5 and then doubled to bring them arbitrarily onto a scale of 1-10.

SPECIES	ESTIMATE OF ABUNDANCE
Triletes areolatus	2
Cutinised sac	2
Caytonia kendalliae (seeds)	4
Amphorispermum pullum	2
cf. Zamites johannae	4
Ptilophyllum hirsutum	2
Pterophyllum thomasii	8
Marskea thomasiana	5

Nilssoniopteris vittata.

Assemblage V occupies the grey clay and the upper parts of the siltstone. It is poorly defined in section 3. The occurrences of the following species are limited almost entirely to it: Marattia anglica, Nilssonia syllis, Nilssoniopteris vittata, whilst the following are almost entirely absent: Cladophlebis harrisii, Clathropteris obovata, Pseudoctenis lanei, Ctenozamites cycadea, Sphenobaiera gyron, Hirmerella crucis, Brachyphyllum crucis, B. mamillare.

Assemblage IV is transitional between III and V but differs from both in having Otozamites penna (= O. gramineus). It occupies the lower part of the siltstone.

Assemblage VI occupies the lithological unit composed of interbedded sandstones, ironstones and siltstones. It resembles assemblages II and VII in having Ptilophyllum hirsutum and Pterophyllum thomasii but differs from both in having Pagiophyllum ordinatum.

Assemblage VII (shown in table 6, opposite) is that of the Hasty Bank main leaf coal. It resembles assemblages II and VI in having Ptilophyllum hirsutum and Pterophyllum thomasii, though differing from both of them in lacking Pachypteris papillosa and Brachyphyllum crucis.

I feel sure that the upwards disappearance of certain species above a particular assemblage was not caused by evolutionary change nor by extinction as nearly every Hasty

Bank species is also known from younger beds.

The assemblages may be compared as follows. III, IV and V.

The greater diversity of assemblage III, the flora of the claystone, is to be expected for statistical reasons as explained in appendix 1 (p.190). Thus the limitation of certain rare species, for example Paracycas cteis, to assemblage III may well have no statistical significance. This certainly seems to be the case for Ctenozamites cycadea: in Figs. 9 -11/pp.56-58 this species is shown limited to the claystone (III) though after much general collecting I also found it in the siltstone (V). Conversely the limitation of certain rare species to the siltstone (V), for example Pterophyllum pruinosum, is likely to be statistically significant.

The main correlation of the species which define these assemblages is with the different kinds of lithology, claystone (III) v. siltstone (IV and V). This suggests to me that the conditions of deposition caused the differences, rather than, at any rate directly, "palaeoecology". I should point out, however, that besides the differences in the floras defining the assemblages they also have a good deal in common. The following species occur abundantly and occur in all of them: Nilssonia kendalliae, Sagenopteris colpodes, Pachypteris papillosa, Ptilophyllum pectinoides Elatides thomasii. This shows that whilst the deposition of some species was affected by the change in lithology from claystone to siltstone that of certain other species apparently was not. It suggests that the differences were not caused by differential preservation.

The extent of sorting and fragmentation of the plant

* as the associations are strong and the fragment size larg

fossils, their cuticle thicknesses and associations of leaves with stems and reproductive organs, are similar in both the claystone and siltstone. The differences in their assemblages can scarcely therefore reflect differences in drifting (sorting) in the sense of Black (1929) and it seems likely that each of the assemblages represents a selection from the nearby vegetation of the delta (and saltwater species). I speculate that those species present and abundant in all three assemblages were possibly dominants in the vegetation , whilst those which define the particular assemblages might be subordinate species (perhaps sensitive to changes of edaphic factors reflected in deposition of claystone v. siltstone). However, equally plausible alternative speculations are possible and it is easy to think of criticisms of both these and the one just given. The plain fact is that there is insufficient evidence to make the conceptual leap from observed fact to palaeoecology a cogent one.

The floras of assemblages III - V represent nearly every species presently known at Hasty Bank. There is no evidence to suggest that any one of the assemblages was drifted more than the others taking them each as a whole. Apart from the component of presumed mangrove and saltmarsh species I will therefore call these assemblages the "normal" Hasty Bank flora, which probably grew fairly nearby. Nevertheless, certain individual species such as Bilsdalea dura and Eretmophyllum whitbiense nearly always occur as drifted remains both in these assemblages at Hasty Bank and also elsewhere. These may possibly have originated somewhat further inland from the majority of species in the

normal flora. Thus although I will refer, for purposes of discussion, to the normal flora as belonging to a single geographical zone of vegetation on the delta, I recognise that in reality it may have originated from several such zones.

The presumed mangrove-like species of Harris (1964) are Brachyphyllum crucis and Pachypteris papillosa. He suggested that since Brachyphyllum crucis is a constant associate of Pachypteris papillosa the two species probably shared a saltwater habitat. However, B. crucis occurs without P. papillosa in the Millepore bed and thus it seems unlikely that they always without exception occurred together when they were alive. It also happens that at Hasty Bank P. papillosa is sometimes abundant where B. crucis is entirely lacking, for example in assemblage V. Like B. crucis two other species, Cladophlebis harrisii and Nilssonia kendalliae are nearly always associated with P. papillosa, both at Hasty Bank and elsewhere in Yorkshire. Neither of these species has in any sense a mangrove-like morphology though from this association with P. papillosa it seems possible that they were also linked with saltwater, perhaps in the way of Acrostichum aureum L.: a plant which grows on tropical salt-marshes at the present day.

Assemblage IV is of sedimentological interest because of its transitional nature and also because, although level-bedded, it slopes, following along the top of the claystone. A possible explanation is that the assemblage IV silts were laid down by a stream (A) which eroded the top of the claystone and that this stream was later exploited by one

(B) whose silts form assemblage V. This latter stream probably eroded another erosion surface marked by the sloping top of assemblage IV. The possible sequence of events is illustrated in Fig. 12 .

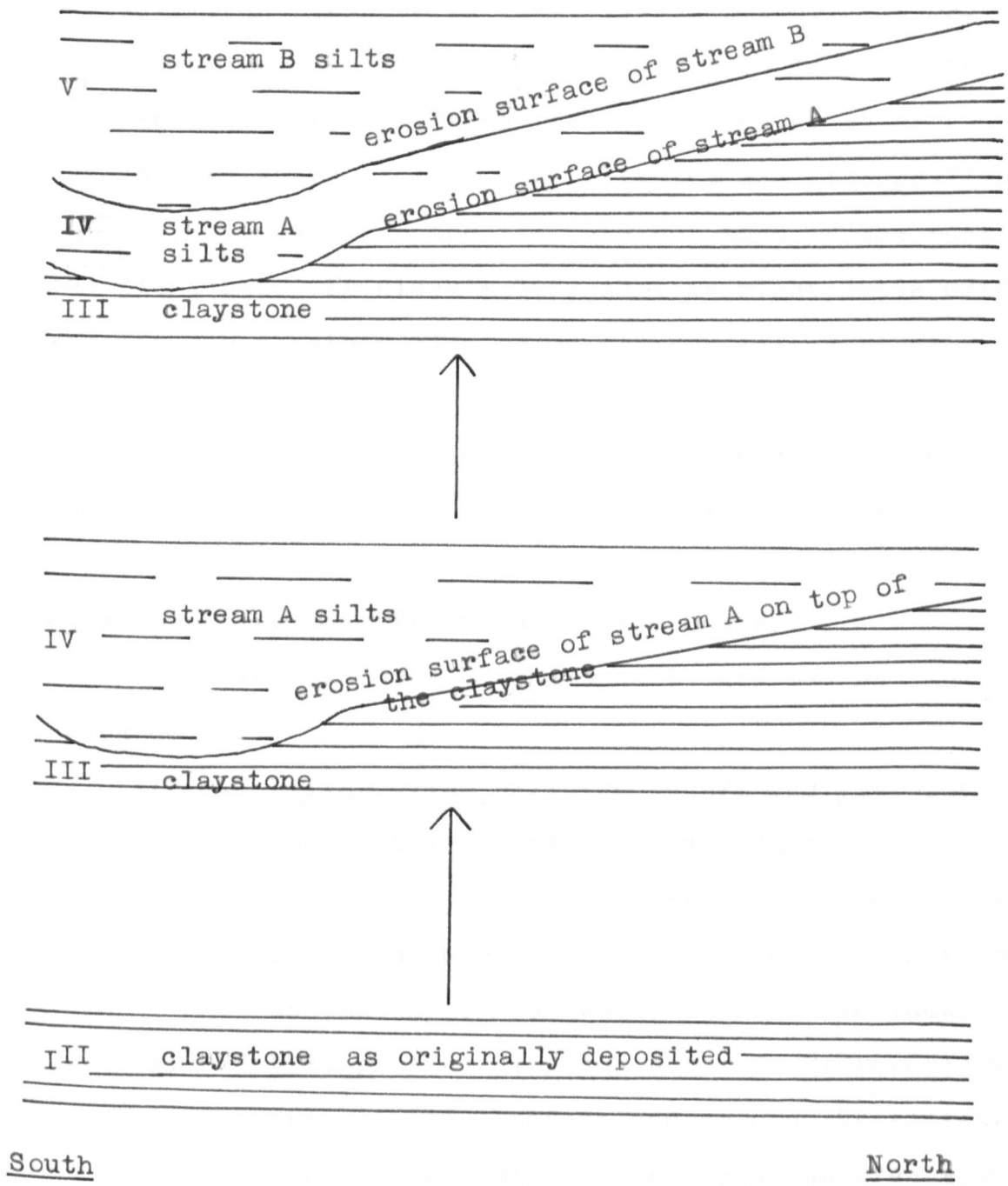


Fig. 12. A possible origin of the sloping yet level-bedded assemblage IV.

II, VI, VII.

In each of these assemblages, unlike III-V, the plant fossils uniformly occur as small fragments and they are associated with deposition of sand. Each assemblage is therefore drifted. Because of their depositional similarity any changes in their floras potentially may be a fairly simple reflection of "palaeoecological" factors.

An interesting fact is that all three of these assemblages share Ptilophyllum hirsutum and Pterophyllum thomasii though these species were not seen in the rest of the plant bed. If Black's 1929 idea is right these drifted species may possibly have grown further inland from the "normal" Hasty Bank flora represented by assemblages III-V. I believe they must have grown in the delta, however, because they are known from hand specimens in other localities at the base of the Saltwick Formation, for example Whitby Long Bight and Marske Quarry.

The chief features of the assemblages may be compared:

VII. Ptilophyllum hirsutum occurs and Pterophyllum thomasii is at its most abundant at Hasty Bank. Their average fragment size is on the whole larger than in the other two assemblages. Saltwater species are lacking.

VI. Ptilophyllum hirsutum occurs. Pterophyllum thomasii is abundant and so are the saltwater species Pachypteris papillosa and Brachyphyllum crucis which are lacking from VII.

II. Ptilophyllum hirsutum and Pterophyllum thomasii are very rare. The size of the fragments seen

was small. Pachypteris papillosa and Brachyphyllum crucis however are overwhelmingly abundant and their fragment size on average is larger than in VI.

This certainly shows that the saltwater species Pachypteris papillosa and Brachyphyllum crucis were replaced upwards in the deltaic rocks at Hasty Bank by Ptilophyllum hirsutum and Pterophyllum thomasii, and there is evidence from their drifted character that these latter species originated from a zone of vegetation growing inland to the normal Hasty Bank flora. The changes upwards represent a succession on one spot though as it is correlated with delta growth this is equivalent to a succession inland (Fig. 13).

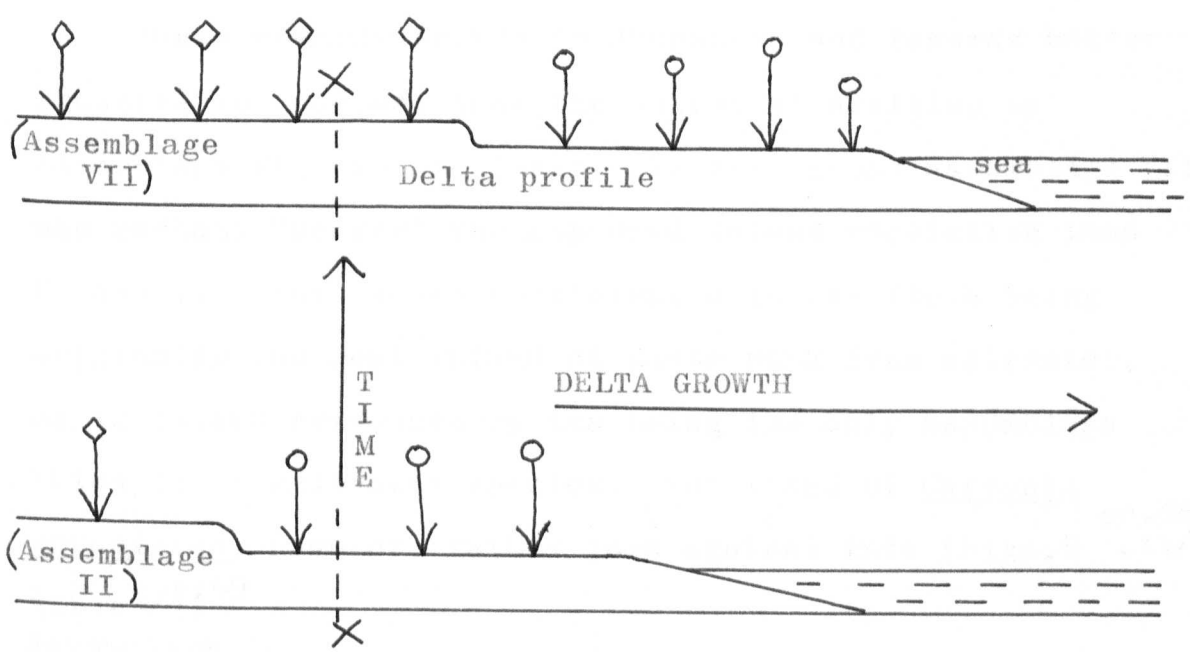


Fig. 13. Diagram showing how a succession upwards (with time) in a growing delta at the point x-x merely reflects a geographical succession. ↓: saltwater species, ↓ : species growing further back on the delta.

As these horizons were studied by bulk maceration full comparison with the channel-samples is limited. Nevertheless it is interesting that one of the species characteristic of assemblage VII (Table 6/ p.59) and abundant there also occurs in assemblages III-V though very rare there: this is Marskea thomasiana (= Taxus jurassica). Like Pterophyllum thomasii and Ptilophyllum hirsutum this species also shows a gradual upwards increase in its fragment size and abundance at Hasty Bank. It was recorded from assemblage III as a single poorly preserved detached leaf and from a few better-preserved leaves in assemblage V. It occurs as abundant and well preserved leaves with occasional shoot fragments in assemblage VII. Marskea may therefore have grown inland along with Ptilophyllum hirsutum and Pterophyllum thomasii.

These upwards trends in abundance and towards better preservation suggest that the extent of drifting in assemblage VII was the least. In this sense assemblage VII was perhaps "nearer" the supposed inland vegetation than VI and II. This seems consistent with its flora being originally the most inland at Hasty Bank from saltwater, as is indeed evidenced by its being the only assemblage which lacks saltwater species. The trend of Caytonia kendalliae, however, rather goes against this (Figs. 9 pp. 56-58 -11/, table 6/ p. 59

Assemblage I.

The occurrence of Phlebopteris woodwardii in marine deposits of the Yorkshire Dogger Black Shales is interesting. It is the only land plant known from these beds and has also been found in them elsewhere by Dr. Knox.

This occurrence doubtless reflects the fact that unlike most other Yorkshire species P. woodwardii is preserved as

fusain (Harris 1958, 1961). It was therefore probably considerably more resistant to water-wear than other species and this would explain why it was carried farther out into the Dogger "sea". Harris (1961:109) suggests that Phlebopteris was probably a plant of inland heaths subject to fires initiated by lightning. I agree.

Summary and discussion of the vertical changes in the Hasty Bank flora.

The lengthy comparisons given above are essentially qualitative, based simply on association with presumed saltwater species and also on evidence for drifting. Cladophlebis harrisii appears to be exclusively associated with Pachypteris papillosa, a saltwater species, whilst Brachyphyllum crucis and Nilssonia kendalliae are much more often associated with P. papillosa than not. This group of species may therefore all be saltwater species. From their succulent and xeromorphic morphology some may have been mangroves but others are more likely to have been saltmarsh plants or perhaps ordinary plants growing very near to the saltwater species. A large group of species, however, called here the normal Hasty Bank flora, whilst commonly associated with saltwater species also commonly occur elsewhere without them, for example Marattia anglica, Sewardiodendron laxum and Brachyphyllum mamillare. These species thus probably grew somewhat inland to the saltwater species. Some of them nearly always occur as drifted remains, for example Bilsdalea dura, and may therefore have grown further inland.

A third group of species occurs only as small (drifted) fragments when associated with the saltwater species, and

at Hasty Bank they are seen as large fragments and in abundance only where the saltwater species are lacking. These species are Ptilophyllum hirsutum, Marskea thomasiana and Pterophyllum thomasii. In certain other localities they are known from even larger fragments and in these localities they do not occur associated with saltwater species. These facts may indicate that Ptilophyllum hirsutum, Marskea thomasiana and Pterophyllum thomasii grew further inland from other species occurring at Hasty Bank.

Although vertically these groups of species overlap they gradually replace each other upwards in the Hasty Bank plant beds. This is a further line of evidence suggesting that they may represent a succession of zones of vegetation on the delta, going away from saltwater. There is no evidence however that any of the species grew a long way inland, except for Phlebopteris woodwardii.

I believe that my ideas about Ptilophyllum hirsutum, Marskea thomasiana and Pterophyllum thomasii need to be tested rigorously by further work on the localities in which they occur as hand specimens, for example Marske Quarry, Whitby Long Bight and Roseberry Topping. If they do sometimes occur as hand specimens in association with saltwater species then the evidence from Hasty Bank that they grew inland to the normal flora would be much weakened.

Variation of species distributions and abundances in the siltstone component of the main plant bed (Figs. 7/, p.26 14p.70).

The siltstone probably represents the deposits of a

Fig. 14.

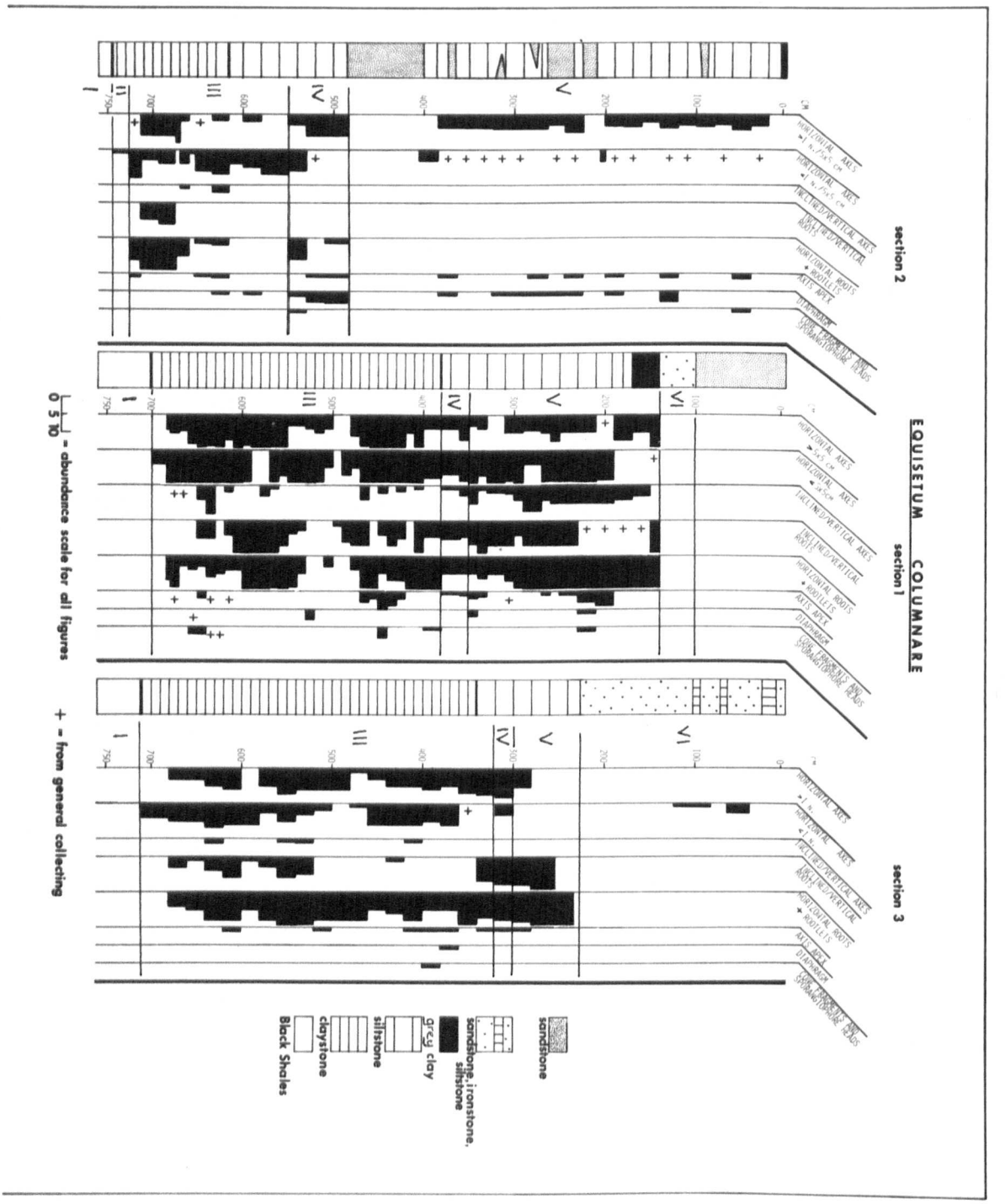

EQUISETUM COLUMNARE
section 2
section 1
section 3
0 5 10 = abundance scale for all figures
+ = from general collecting
sandstone
sandstone, ironstone, siltstone
grey clay
siltstone
claystone
Black Shales

Fig.14.

single stream channel, at any rate that part of it characterised by assemblage V (p.39). I would thus expect that the silts were laid down more or less contemporaneously in the three sampled sections. There is a marked decrease in grain size in the sequence section 2 > section 1 > section 3 (Fig. 7, p.26).

Equisetum columnare (Fig. 14, p.70)

This is the only species from Hasty Bank for which there is direct evidence that it grew there (Halle 1913). It occurs abundantly in parts of the siltstone as upright stems (either inclined to the bedding or vertical to it) and these gave out horizontal roots at successively higher levels.

At section 2, nearest the channel, large fragments of stems occur but none of these are upright and roots are neither attached nor associated. Clearly this material was washed or floated to the place of burial; presumably the water was too deep, and the sediment too coarse or deposited too rapidly, for the plant to grow. But where the water was presumably shallower, in sections 1 and C, there are abundant stems in position of growth. Presumably here there was a swamp of Equisetum like those seen along the margins of many modern streams and swamps. In section 3,

Fig. 14 (opposite) Comparison of abundances of Equisetum columnare Brgt. in sections 1, 2 and 3 of the Hasty Bank main plant bed.
1 N = 1 leaf sheath attached to the adjacent portion of internode.

where the water was shallowest, there are no upright stems but a dense truncated mass of horizontal and vertical roots is indirect evidence that E. columnare once grew there. I assume the stems grew at a slightly higher level than those in section 1 and they would thus be removed preferentially by erosion.

Though these long upright stems in the siltstone were almost certainly growing there I am uncertain about those in the claystone component of the main bed. Here they occur as short pieces of stem which may possibly have floated there like little boats, particularly in section 2 where no attached roots were seen. Coffin (1971) has shown experimentally that stems of living E. arvense L. can float upright in water for some time and thus floating of morphologically similar fossil plants before their burial would seem to have been a likely possibility.

Other species.

The floras of sections 1 and 2 are qualitatively similar though nearly all the reasonably common species are much more abundant in section 1, in particular Sagenopteris colpodes, Nilssonia kendalliae, N. syllis, Ptilophyllum pectinoides, Eretmophyllum whitbiense and Elatides thomasii. I think this almost uniform increase in abundance is probably a direct reflection of depositional factors. The average grain size in section 1 is smaller than that of section 2 and the thickness of the siltstone is about half, doubtless doubling the concentration of bedding planes. Given a uniform supply of leaves and silt an abundance increase by about 8 times in section 1 compared with section 2 might therefore be expected in comparable volumes of sediment. Size of the plant fragments probably also

contributes to the increased abundance because in section 1 they are on the whole more fragmented than in section 2.

The change in abundance of Pachypteris papillosa is strikingly contrary to the other species as its greater abundance is emphatically in section 2. Interpreting this against Fig.8/ facing p.54 I can think of at least four explanations which seem possible and they are all speculative:

1. Rotting and sorting

   As the leaf cuticle is thick it may have formed a strong sac around bubbles of gas produced on rotting of the succulent mesophyll. Possibly the cracks regarded by Harris (1964:129) as products of shrinkage were produced by bursting. If this idea is right P. papillosa leaves would be more buoyant than those of the other species with which it occurs and which were not succulent. Pachypteris papillosa might thus have been preferentially whisked away downstream compared with other species. Its gradual increase in abundance upwards in section 2, as the stream became increasingly sluggish, seems consistent with this.

2. The Pachypteris papillosa plant may have grown in the stream as floating masses like the modern Water Hyacinth (Eichornia). Such mats would probably not penetrate very effectively into the Equisetum swamp of section 1.

3. Leaves of Pachypteris may have been deposited in abundance in the Equisetum swamp but the juicy leaves

preferentially eaten by scavenging animals. . . .

4. As a mangrove P. papillosa may have grown downstream from the other species and thus have been deposited by the flow of tidal flooding whereas the other species from upstream would be deposited in the seawards flow of the stream.

This range of possible explanations exemplifies, at any rate to me, the unsatisfactory nature of trying to interpret palaeoecology from limited evidence. There seems to be too little evidence at Hasty Bank to make a sensible choice and the only solid fact is that P. papillosa obviously behaved peculiarly in deposition in relation to other species which occur with it in the siltstone. This increases the air of mystery already surrounding a plant of bizarre morphology.

Mode of deposition of the fossil plants at Hasty Bank

Where the fossils occur as large fragments (assemblages III-V) marked associations often occur between leaves with the appropriate fructifications and often also the stems. As these detached organs were of different size and presumably density this suggests that sorting of the plant debris was very slight. Hydrodynamically I would expect this if the majority of the species grew fairly near to Hasty Bank, the essence of the idea expressed by Black (1929) for the Gristhorpe bed.

The modern analogy of deposition in a tropical river may be an instructive one. In these rivers flooding after summer storms is commonplace. The floods erode and

swamp the river banks, trees are thus torn down and they are sometimes uprooted. In this way large numbers of branches and some whole trees with roots are swept downstream where they gradually become broken up. Under favourable conditions branches may sometimes be carried by water for over 50 km before finally breaking up into their separate organs (Ridley 1930) though after such long distances of transport the wood, fruits and seeds usually dominate, being the most resistant organs to wear, whilst the more delicate leaves are insignificant having been worn away.

The occurrence of two kinds of roots which are not in position of growth (p.188) and of fern rhizomes to be described elsewhere lends some support to the idea of uprooting and erosion of river banks. Nonetheless it is possible that these roots fell placidly from epiphytes which grew on trees overhanging the deltaic streams. Equally, although they look like roots they may have been tendrils.

Support for transport as whole plants and branches rather than from natural abscission of the organs comes from the marked associations of some species with their stems, often very thick trunk-like ones (p.52). These might have been carried in water for some distance though if this had been far I would expect there to be a greater amount of concentration separately of the organs into different horizons, owing to sorting, than in fact occurs at Hasty Bank.

Notably there are a few species whose leaves are often abundant but their stems and fructifications are unknown, at any rate at Hasty Bank. These species are Sphenobaiera gyron, Ctenozamites cycadea and Eretmophyllum

whitbiense. They also tend to vary in abundance more erratically than the majority of Hasty Bank species, often being abundant in one section whilst virtually absent at a comparable horizon in another just a few metres away. These leaves may perhaps have fallen as a result of natural abscission to form mats of leaf litter which only then became subjected to erosion and were carried downstream in chunks. Sphenobaiera gyron leaves are frequently oxidised, implying that they were redeposited and or rotted at some stage before their final burial.

The implication of this discussion is that the mode of deposition might not have been uniform for every species at Hasty Bank. I imagine some species were deposited as a direct result of erosion of the stream banks, doubtless because they grew there. However if this idea is right those species known solely from abundant leaves without either fructifications or stems may have been in some way protected from direct erosion, though their leaf litter was not. These species may have grown on slightly higher ground. Such ground might occasionally have been flooded (and thus the litter dredged and drained into the stream) but not so drastically eroded and dredged as the stream banks, which being on lower ground would be more deeply flooded. Alternative explanations are, however, possible and my ideas may be fundamentally wrong.

Classification of the plant beds at Hasty Bank

All five of Harris's (1952) plant beds occur at Hasty Bank though intergrading at one or more horizons. Redeposited fragments of Eretmophyllum whitbiense, for example, are present in abundance in the autochthonous Equisetum swamp of section 1 and both species occur in river-channel deposits. As mentioned on p.15 similar considerations apply to the Gristhorpe bed. Harris's classification clearly breaks down when applied to these rich localities.

Inland v. delta floras

The species known as drifted fragments from assemblages II, VI and VII also occur as hand specimens, either in the normal Hasty Bank flora (*Pachypteris papillosa*, *Brachyphyllum crucis*) or in other localities of comparable sedimentology and of similar age (*Ptilophyllum hirsutum*, *Pterophyllum thomasii*, *Marskea thomasiana*). This supports the view expressed on p.14 that drifted plants might have grown only a short distance inland from species growing in the "*in situ*" flora, rather than at great distances as has often been supposed.

Conservation of hand specimens

The more fragile hand specimens were strengthened by coating with an approximately 50% aqueous solution of "Polybond". This product is a water-based emulsion of polyvinylacetate (PVA) containing 55% solids and plasticised with 10% di-Butyl phthalate. It is made by Polybond Ltd., 42-44 Warsash Rd., Warsash, Southampton, to whom I am grateful for information about chemical composition. It is used widely as a concrete sealer and bonding agent.

The 50% solution was applied with a brush to the back of the less fragile blocks and on the more fragile ones to all areas except those of interest for observation and subsequent cuticle preparation. Coating of the more fragile specimens was carried out in the field but it was usually done in the laboratory. Undiluted Polybond was also used as a glue for repairing cracked and broken specimens.

Durability of the Polybond was crudely tested by observing the effects of various treatments on completely sealed specimens of matrix: heating at 35°C and 80°C for several days in air, in water to 100°C for a few minutes, standing in water at 20°C for 24 hours and in paraffin also for 24 hours. There was no net effect on the Hasty Bank matrix (claystone and siltstone) though swelling and disintegration of Gristhorpe matrix (claystone) occurred in the water treatments. This swelling also occurred in uncoated control specimens and thus the PVA coat can not have been the cause of it.

Maceration of completely coated specimens after one year showed that the PVA had no adverse effect on their

cuticles compared with uncoated ones. Nevertheless, in view of possible long term deleterious effects the area of interest was normally left uncoated. Cracks in the fossil substance itself were mended and crumbly fossils glued to the matrix using a paste of flour in water. This disappears on maceration and does no harm to the cuticles.

Comparison with other sealing agents, such as polyvinylchloride (PVC) and polybutylmethacrylate, showed that Polybond (PVA) was preferable. Polybutylmethacrylate is messy and PVC as applied from aerosol sprays is both toxic and not very effective. Varnishes such as Shellac were often used in the past but have generally been found destructive in the long term rather than conservative. In many cases the matrix of varnished specimens has become blistered, the film of varnish has lifted from the matrix and cuticles were destroyed or damaged by the treatment. Damage by varnishing has sometimes been so great that it has considerably impeded cuticular studies on old collections (Watson 1969:211). The use of ordinary varnishes is therefore to be strongly discouraged.

Hand specimens and cuticle preparations described in the taxonomic part of this thesis are located in the palaeobotanical collections of the Palaeontology Department, British Museum (Natural History) where they are to be registered after publication. Those forming the reference collection for the quantitative work are either in the palaeobotanical collections of Leeds University (hand specimens) or the British Museum (cuticle preparations).

Laboratory study of hand specimens

The gross form of the specimens was examined using good quality binocular microscopes. Commercial paraffin

(Kerosene) decolourised with animal charcoal was applied to the specimen when an increase in colour contrast with the matrix was required (Harris 1938:7). This proved a valuable technique and was specially useful when the fossil substance was preserved only as a very thin film. Paraffin is preferable to xylol which is more costly and is carcinogenic. Excavation of the matrix with needles (Lacey 1963:216) was occasionally useful.

Measurements of taxonomic characters were taken using either dividers or a calibrated eyepiece graticule.

Transfers of specimens were prepared when it was desirable to observe the surfaces facing the matrix and thus normally hidden from view. They were successful only with the flatter specimens and there were many failures on fossils such as Mariestopesia in which the coaly substance is fragile. A variation of Walton's technique, developed by Professor Harris (unpublished) for fragile specimens, gave the best results. The specimen to be transferred was painted thinly with one or two coats of a 1% solution of gold size in toluene, allowed to dry in dust free conditions and then transferred by the Walton method (Lacey 1968:247-249). Lakeside resin, obtained from the Cutrock Engineering Co. Ltd., 35 Ballards Lane, London N3, was preferred to balsam as it is simpler to use and less costly.

Cuticles and spores

Cuticles were prepared by Schulze maceration. This was carried out in a watch-glass kept inside a petri-dish lined with moist filter paper, a method described fully by Wesley 1954:169. Spores from sporangia were also prepared by this method though on a cavity slide and using 5% Schulze

solution (5g powdered $KClO_3$ in 100 ml nitric acid of sp.G.1·42). For delicate cuticles 5% Schulze was used and for robust ones a saturated solution. Because of the humid conditions of maceration the nitric acid becomes diluted, thus progressively slowing the reaction and in most cases preventing over-maceration. Nevertheless the progress of maceration was always periodically monitored using a binocular microscope. A 5% aqueous solution of 0·88 NH_4OH was used for the alkali stage of maceration.

In the many instances where they were fragmentary the cuticles were concentrated by centrifugation in an MSE bench centrifuge at settings 2-6. No observable damage was caused by this treatment. Spores were concentrated at settings 6-8.

For the routine quantitative work, where cuticles of many hundreds of specimens had to be prepared with maximum speed, the humid conditions of maceration were dispensed with. These macerations were done on porcelain staining tiles thus minimising time spent on washing apparatus, but there was inevitably less control over the rate of reaction. In this way up to 50 preparations per day were made.

The method of Harris (1926) was used for bulk macerations though Harris (1966) gives rather more refined methods.

After washing thoroughly in distilled water the macerated cuticles and spores were mounted in glycerin jelly (formula of Bradbury 1973:220). Any air-bubbles were removed from the jelly by applying a small drop of alcohol to them from the point of a needle. The mount was warmed for at least 30 minutes on a hot-plate at 30°C before application of the cover-slip, in an attempt to reduce long term drying

out of the glycerin jelly. To this end also the cover-slips were finally sealed with gold size.

1% safranin was sometimes used to stain the cuticles though staining was usually unnecessary.

Botryococcus and other acid-resistant microfossils were prepared using standard palynological techniques (Kummel & Raup 1965:530-587). 5% Schulze extraction was followed by centrifugation with bromoform-acetone to remove the bulk of the mineral particles and any remaining clay particles were finally removed with 48% aqueous HF.

Scanning electron microscopy

Standard techniques (Alvin 1970) were used except for the preparation of a Durofix replica of Mariestopesia as follows (pl.6).

1. The Counterpart impression surface (pl. 6 fig. 1) was flooded with acetone.
2. Before the acetone had evaporated an acetone-based nail varnish was gently brushed on.
3. 1. and 2. were repeated to ensure good penetration of the varnish into the cavities of the impression.
4. A solution of 1:1 Durofix glue (celloidin) and amyl acetate was applied until a tough film about 1mm thick was formed. This gave the replica a rigid base which was essential to prevent distortion during subsequent treatment.
5. The replica was pulled off the specimen and treated as a Walton transfer, in 48% HF, to remove all traces of matrix (Lacey 1968:247-249).
6. The replica (Pl.6 fig.2) was dried in dust-free conditions at room temperature.
7. After mounting on a specimen stub the replica was

coated with 200 A gold/palladium and viewed in the SEM.

Because replicating materials dissolved in mobile organic solvents were used this method gave good penetration of narrow crevices left in the matrix by the sporangia. A severe disadvantage, however, compared with other materials such as latex, is that the original specimen was disfigured. Chaloner & Gay (1973) have obtained moderately good replication with latex but the unpublished results of other workers suggest that silicone-rubber solutions of low viscosity may prove more useful in the future.

Replication of suitable impressions for study in the SEM is likely to prove a widely useful technique for studying their cellular patterns. These can rarely be seen clearly by the analogous method of reflected light because of light-scattering effects.

Illustrations

Drawing of hand specimens was done chiefly using a Lechetier-Barbe camera lucida. A few specimens were drawn free-hand and where done this is indicated on the captions to the relevant figures.

Photography of the hand specimens. Many of the Hasty Bank specimens are in a brown or dark brown coloured matrix against which they show poor contrast of colour. Contrast was therefore enhanced for photography by immersion of the specimens under decolourised paraffin. When details of surface relief were required the specimen was photographed dry in grazing light. The photographs were taken on a Focomat II with appropriate lighting (Blaker 1965). Ilford N30 and N40 plates or Agfa Scientia film were used.

Cuticles and spores were photographed using a Zeiss "Ultraphot II" photomicroscope in the Dept. of Plant Sciences of Leeds University and a Zeiss "Universal" photomicroscope at the British Museum (Natural History). In most cases the position of the photographed cuticle or spore is indicated on the slides by a mark in Indian ink. Kodak Panatomic-X or Ilford FP4 film was used.

7: SYSTEMATIC DESCRIPTIONS

The eighty species of plant fossils so far recorded from Hasty Bank have recently been listed by Hill & van Konijnenburg (1973) and Hill (1974). In the following pages a number of them are described and discussed. Formal synonymies are only given where they add to those given by Harris (1961, 1964, 1969).

ALGAE

CHLOROPHYCEAE

CHLOROCOCCALES

Genus Botryococcus Kützing 1849: 982

Botryococcus braunii Kützing
(Pl. 1)

1849.	Botryococcus braunii Kützing.	Kützing 1849:982
1955.	B. luteus Traverse,	Traverse 1955:79, pl. 13, fig. 148.
1972.	B. luteus Traverse.	Pocock 1972: 122, pl. 29 figs. 1-4.

Other references are nearly all to B. braunii Kützing.

DISCUSSION.

Botryococcus braunii is a planktonic colonial alga of long geological history, ranging from the Ordovician to the present day (Pocock 1972). The fossil material is morphologically indistinguishable from the living and thus the name B. luteus Traverse is here regarded as superfluous. The only difference from living material is in the colour of the cups and this merely reflects chemical changes which have occurred with time, the cups of macerated living and Quaternary material being colourless whilst in most of the older material when macerated they vary from yellow to brown.

This is the first record of B. braunii from the

British Lower and Middle Jurassic.

DISTRIBUTION

The Hasty Bank material was found in palynological preparations made from the marine rocks of the Lias, the brackish Black Shales and the "freshwater" plant beds (Fig. 7 , p. 26). It is rare in the Lias and increases in abundance upwards to the top of the main plant bed (assemblage VI) where it is associated with algal microfossils assigned to the genera Tasmanites, Crassosphaera and Pterospermopsis.

PTERIDOPHYTA

SPHENOPSIDA

EQUISETALES

Genus Equisetum L.

Equisetum columnare Brongniart
(Pl. 2. Fig. 15, p. 89)

BRANCHING (Pl. 2.)

A stem fragment from the siltstone shows the previously unknown branching of E. columnare. The fragment must have been orientated vertically when compressed because it approximates to a cross-section, showing the nodal diaphragm of the main stem surrounded by the bases of the branches.

The thick and coaly diaphragm of the main stem is smooth and is 9 mm in diameter. It is surrounded by a radially striated cortical zone 3 mm deep and this in turn by an incomplete whorl of branches. One side of the specimen broke off and was lost during collecting but the arrangement of the remaining branches suggests that originally the whorl completely encircled the stem.

At the base of each branch is a centrally placed cast of its nodal diaphragm which is < 1 mm in diameter. The

diaphragm is surrounded by a ring of tiny masses of coal which probably represent the nodal metaxylem. These masses in turn are surrounded by a cortex 1 mm deep which is invested in a leaf sheath like that of unbranched E. columnare (Harris 1961).

DISCUSSION

Attempts to prepare the cuticle were unsuccessful. The specimen is determined because it agrees with E. columnare in size, is associated with it in the field, and the form of the leaf sheaths is very similar. The diaphragm of the main stem, however, is atypical in lacking tubercles and in its substance being smooth and thick rather than thin and granular. The metaxylem masses of the branches are more coaly than the "tubercles" which are their equivalent in unbranched stems. I suggest that these differences are unlikely to indicate a taxonomic difference from E. columnare and probably represent modifications connected with the branching; I would expect increased vascular tissue to give a more coaly fossil.

The main stem of the branching specimen is 1.5cm wide and this is narrower than the average for E. columnare. If the stem tapered upwards as it does in living species this suggests that the branches were borne fairly high up. Evidently the branching was rare for although many hundreds of diaphragms from unbranched stems are known only the one just described shows the branching.

Harris (1961:19) describes fragments of slender detached "stems" sometimes found in association with E. columnare and I have found a few of these at Hasty Bank. As they are similar to the branches described above I

Fig. 15(opposite). Roots of Equisetum columnare Brongniart, from Hasty Bank.

a,b, fragments of rhizome showing attached roots.

c, fragment of a detached root showing its branching.

All the figures are x1.

identify them as such. Their scarcity compared with other parts of the plant again suggests that E. columnare rarely produced branches.

LEAF TEETH. (Harris 1961: p. 18; fig. 4I)

The leaf teeth of Hasty Bank E. columnare are commonly adpressed to the rhizomes, though referring to stems from several localities Harris (1961) states that this is unusual. Although he gives the maximum length of the leaf teeth as 5 mm they reach 12 mm in some of the specimens.

ROOTS (Fig. 15)

The roots of E. columnare have been described in detail by Halle (1913) and briefly by Harris (1961). Halle figures horizontal and vertical roots attached to stems.

Roots attached to Hasty Bank stems commonly branch three or four times, typically at angles of roughly 90°. The main roots and their branches may be either horizontal or vertical and are about 4 to 10 mm wide, whilst the smallest rootlets are about 0·5 to 1·0 mm wide. These rootlets usually run horizontally and often form a dense mat impressed upon the surfaces of larger fossils.

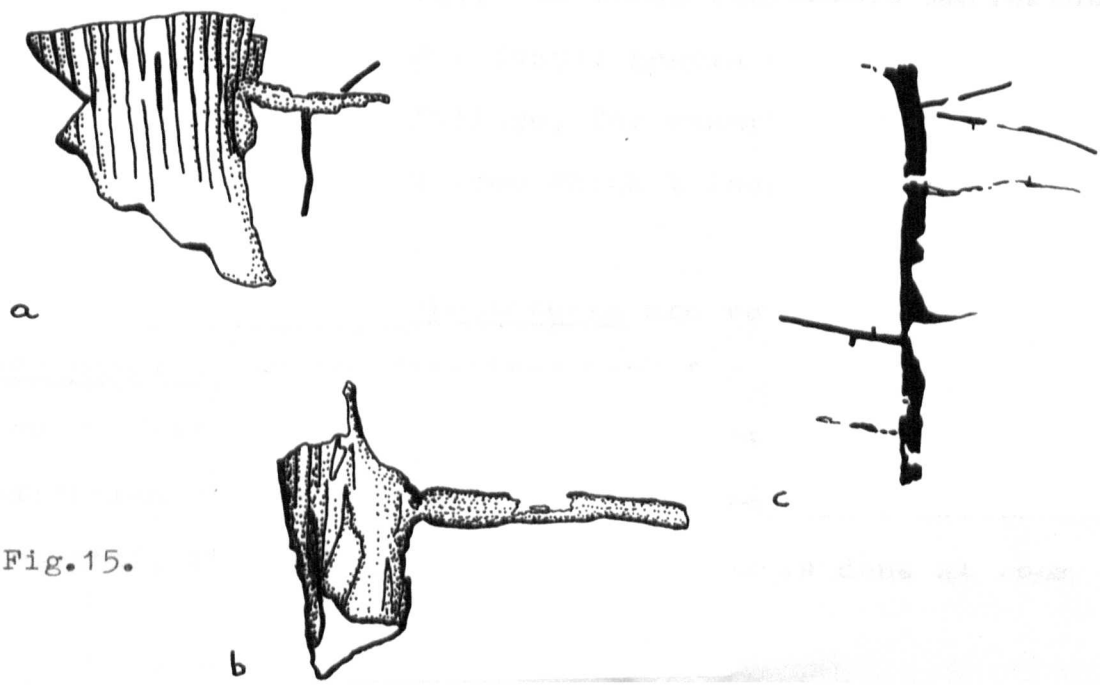


Fig.15.

FILICOPSIDA

EUSPORANGIATAE

MARATTIALES

Angiopteridaceae Christensen

Genus Mariestopesia nov. (manuscript name)

Mariestopesia blackii comb. nov.
(Pls. 3 - 9 Figs. 16- 22).

INTRODUCTION

This fern is one of the few Hasty Bank species which has been found nowhere else. It was first described from a single fertile frond fragment by van Cittert (1966) and assigned by her to the living genus Angiopteris. I have since collected 200 further fragments at Hasty Bank and study of these indicates that the form and arrangement of their sporangia was probably somewhat different from Angiopteris. The differences are here considered to be generic and the new genus Mariestopesia is instituted and described for the fossil.

The new genus differs from Angiopteris in having less compact sori and sporangia which are narrower in relation to their width. The sporangia were circular in transverse section rather than oval. In these characters Mariestopesia approaches certain older fossil genera of the Marattiales which had pecopterid foliage, for example Asterotheca and Eoangiopteris, and from which I imagine it might possibly have evolved.

The spores of Mariestopesia are very like those of Angiopteris and are described here for the first time. Under certain conditions they become swollen after Schulze oxidation at high temperatures (followed by extraction in ammonia), though not when the oxidation is done at room

* sori situated one on each vein or vein branch near

temperatures. Dispersed spores similar to those extracted from sporangia of Mariestopesia are known from the Jurassic of the Soviet Union.

Many of the pinnules are imperfectly preserved and often the tissue between the veins has disappeared. Where the veins have shifted laterally away from their usual angle to the midrib this suggests that the tissue between them disappeared before final compression.

In the following diagnoses and discussion the wall of the sporangium next to the lamina is termed dorsal and that nearest the placenta ventral.

Genus Mariestopesia nov.

DIAGNOSIS

[Fern frond whose ultimate segments ("pinnules") are known only].

Pinnules simple, lanceolate, having parallel single or once-forked veins arising from a central midrib and extending to the margin. Fertile pinnules bearing two rows of oval sori on the presumed lower side, * the pinnule margin. Ratio of length of sori to pinnule width not smaller than $\frac{1}{4}$. Sorus composed of several eusporangiate sporangia which are scarcely compressed laterally against each other. Sporangia narrowly ovoid in shape, probably circular in transverse section, dehiscing by a single longitudinal slit in the ventral wall. Cells of the sporangium wall uniformly elongated.

Spores formed in large numbers per sporangium, trilaesurate, sculpture predominantly verrucose.

Sterile pinnules similar to fertile in size and venation. [Pinnule base unknown].

The generic name is in honour of Dr. Marie C. Stopes, a famous palaeobotanist.

Mariestopesia blackii (van Cittert) comb. nov..

1966. Angiopteris neglecta van Cittert (non Ching et Wang 1959). van Cittert 1966, hobtype: pl. IIB

1973. A. neglecta van Cittert. Hill & van Konijnenburg 1973: 60, name in list

?1975. A. blackii (van Cittert). van Konijnenburg - van Cittert ?1975 (in MS), change of name to replace the invalid homonym A. neglecta van Cittert.

Emended diagnosis

Pinnules (known from fragments only) at least 6 cm long. Pinnule width 6.5 to 12 mm, uniform or slightly tapering, contracting over the distal 1 to 2 cm to an obtuse apex. Margin entire or slightly lobed, usually flat. Midrib more prominent on the (presumed) lower side, striated longitudinally, up to 1.6 mm wide and tapering to the apex. Veins parallel, arising at a small angle from the midrib and curving outwards to 60°-90° to the midrib (20°-60° near the apex), reaching the margin at a concentration of 6-13 per cm. Point of forking of the veins usually near the midrib. No fibrous strands (venuli recurrentes) seen between the veins.

Sterile pinnules similar to fertile in size and venation.

Sori oval, elongated in the direction of the veins, ending at about 1 mm from the margin and taking up about $\frac{1}{4}$ to $\frac{2}{3}$ of the pinnule width. Length of sorus 1.4 - 2.9 mm, length of placenta 0.2 - 0.9 mm.

Sporangia typically 6-9 (rarely up to 12) per sorus, each attached separately at its base to the placenta and tending to point radially from the centre of the sorus; circular in transverse section before compression; typically broadest at or below the middle (rarely above) and narrowing distally to an obtusely pointed tip which is often curved

towards the ventral side of the sporangium. Sporangia usually about twice as long as broad, ratio of length to breadth 1.4 - 3.2, length typically 0.8 mm and breadth 0.4 mm (range 0.5 - 1.1 x 0.3 - 0.6 mm). Ventral wall of sporangium showing a single slightly sunken dehiscence-slit along most of the length; cells of wall uniformly thickened and elongated longitudinally, becoming shorter towards the tip of the sporangium.

Spores about 3000 per sporangium, 20 - 30 µm wide, compressed to a round or oval shape with typically one, and sometimes two, strongly marked arcuate folds in the exine. Laesurae three low ridges on the exine, extending to a variable length and often at unequal angles to one another. Exine about 1 µm thick, composed of a very thin continuous basal layer bearing closely placed small verrucae which are of uniform size (about 0.5 to 1.0 µm) both proximally and distally. Neighbouring verrucae commonly fused to form short rugulae.

The majority of the specimens are located in the collections of the Palaeontology Dept. of the British Museum (Natural History), London, though the holotype is in the collections of the Botanical Museum and Herbarium, The University of Utrecht.

DESCRIPTION and DISCUSSION

Pinnule length. As there are no complete pinnules their length was estimated indirectly. Two methods were used. In the first the total length of the fragments was divided by the number which show the apex. This gave a length of 3.7 m which I feel sure is likely to be a gross overestimation. Perhaps the basal parts of the pinnules were preserved more often than the apices, as out of the total sample of some two hundred fragments there are only seven showing the apex.

FIGS. 16-18.

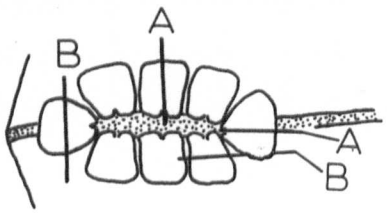


Fig.16. Plan view of a typical Angiopteris sorus, showing the orientation of planes of section A and B through the sporangia.

Angiopteris evecta Mariestopesia blackii

Fig.17. Diagrams of the typical appearance of sporangia viewed in planes A and B.

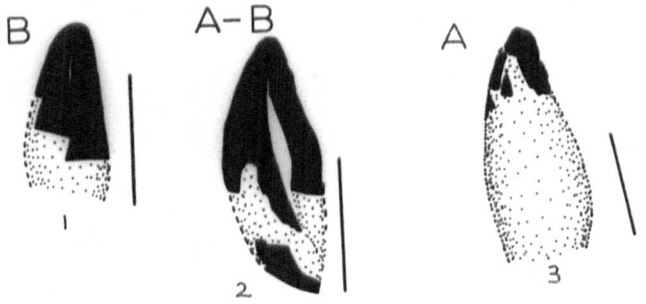


Fig.18. Shapes of Mariestopesia sporangia as observed when compressed in orientations A and B. 1,2 are from a transfer of specimen no. 32, and 3 from specimen no. 74. The vertical lines each represent 0.5 mm.

The second method uses measurements of midrib taper to match fragments of known length and similar width. Difficulties caused by unequal preservation are thus eliminated. When used for sixteen of the longer fragments this method gave estimates of pinnule length up to 10 cm, excluding the unknown base, and I regard this as reasonable.

Pinnule margin When clearly seen the margin is usually flat and it often looks entire. Sometimes, however, it is recurved, though the curve is directed either upwards or downwards and sometimes it is in both directions in one pinnule. Occasionally the margin is lobed (Pl. 4 fig. 2) though I think the lobes may sometimes have been produced by uneven wear of the pinnule margin during burial.

Sporangia Many of the sporangia are compressed in the planes A and B, as shown in Figs.17,18 /p.94. Since their width in the two planes is equal I conclude that before compression they were circular in transverse section (Walton 1936).

Frequently the dorsal wall of the sporangia is more strongly curved than the ventral (Pl. 5, figs. 4,5), and commonly a rather marked continuation of the curve forms the incurved tip seen in Pl. 5, fig. 4 and Pl. 6, figs. 5-7. In lightly compressed pinnules the parting planes pass through the substance of these curved sporangia and thus when such specimens are split the tips of the sporangia become broken off. Owing to their curve the tips are left embedded at an angle in the matrix of the Counterpart, hidden from direct view. As a consequence the residual parts of the sporangia exposed plane with the surfaces of the Part and Counterpart often look broader in shape than they actually are, looking somewhat like sporangia of Angiopteris. Pl. 6 fig. 1 shows the Counterpart of such a specimen. When a celloidin replica (p. 83) was prepared from it the otherwise invisible tips embedded in the

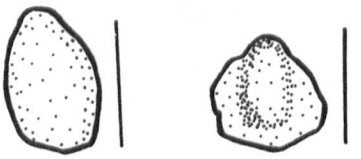


Fig. 19. Immature or aborted sporangia of Mariestopesia blackii, from specimen no. 36. The vertical line represents 0.5 mm.

matrix were retrieved and the narrow shape of the sporangia thus demonstrated (Pl. 6, figs. 2-5).

In heavily compressed pinnules the parting planes pass over the top of the more flattened sporangia rather than through them. Thus in these pinnules the shape of the whole unbroken sporangia is seen from the exposed surfaces of both Part and Counterpart. When present in such pinnules the incurved tip is compressed to a small lump (Pl. 6, fig. 6).

Immature or abortive sporangia

A few specimens have sporangia which although whole are broader than usual and thus look very like those of Angiopteris (Fig.19). These sporangia range in shape from a broad oval to circular, and are often folded or crumpled. They are of the smallest size seen in Mariestopesia and as they contain remarkably compact spore-masses are easily displaced entire from the matrix. Their spores not only show poorly developed exine sculpture but also were difficult to separate after Schulze maceration (even when treated with detergents and vibrated ultrasonically).

Rather than indicating identity with Angiopteris I think the facts just given show that these sporangia were probably immature or abortive.

Cells of the sporangium wall. The outlines of the thickened cells of the sporangium wall form strong ridges and grooves on both impressions and compressions (Pl. 6, figs. 4-7). Transfers of specimens in which the tissue between the veins is lacking display similar cells on the dorsal wall to those of the ventral, though because the sporangia are fragile transfer of their tips was unsuccessful. I have not seen a clearly defined patch of isodiametric cells on the dorsal wall such as occurs in Angiopteris.

Spores (Pls. 7,8,9)

The sporangia of most of the pinnules are fractured into tiny pieces and yielded only a few stray spores on maceration. Presumably these sporangia had shed most of their spores before burial. However, in about 10% of the specimens the fracturing is slight and as the sporangia of these contain large numbers of spores in the form of compact masses I presume they were undehisced.

The number of spores produced by Mariestopesia was counted from undehisced sporangia, using ones in which the spore masses separated into individual spores fairly readily in the ammonia stage of maceration. It proved impossible to prevent some loss of fragments during handling of the sporangia and thus the counts are almost certainly too low. The following counts, given to the nearest 100, were obtained from five sporangia of specimen no. 21:

1200; 3000; 3000; 1700; 2000.

The laesurae of the tetrad mark in Mariestopesia spores are typically of unequal length. Whilst in this they approach the monolaesurate condition I have not seen any properly monolaesurate spores.

Comparison with dispersed spores. (Pl. 7, figs. 4,5).

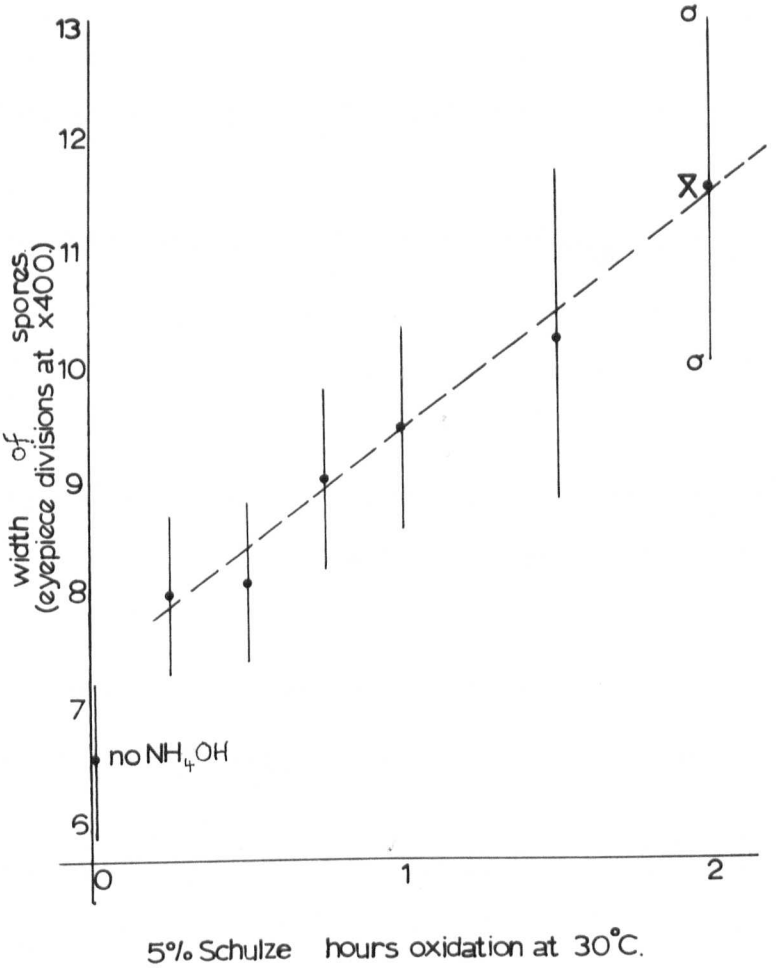
Mariestopesia spores sometimes show a symmetrical tetrad mark and then agree broadly with Verrucosisporites (Ibrahim & Kremp) Smith & Butterworth (Smith 1971). The more typical spores of Mariestopesia, which have an asymmetrical mark, could be confused with Marattisporites scabratus Couper, the presumed dispersed spore of Marattia anglica (Harris 1961, Couper 1958). However, both Marattisporites and spores extracted from Marattia anglica synangia typically have a

Fig. 20.

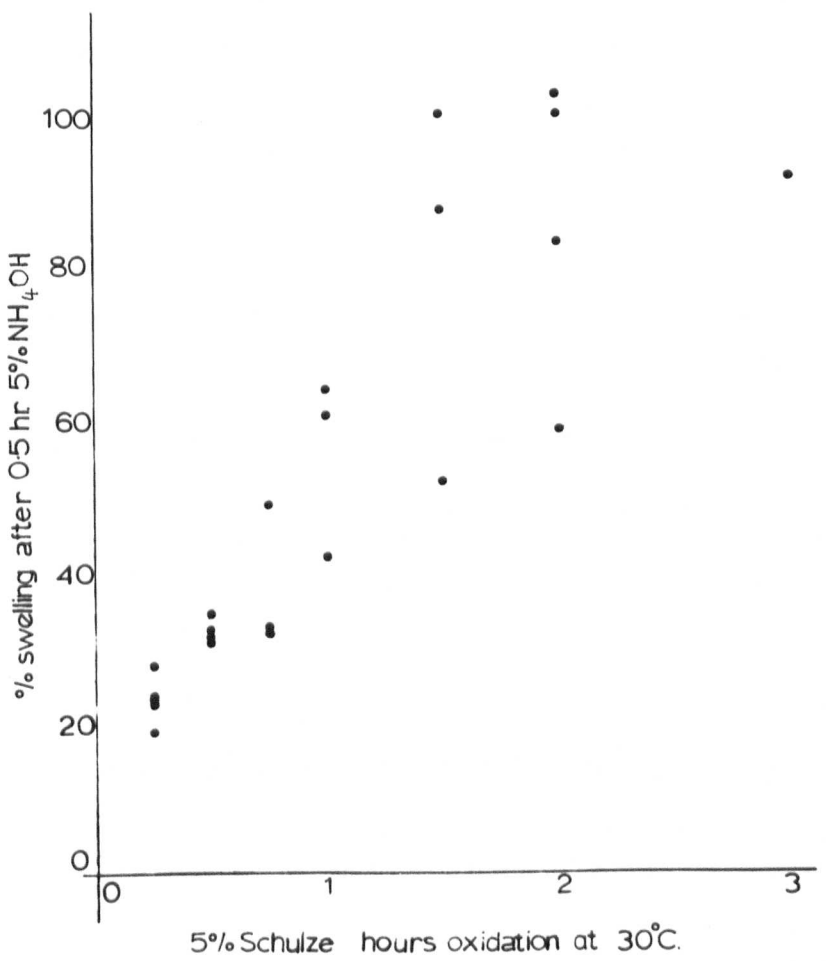
Schulze-Ammonia macerated spore-masses of Mariestopesia blackii, graphs showing the relationship between size of spores and duration of oxidation in Schulze solution.

A. Increase in the greatest width of spores situated at the outside of compact spore-masses. $\bar{x}$ = arithmetic mean, σ = standard deviation.

B. Scatter diagram showing the progressive increase in size of spore-masses with increasing duration of oxidation.


13
12
11
10
9
8
7
6
σ
X
σ
width of spores (eyepiece divisions at x400)
no NH_4OH
0
1
2
5% Schulze hours oxidation at 30°C.

A


100
80
60
40
20
0
% swelling after 0·5 hr 5% NH_4OH
0
1
2
3
5% Schulze hours oxidation at 30°C.

B

Fig.20.

thicker continuous exinal layer which bears much less uniform verrucae and granules.

As far as I know the only described dispersed spores which closely resemble those of Mariestopesia are certain ones named Angiopteris, recorded by Faddeeva from the Jurassic of Russia (Andreeva et al 1966).

I have only ever seen two spores in dispersed miospore preparations from Hasty Bank which agree fully with Mariestopesia spores, yet I must have looked at well over a hundred thousand spores in all. Clearly this occurrence is so low that it may have been the result of contamination. Spores similar to Mariestopesia in size and sculpture were more common, though well under 1%, but as their tetrad mark was not seen I did not feel confident about their determination.

Swelling of the spores (Fig. 20 p.99) Spore-masses were oxidised in a 5% Schulze solution (p.81) and then treated with 5% ammonium hydroxide for ten minutes. At a room temperature of 20°C even long oxidation for 1 to 4 days produced negligible swelling. However, increases in temperature of the oxidation resulted in marked swelling and at only 30°C up to 40% increase in size was recorded (Fig.20). At 100°C the spores were usually destroyed after a few minutes oxidation, though this method has been used for Jurassic gymnosperm microspores without apparently affecting their size (van Konijnenburg 1971).

Fungi

Circular or oval rings of coal, up to 5 mm across, occur in four pinnules (Pl. 4 fig. 2). They are identified as rims of leaf-spot fungi (Harris 1961) though maceration failed to

give either fungal hyphae or cutinised host-tissue.

COMPARISON

The only Yorkshire Jurassic fern which could be confused with Mariestopesia is Marattia anglica (Thomas) Harris (Harris 1961) and both species occur in association in the siltstone of Hasty Bank. However the synangia of Marattia (in which the sporangia are fused) are different from the sori of Mariestopesia (in which the sporangia are separate). The rather similar sterile pinnules of Cladophlebis aktashensis Turutanova-Ketova (Harris 1961) are distinguished by their typically twice-forked veins and their more slender midrib.

Marattiopsis bowerii Seward (Seward 1911) from the Upper Jurassic (Kimmeridgien) of Scotland looks similar in gross form to M. blackii and I have extracted a few spores from its sporangia which look similar to those of Mariestopesia. The preservation of the sporangia and "synangia" of M. bowerii, however, seems to me too poor for there to be any certainty about its proper generic position.

The preservation of Mariestopesia blackii (Pls. 3,4)

In many pinnules of M. blackii the tissue between the veins has disappeared. When this is in specimens whose sporangia are poorly preserved or preserved only as impressions I suspect that Recent weathering may have caused the loss of tissue. However, in some specimens the veins have become separated or squashed together at up to 20 per cm and sometimes they have become displaced from their usual angles to the midrib. Where the pinnules lie flat on the bedding planes this displacement and the other distortions must have occurred before final compression. It could only occur after liquefaction of the waterlogged mesophyll and presumably took

place either before burial or soon after. In these pinnules it thus seems likely that the tissue between the veins disappeared contemporaneously with deposition.

An interesting feature of Mariestopesia is the occurrence of tilted sori, known also in Marattia anglica (Harris 1961). The tilting occurs in about a third of the specimens and is directed equally towards the bases of the pinnules (seen clearly in 22 pinnules) and their apices (24 pinnules). Occasionally it occurs in both directions within one pinnule. A possible explanation of these facts is that the sporangia were tilted in life, persisting in their position during burial, but if this was so I would expect more specimens to show the tilting. I would also expect the direction of tilt to show a numerical bias towards either the base or apex of the pinnule. I imagine instead that the tilting was produced by currents acting on the waterlogged and softened placenta during and soon after burial. Other explanations, however, are possible, for example shrinkage of the tissues after burial.

Distortions of the kinds mentioned above are not shown so often in Hasty Bank ferns other than Mariestopesia, though Marattia anglica does occasionally show vein displacement as well as soral tilting. Two explanations seem possible for this. Presumably compared with the other species Mariestopesia was either carried in the deltaic streams somewhat further because it grew further away, and processes causing distortion thus had a longer time to act on it, or it may simply have been more susceptible to distortion. From the point of view of "palaeoecology" it is interesting to guess which of these explanations might be nearer the truth. The fossil evidence which can be seen shows that the

pinnule of Mariestopesia looks at least as robust as in other Hasty Bank ferns, its fragment size is similar to them and well-preserved pinnules occur with those showing changes in form. This goes against the idea that Mariestopesia was carried further than the other species.

Simple experimentation provided a second line of approaching this "palaeoecological" problem. Living pteridophyte fronds comparable in gross form to Hasty Bank ones were immersed in muddy pond water of pH 5 to 7 (the pyritic matrix at Hasty Bank indicates that acid conditions probably occurred there during or after burial). Destruction of Angiopteris (cf. Mariestopesia)was compared with that of living species of Marattia, Equisetum and Dicksonia, which are represented at Hasty Bank by fossil species.

Over a 13-day period the Dicksonia and Equisetum showed no visible damage or distortion and some stems of the Equisetum even grew to produce new stems. However, in both Marattia and Angiopteris extensive destruction of the mesophyll occurred within 7 days. This allowed the veins to shift in response to the slightest disturbance of the water, though more readily in Angiopteris than Marattia. Indeed the appearance of the experimentally decayed material after 7 days was remarkably like that of the comparable fossil species at Hasty Bank. Thus within the limits of an experiment based purely on similarity in morphology and a simple imitation of some of the conditions of deposition the results imply that Mariestopesia was simply more susceptible to distortion than the other ferns and did not necessarily grow further away from the place of burial.

This experiment might possibly explain why several pinnule apices of Mariestopesia are known yet not their bases

or attachments to the rachis, whereas in Marattia anglica all parts of the pinnules and their attachment are known (van Cittert 1966; Harris 1961). The pinnules of the living Marattia remained attached to their rachises throughout the duration of the experiment whilst in Angiopteris they were shed during the first 9 days, by separation from the rachis at the swollen gelatinous bases of the petioles.

The Systematic position of Mariestopesia

The family Angiopteridaceae encompasses the living genera Macroglossum, Archangiopteris, and Angiopteris. Of these the genus Angiopteris is the closest to Mariestopesia; the pinnules of many living species agree in gross form and venation with M. blackii and like it they may also lack fibrous strands between the veins. Tiny hairs which occur on the underside of the pinnule in Angiopteris are lacking in Mariestopesia, though as they are delicate they may well not have been preserved.

The differences between the two genera are in their sori and sporangia. The sporangia of Angiopteris are spaced closely next to one another, giving a compact sorus, whereas in Mariestopesia they are spaced more diffusely and the sorus is less compact (Pl. 5).

Perhaps because the sori are more compact the sporangia of Angiopteris are oval in transverse section whilst those of Mariestopesia were circular in transverse section.
The sporangia of Mariestopesia are longer in relation to their width, looking much narrower and more pointed than those of Angiopteris.

The following are further differences. In Mariestopesia the sori typically extend further across the pinnule, taking up about $\frac{1}{4}$ to $\frac{2}{3}$ of its width, whereas in Angiopteris

they take up only ¼ (or less) of the pinnule width. The cells throughout the sporangial wall of Mariestopesia may well be uniformly thickened and elongated, unlike in Angiopteris where a patch of thin-walled isodiametric cells occurs on the dorsal wall (Pl. 6, fig. 8). Finally the number of spores produced by the sporangia of Mariestopesia is higher, about 2000-3000; Bower (1926) gives 1500 for Angiopteris evecta.

A perine is characteristically present surrounding the spores of Angiopteris (Pl. 9) though I have not seen one on Mariestopesia spores. Whilst this constitutes an apparent difference it should be remembered that owing to lack of preservation the perine is as a rule lacking in fossil spores (Tschudy & Scott 1969).

In the available literature Angiopteris is portrayed as a neatly circumscribed genus from which Mariestopesia seems to me justifiably separated generically, on the basis of the differences given above. I should point out, however, that full comparison of the sori and sporangia of Mariestopesia with those of Angiopteris is at present limited. Though over 100 species of Angiopteris have been described rather scant attention has been given to the range of variation in the morphology of their sori (de Vriese & Harting 1853; Ching et al. 1966; Holttum 1954; Copeland 1947). As far as I know the sori of only the type species A. evecta Hoffmann have been described in any detail (Strasburger 1874; Bower 1898). However, when I looked through the herbarium specimens at Kew there certainly seemed to be noticeable differences between the sori of the different species, especially in the patch of thin-walled cells on the dorsal wall of the sporangium. Proper study might well show that the morphology

of the sorus and sporangia in Angiopteris varies more than has been supposed, and indeed it might possibly encompass that seen in Mariestopesia.

The long and narrow, somewhat cigar-shaped, sporangia of Mariestopesia, arranged rather diffusely in the sori, are rather similar to those of certain fossil Marattialean pinnules of Palaeozoic to early Mesozoic age, for example Eoangiopteris Mamay (Mamay 1950) and Asterotheca Presl. The pecopterid pinnules of these Palaeozoic genera were typically smaller and narrower than those of Mariestopesia and in some species the sporangia were even longer and narrower. Their spores differ from Mariestopesia in a number of ways (Bhardwaj & Singh 1956; Pfefferkorn et al 1971; Laveine 1969 and 1970; Doubinger 1961). Eoangiopteris differs from Mariestopesia in having a basal cushion in the sorus, and Asterotheca in its radial rather than oval, synangiate, sori.

Of the Mesozoic genera which are like Mariestopesia in having a more expanded taeniopterid pinnule Danaeopsis is the only one I know which is at all similar. Halle (1921) points out, however, that in the only properly studied species D. fecunda Halle the arrangement of the sporangia in double rows over the whole width of the pinna is, if anything, nearest to the living Archangiopteris. Though Banks et al (1967) have suggested that Danaeopsis may have given rise to Angiopteris the arrangement and squat conical shape of its sporangia are rather different from both Angiopteris and Mariestopesia.

The comparisons given above suggest that the resemblance of the sorus of Mariestopesia is closer to Angiopteris than it is to any other known genus. The sporangia, however, show some approach to certain Palaeozoic genera which had pecopterid

Fig. 21.

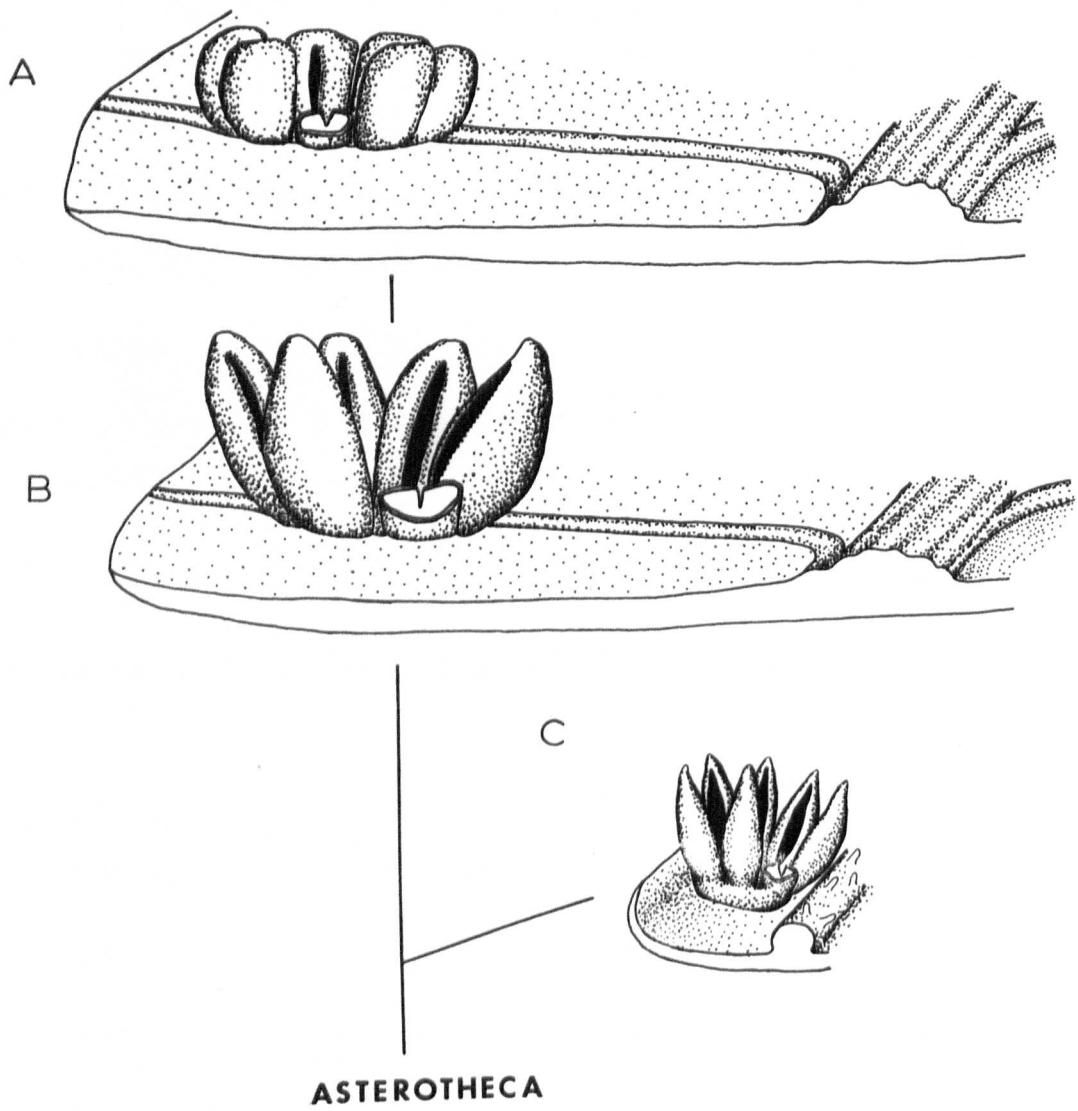


Fig. 21.

Fig. 21. Postulated evolution of the living Marattialean fern Angiopteris (A) from Palaeozoic ancestors like Asterotheca and Eoangiopteris (C), imagining the Mesozoic genus Mariestopesia (B) as an intermediate.

In the early Asterotheca (Carboniferous to Trias) the circular synangia composed of elongate sporangia were not very compact. They were borne on narrow (pecopterid) pinnules. The contemporary Eoangiopteris was similar except that as in the later genera its synangium was oval.

Whilst the younger Mariestopesia (from the Jurassic) was like Angiopteris in that the oval sori were borne on an expanded (taeniopterid) pinnule, its long and pointed sporangia arranged in rather diffuse sori were more like those of the synangiate earlier genera. Thus a final degree of reduction in length of sporangia and their greater compaction into the sorus would be required to give the living Angiopteris.

Further expansion of the lamina and elongation of the sorus of Angiopteris would give rise to the living genera Archangiopteris and Macroglossum.

pinnules. I speculate that Mariestopesia might have evolved from early forms like Asterotheca or Eoangiopteris which in their turn might conceivably have been derived from a coenopterid genus such as Chorionopteris (Mamay 1950). The trends which I imagine might have occurred (Fig.21/ p.107) would be expansion of the pinnule from pecopterid to taeniopterid, elongation of the sorus from circular to oval, increasing compaction of the sporangia into the sorus, separation of sporangia in the synangia and specialisation of the cells of the sporangium wall. Thus expansion of the pinnule of Asterotheca coupled with elongation of its sorus and separation of the sporangia would give Mariestopesia. Greater compaction of the sporangia of Mariestopesia into the sorus and specialisation of the sporangial wall would give Angiopteris. A continuation of these trends, involving further expansion of the pinnule of Angiopteris and elongation of its sori to take up more of the pinnule width, would give rise to the living genera Macroglossum and Archangiopteris (Bower 1926).

Further evidence is needed as the presently available facts allow other speculations, such as derivation from Radstockia, a Palaeozoic fern which had elongate synangia and an expanded pinnule (Taylor 1967).

LEPTOSPORANGIATAE

FILICALES

Matoniaceae

Genus Phlebopteris Brongniart

Phlebopteris woodwardii Leckenby
(Pl. 10, figs. 1-3)

DISCUSSION

Because the Yorkshire material of this fern is almost always fusainised the tissues are scarcely compressed and the anatomical details are remarkably well-preserved (Harris, 1961). Such material is opaque and thus is not very suitable for study by light microscopy though as the shape of the cells is preserved it is ideal for study by scanning electron microscopy (SEM). SEM photographs in Pl. 10, figs. 1 and 2, show the previously unknown stomata (which avoid the veins). Pl. 10, fig. 3 shows cells of the spongey mesophyll. Alvin (1974) has recently reported a similar though more detailed SEM study on fusainised material of Weichselia.

Distributions and abundances of Pteridophyta and Caytoniales at Hasty Bank

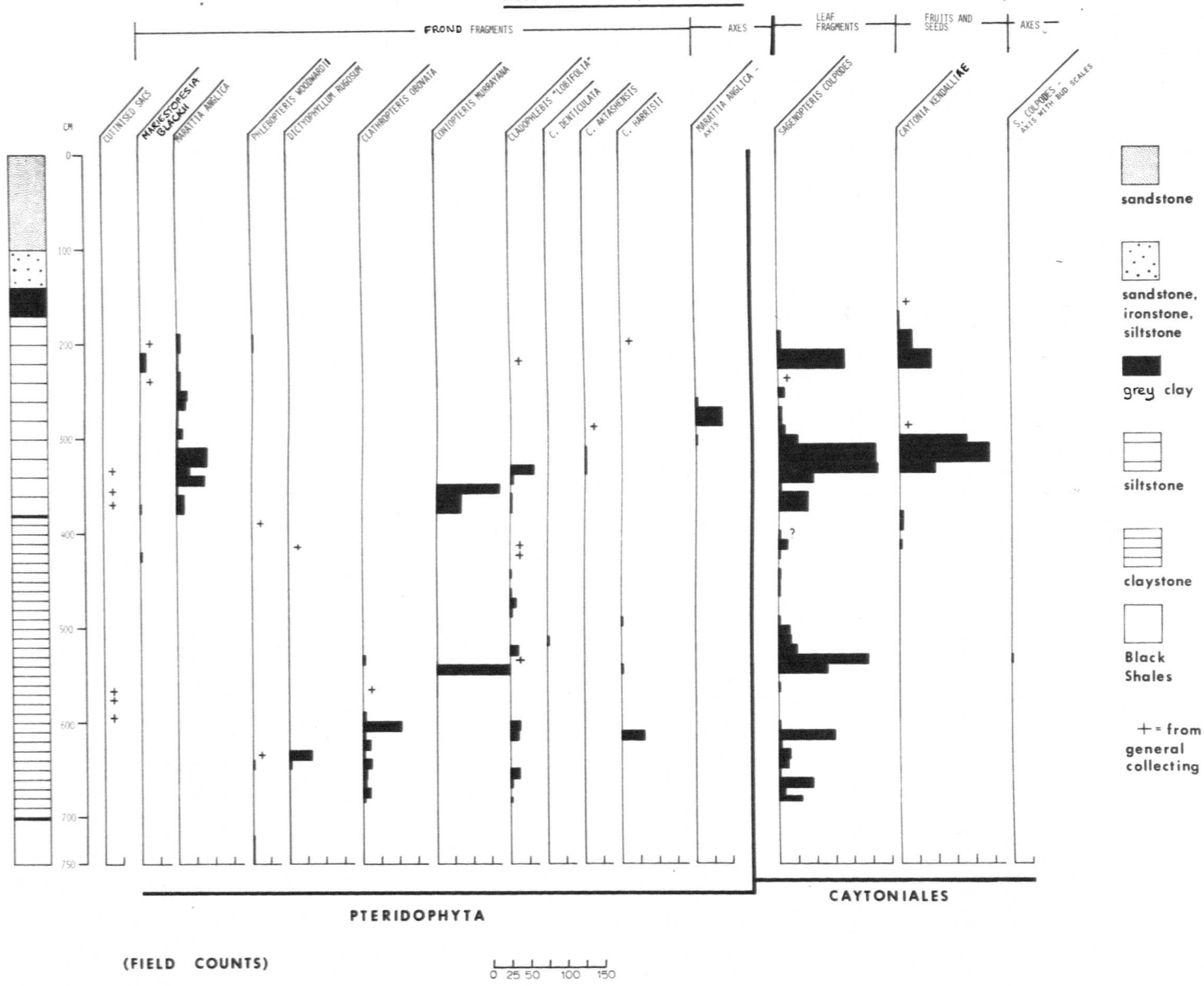


Fig. 22.

CAYTONIALES
(Fig 22p.111)

Associations between detached organs

The quantitative agreement between counts of the leaf Sagenopteris colpodes Harris in section 1 with those of the associated fruits and seeds Caytonia kendalliae Harris is impressive. No other determinable fructification is associated with S. colpodes at Hasty Bank so strongly as C. kendalliae.

This confirms the view of Harris (1964)who inferred from qualitative collecting that these organs occur in association in the field. Taking this evidence together with that from structural agreement in their cuticles he suggests that the organs belonged to the same plant (Harris 1964:8).

CAYTONIALES?

Genus Amphorispermum Harris

Amphorispermum pullum Harris
(Pl. 11, fig. 1)

Amphorispermum pullum was classified by Harris (1964:28) in the Caytoniales because of similarities in its structure to seeds of Caytonia. It was then known only from isolated seeds.

Besides finding such isolated seeds of A. pullum at Hasty Bank I have also occasionally found them aggregated into clumps composed of three seeds. As the seeds in these clumps are stuck together side by side this implies that they were borne next to each other when alive, though probably not partitioned off as in Caytonia where dispersed seeds are always found separate from one another.

These facts indicate that the unknown fructification of A. pullum was possibly rather unlike Caytonia.

Distribution and abundances at Hasty Bank of Cycadales and pteridosperms other than Caytoniales.

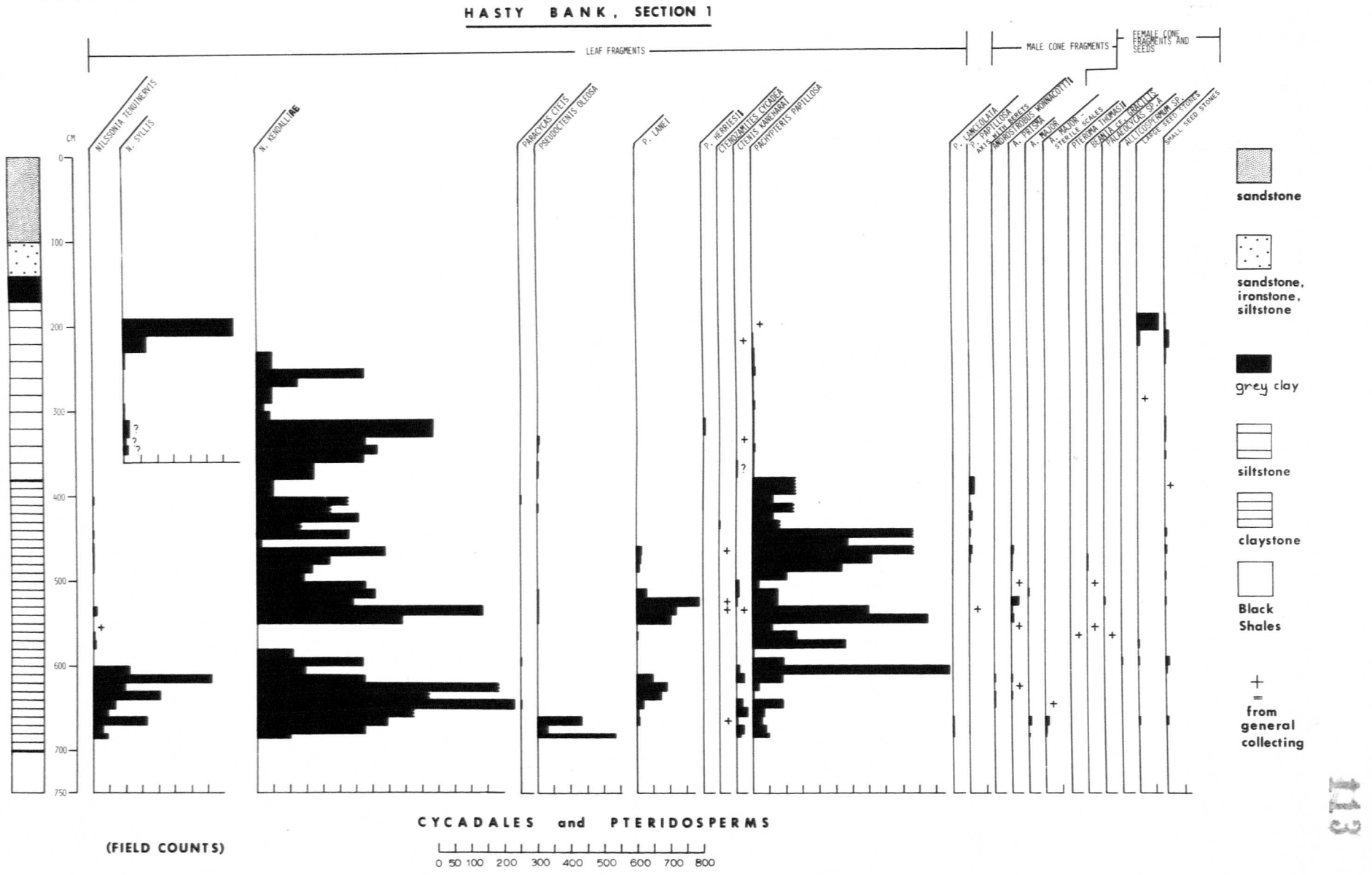


Fig. 23.

The family Nilssonieae (Thomas & Harris 1960)

This extinct family encompasses a number of cycads which were partially reconstructed from their detached organs by Harris (1941) and Thomas & Harris (1960). Their cones (Beania and some species of Androstrobus)are rather similar to those of the living Zamiaceae though differing considerably in being less robust and more loosely constructed. The leaves (Nilssonia)are often segmented and their segments show parallel venation like those of the modern Zamiaceae. Unlike the Zamiaceae, however, the leaf segments of Nilssonia are often short, and their attachment to the very top of the rachis is quite unlike any living Cycad. The pollen of the Nilssonieae broadly resembles that of living Cycadales though details of the exine differ (van Konijnenburg 1971).

Associations between detached organs of the Nilssonieae at Hasty Bank (Figs.23[p.113], 9, 10, 11,[p.56-58])

1. Androstrobus wonnacottii Harris + Nilssonia tenuinervis Seward.

Although A. wonnacottii is associated at Hasty Bank with N. tenuinervis it is also just as strongly associated there with other cycad leaves, especially Nilssonia kendalliae. Thomas & Harris (1960:146), however, have shown that the association A. wonnacottii + N. tenuinervis is shown more strongly in certain other localities. Harris (1941:95) has also shown that there is greater agreement in cuticle structure and resin between A. wonnacottii and N. tenuinervis than with any other associated leaf. Taking association together with agreement in structure there is thus no reason to doubt that these organs belonged to the same plant. The

weakness of the evidence of association at Hasty Bank is nevertheless instructive. It shows that association between organs if considered without reference to structure and in only one locality could sometimes be misleading.

2. Beania cf. gracilis + Nilssonia kendalliae Harris (Fig. 23 p. 113; 27 p. 148, E, F. Pl. 11, figs 3,5)

Beania gracilis at Gristhorpe is associated with Nilssonia compta with which the structure of its cuticle agrees. On this basis Harris (1941) has referred these organs to the same plant. Specimens of female cones occurring at Hasty Bank and Roseberry Topping which show "no distinguishable character" from B. gracilis but which are associated with Nilssonia kendalliae were also mentioned by Harris (1964: 169; his Pl. 5, fig. 9). The Hasty Bank specimens are all fairly uniform in size and the seeds are lacking, presumably having been shed before preservation.

Harris points out that these cones are probably distinct from Gristhorpe B. gracilis because none are so large as those of the full size found at Gristhorpe. They are therefore named here Beania cf. gracilis.

There is very little to add to this. The association of B. cf. gracilis with N. kendalliae is indeed strong, particularly in section 2. The only other leaf with which it is associated and to which it conceivably might belong is Pachypteris papillosa. P. papillosa differs, however, in its thick and papillose cuticle.

Cuticle preparations from the cone axis of B. cf. gracilis show trichome bases and ordinary epidermal cell outlines like those seen in many species of Nilssonia though stomata are lacking (Pl. 11, fig. 5). The sporophyll head, however,

shows a few stomata and in lacking subsidiary cell papillae these agree with N. kendalliae rather than N. compta. This evidence from the cuticles taken with that of association points to N. kendalliae being a possible leaf of Beania cf. gracilis. However, as the stomata mentioned above look rather like trichome bases they are not very convincing and the cuticular evidence is therefore weak.

Cycadales not referable to the Nilssonieae.

1. Androstrobus prisma Thomas & Harris + Pseudoctenis lanei Thomas, reconstructed by Thomas & Harris (1960).

DISCUSSION

This plant had compact rather robust male cones (A. prisma) and it bore large once-pinnate leaves (P. lanei). The leaf pinnae of P. lanei are much longer than broad and have parallel veins which fork but do not anastamose. In these characters the plant approaches closer than any other Yorkshire Jurassic cycad to certain genera of the living Zamiaceae such as Encephalartos and Zamia. The pollen grains of A. prisma, however, lack a colpus and have grana in the exine, in these characters differing sharply from both the Nilssonieae and the living cycads (van Konijnenburg 1971:18-28). They differ from the Nilssonieae in being more or less round in outline rather than oval.

The attribution of Alvinia florinii gen. et sp. nov. to this plant is discussed on p. 137 et seq.

At Hasty Bank Androstrobus prisma is strongly associated with Pseudoctenis lanei in section 1 and less strongly in sections 2 and 3 (Figs. 23 (p. 113); 10, 11, (p. 57, 58)). In section 1 there is quantitative agreement in so far as A. prisma is commonest where P. lanei is at its most abundant. Of the range of associated cycad-like leaves only P. lanei and P. oleosa have similar cuticles, and P. lanei is the more similar to A. prisma (Thomas & Harris 1960; Harris 1964). Thus the evidence from my work at Hasty Bank supports the reconstruction P. lanei + A. prisma as proposed by Thomas & Harris (1960).

ANDROSTROBUS MAJOR van Konijnenburg

Fig. 24.

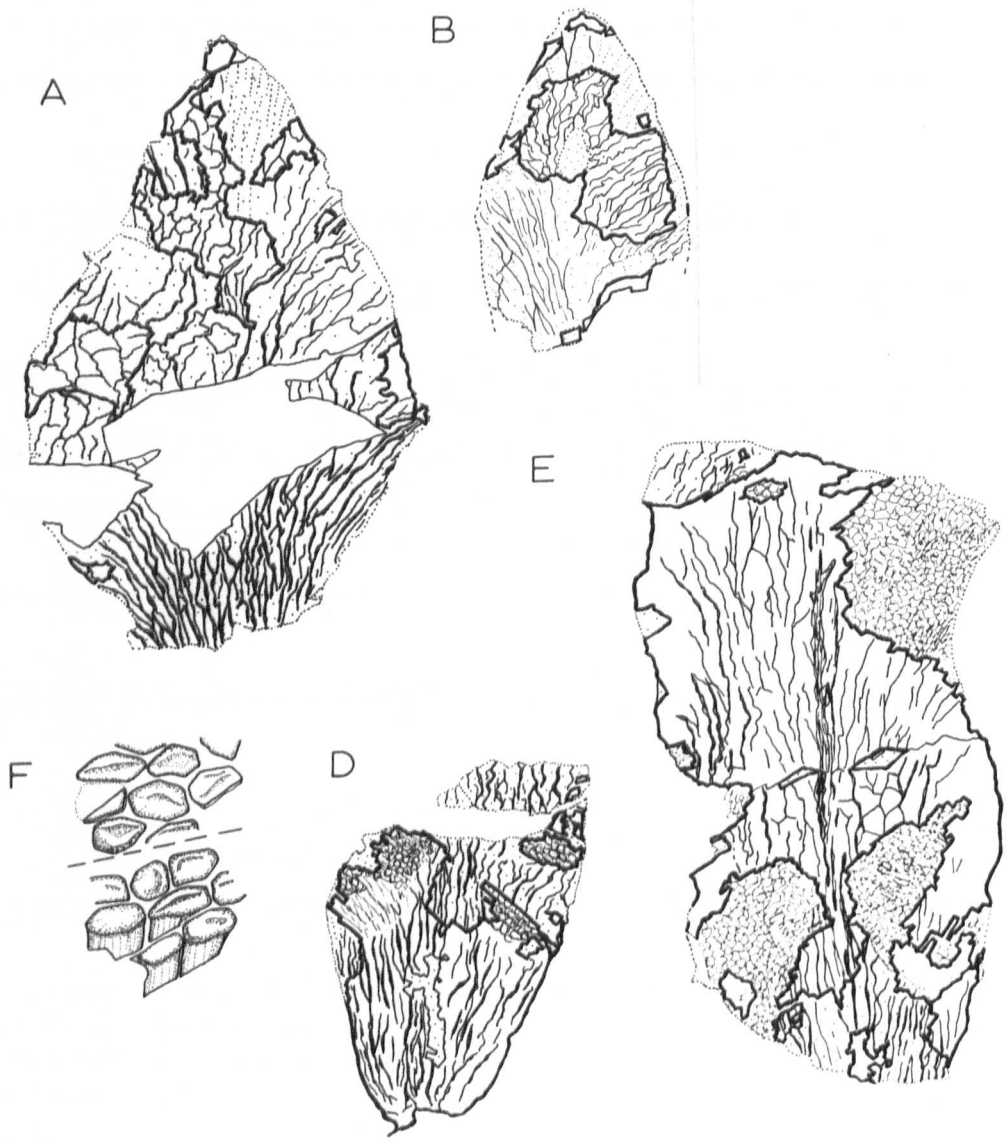


Fig. 24.

Fig. 24.

Androstrobus major van Konijnenburg

A - B, sterile scales.

A, specimen no. 9, from section 1: 660-670 cm, x2.

B, specimen no. 5, from section 1: 660-670 cm, x1.

D - F, fertile scale (microsporophyll), specimen no. 1, from section 1 ca. 520 cm.

D, E, the two largest of several fragments, both x2. The lower half of D is the sterile base of the scale. Its upper half is the Counterpart of the Part, E, which is the fertile distal region of the scale. F, details of the free ends of the microsporangia, from two small areas of the Part, x20, drawn freehand.

2. Notes on Androstrobus major van Konijnenburg and its attribution to the leaf Pseudoctenis oleosa Harris.

Androstrobus major van Konijnenburg (Fig. 24/p.118, Pl. 12).

1968. Androstrobus major van Konijnenburg. van Konijnenburg-van Cittert 1968: 267; Figs. 1,2; Pls. I,II, (description of holotype and pollen).

1971 A. major van Konijnenburg. van Konijnenburg- van Cittert 1971: 22-23; Pl. IV, fig. 5, (pollen).

1973. A. major van Konijnenburg. Hill & van Konijnenburg 1973: 61 (name in list).

FERTILE SCALES (MICROSPOROPHYLLS) (Pl. 12, fig. 1. Fig. 24/p.118, D-F).

Like Mariestopesia blackii the male cycad cone Androstrobus major van Konijnenburg is known only from Hasty Bank. Several detached microsporophylls from the claystone of sections 1 and 3 add to the only previously known specimen, the holotype, which was described by van Konijnenburg (1968). The new specimens agree with the holotype in essential features of their gross form, cuticle and pollen, though the one shown in Fig. 24/p.118, D, E, is larger (greatest width 2 cm). In all of the new specimens the microsporangia seen in end view are predominantly oval or polygonal rather than circular (Fig. 24 ,F), whilst both surfaces of the scale are wrinkled rather than just one; and in these characters the new specimens differ from the description of the holotype.

The cuticles of the microsporangia are typical of the genus. There is a thin external cuticle showing elongate cells with delicately marked walls and a thin inner one which is granular and shows faintly marked cell outlines.

STERILE SCALES (Pl. 12, figs. 2-4; Fig. 24/ A, B).

These previously undescribed scales occur associated intimately with the fertile ones in section 1 and were at first confused with them. They agree strikingly in their shape and wrinkling with the fertile scales, differing from them only in the absence of microsporangia and in having better-preserved cuticles.

Description (Fig. 24/ p.118 ,A,B)

The scales overlap one another (the basal end of the scale and its attachment are unknown). In the part known they are broad-lanceolate in shape and end in an obtuse apex. Their length is at least 4 cm and the width up to 2 or 3 cm. The substance is thick and the surfaces are strongly wrinkled, the wrinkles being of variable length and diverging from the base of the scale. Occasionally these irregularly waved wrinkles become fused laterally to form an irregular reticulum.

The scales on maceration yield abundant resinous matter, the resin occasionally occurring as rounded casts 30-50 µm wide which adhere to the cuticle.

The cuticle is fragmentary and about 1-2 µm thick (measured in folds). The epidermal cells are polygonal, isodiametric or slightly elongated, and their corners are rounded. Their periclinal walls bulge slightly, are minutely pitted, and often show irregular thin areas and longitudinal thin strips, sometimes also showing faint longitudinal striae. The anticlinal cell-walls are prominent on the inner surface of the cuticle. Trichomes and papillae are lacking.

The stomata are sunken and occur at a density of about 40 per mm square. Their orientation is variable and they are

each surrounded by a ring of 6 to 8 (rarely up to 12) uniform subsidiary cells. The subsidiary cells are commonly either equally thickened next to the stomatal pit or the terminal ones are unthickened (the thickening in both cases is rather weakly developed). The pit is oval or circular, 15-35 µm across. The guard cells are sunken, thickened in the middle and usually extend beyond the pit, though the poles were not clearly seen. The poles occur at a higher level than the middle part of the guard cells. Encircling cells are absent or present in an incomplete ring and unspecialised.

DISCUSSION

Sterile scales + fertile scales (Figs. 23, p. 113, 24).

The association of the sterile with the fertile scales is intimate. They are remarkably similar to one another in form and wrinkling and agree in the details of their epidermal cells. This is strong evidence that they occurred on the same kind of plant and possibly both types of scale occurred together in the cones, as I imply by naming both of them A. major. There is, however, no direct evidence of attachment. One of the new specimens shows four sterile scales overlapping in an arc and though this is as might be expected from arrangement on the slender axis of a cone it is possible that they were borne on ordinary stems, if these were also slender (they are unknown).

Comparison

There is little possibility of confusing these sterile and fertile scales with other Yorkshire Jurassic species as no species other than A. major shows wrinkling of the kind and intensity seen in them.

The leaf attributed to A. major

There is new evidence from both association and agreement in cuticle structure to suggest that A. major was borne on the same plant as the leaf Pseudoctenis oleosa Harris. The agreement of the leaf cuticle is chiefly with the sterile scales, and the evidence is as follows.

Association with P. oleosa

The following leaves of cycad or pteridosperm affinity are associated with A. major at Hasty Bank:

Nilssonia tenuinervis	(common)
N. kendalliae	(abundant)
Pseudoctenis oleosa	(common)
P. lanei	(rare)
Ctenis kaneharai	(rare)
Ctenozamites cycadea	(rare)
Pachypteris papillosa	(common)
P. lanceolata	(rare).

Of these leaves only P. oleosa is strongly associated with A. major (Figs. 23/p.113, 11/p.58) and near the bottom of section 1 this association is impressive: A. major is at its most abundant where P. oleosa is also at its most abundant.

Thus the evidence of association points to P. oleosa being the leaf of A. major.

Agreement in cuticle structure of the sterile scales and P. oleosa.

Of the associated cycad or pteridosperm-like leaves none are identical with the sterile scales in their cuticular structure. Nilssonia tenuinervis and N. kendalliae differ greatly in their much thinner cuticles, the characters of their epidermal cells and also in having much simpler stomata.

Ctenis kaneharai differs in having cutin ridges on the periclinal walls of its epidermal cells and also in other details. Ctenozamites cycadea has a quite different stomatal morphology, with a rampart of cuticle around the top of the stomatal pit. Both Pachypteris papillosa and P. lanceolata differ strongly from the sterile scales in their much thicker cuticles having epidermal cells which show strongly marked striations, and they also differ in their subsidiary cells which in P. papillosa are developed into papillae next to the stomatal pit.

Only Pseudoctenis lanei and P. oleosa are at all similar to the sterile scales. The epidermal cells of these leaves show thin patches and strips, faint longitudinal striae and prominent anticlinal walls, very similar to the scales. In their essential features the stomata also agree with those of the scales. However, in the scales the subsidiary cells are more often thickened equally next to the pit rather than on opposite sides as in the leaves, and the thickening is also weaker than in the leaves. They form a more uniform ring than in the leaf cuticle. Though stomata showing equally thickened subsidiary cells also occur in P. oleosa and P. lanei (Pls. 18 , fig. 4; 20 , figs. 2,3) they are rare.

The occurrence of large resinous cell-casts adhering to the cuticles of the sterile scales agrees with typical specimens of P. oleosa rather than P. lanei and a further point of agreement with P. oleosa is the absence of trichomes and papillae from the scales. However, it should be noted that A. prisma, the cone which probably belonged to P. lanei, also lacks them.

Thus the evidence from cuticular structure shows that

the closest agreement of the sterile scales is with the leaf Pseudoctenis oleosa. Whilst this agreement is not perfect it seems close, and indeed is the closest seen amongst the associated leaves. As the sterile scales were almost certainly produced by the same plant as the fertile ones, if not in the same A. major cones, this cuticular evidence suggests that A. major belonged to P. oleosa.

The Systematic position of Androstrobus major

Though poorly known the pollen of A. major resembles that of the Nilssonieae (van Konijnenburg 1971). However, A. major stands apart from all other described species of the genus in its large size and also in having more flattened and expanded microsporophylls. In a general sense the sporophylls are thus considerably more leaf-like than those of other species. A further difference from other species, pointed out by van Konijnenburg (1968:270) is that the microsporophylls of A. major are sterile at the base as well as distally.

These differences set Androstrobus major well apart from the Nilssonieae or A. prisma. Indeed the nearest approach to it is seen in living Cycas L., particularly in the microsporophyll of C. circinnalis L. (comparing Fig.[24,p.118] with Schuster 1932, Fig. 10,B), whose cuticles also agree rather well. The chief difference is that the microsporophyll of C. circinnalis is less expanded than that of A. major and this is interesting in relation to the theory of evolution of cycad sporophylls from fertile leaves (Chamberlain 1935, Fig. 100, p. 100-103). Adherents to the theory claim that the microsporophyll of C. circinnalis is a primitive form because it is the most leaf-like seen amongst the living

cycads. Clearly if this is right A. major may be interpreted as a convincingly more leaf-like form and therefore more primitive. In this sense it is plausibly an ancestral form of the Cycas microsporophyll. However, in reality it can hardly be considered ancestral to the living cycads as a whole for it was a contemporary of other Androstrobus spp. (the Nilssonieae and A. prisma) which supporters of the above theory would regard as advanced.

The chief fact is that the microsporophyll of A. major is more like a leaf than that of any other known cycad, living or fossil.

The systematic position of the partially reconstructed plant Androstrobus major + Pseudoctenis oleosa.

The leaf Pseudoctenis oleosa approaches that of living Zamiaceae rather closely whilst the male cone A. major resembles Cycas rather than the Zamiaceae, more especially so if the sterile scales belonged in the cones. P. oleosa + A major thus approaches both the living Zamiaceae and Cycadaceae, combining certain features found in two living families which are now quite distinct from one another. As such its individual organs support Harris' (1961a:322) contention that the cycads may have essentially completed their evolution by Jurassic times, and extend this to include the male cone of the Cycadaceae. However, the reconstruction also shows that the Jurassic cycads, considered as whole plants, do not appear to have become selected into the distinct and presumably relict families we know today. I imagine a monophyletic ancestry of the Cycadaceae with Zamiaceae.

The evidence for linking Androstrobus major with Pseudoctenis oleosa seems to me strong though it is, of course,

circumstantial. If the leaves and cones were unrelated I find it difficult to imagine how the coincidence came about that they could agree so closely in structure and at the same time be buried in intimate association, especially as they are of different shape and presumably density.

Notes on Alvinia florinii gen. et sp. nov., a Cycas-like megasporophyll known only from Hasty Bank.

INTRODUCTION.

In its vegetative parts the fossil Alvinia florinii gen. et sp. nov. is remarkably like the megasporophyll of Cycas revoluta Thunberg, indeed its resemblance to it is stronger than that of any other known fossil. It has a stalk and a flattened segmented head. The stalk has two rows of lateral bulges, each bulge having a round scar which I presume bore an ovule. Only one ovule is known and though this looks as if it was originally attached to a bulge it is slightly separated from the nearest one. My suggestion that this ovule belonged to Alvinia is therefore presumptive. The head of the megasporophyll is dorsiventrally flattened. Unlike Cycas the stomata and trichomes are limited to its lower surface.

Reasons are given for separating Alvinia generically from Cycas L. and also for excluding it from Cycadospadix Schimper.

The species of leaf to which Alvinia might be attributed is considered. A Zamia-like leaf, Pseudoctenis lanei Thomas, seems the most likely candidate on grounds of association in the field and its similarity in cuticle structure. The Cycas-like leaf Paracycas cteis Harris, however, is also a possibility.

SYSTEMATIC DESCRIPTION

p.129

Genus Alvinia nov. (manuscript name). Fig. 25/, Pls. 13-17.

Diagnosis

Megasporophyll composed of a stalk and a distally expanded part (the head). Head dorsiventrally flattened,

Fig. 25

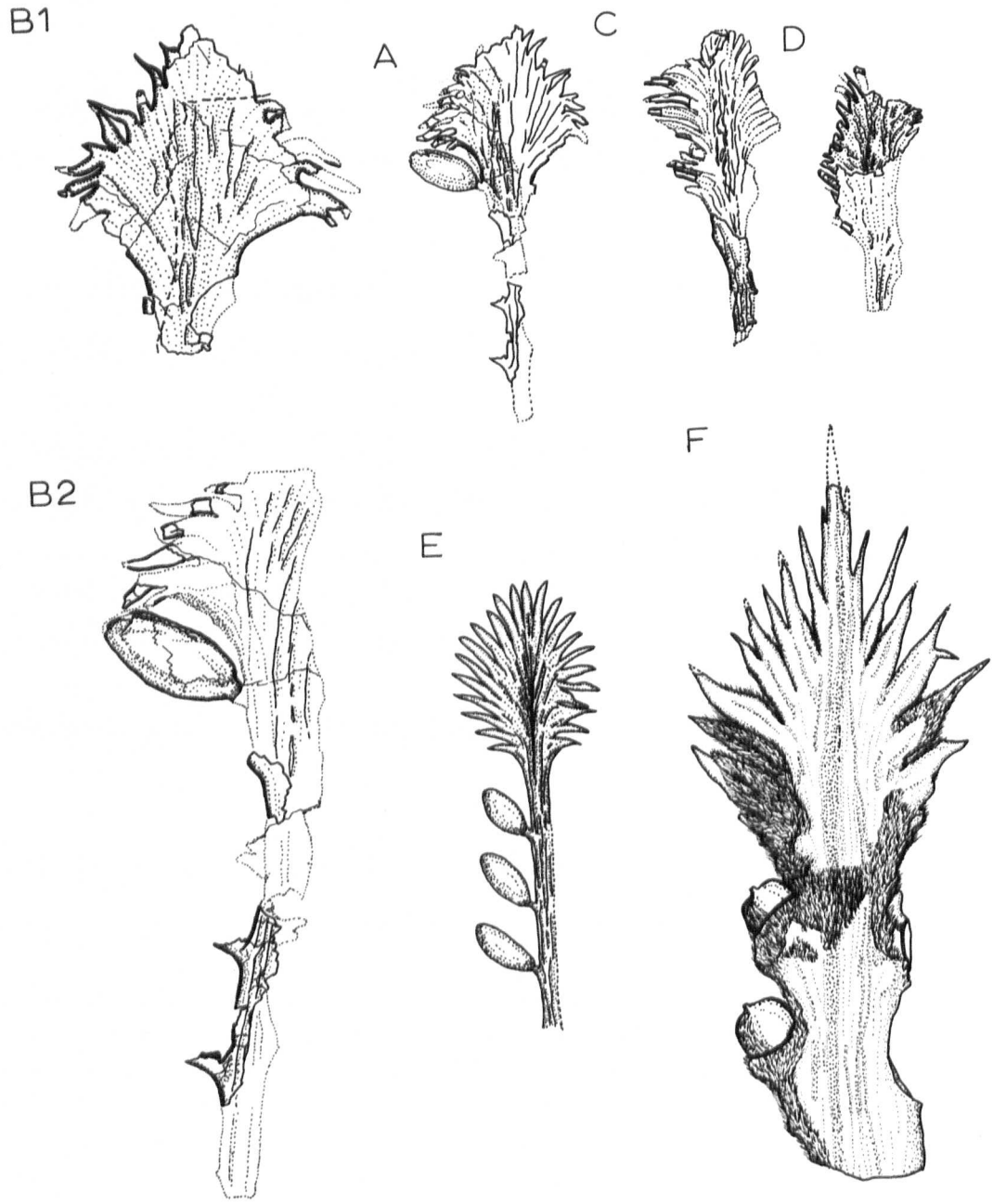


Fig. 25.

Fig. 25.

Alvinia florinii gen. et sp. nov.,

Cycas cf. *siamensis* Miquel.

A-E *Alvinia florinii* (fossil)

A,B. Holotype, specimen no. 4, from section 1: 560-570 cm.
A, drawing from Part and Counterpart, x 1.
B1 (Part) and B2 (Counterpart), x 2.

C,D. Specimen no. 1, from section C claystone.
C, Counterpart, x 1;
D, Part, x 1.

E. Restoration, x ca. 1.

F. *Cycas* cf. *siamensis* Miquel (living). Megasporophyll, x 1.

oval or rhomboidal, margin divided into pointed segments. Stalk showing two lateral rows of bulges, the bulges each having a circular scar [to which a single ovule was attached].

[Ovule orthotropous, ovoid. Base of megasporophyll and its attachment unknown].

Stomata limited to the lower surface of the head, haplocheilic, surrounded by a ring of uniform subsidiary cells which are thickened uniformly next to the stomatal pit. Trichomes limited to the stalk and the lower surface of the head.

The genus is named after Dr. K.L. Alvin .

Alvinia florinii sp. nov. (manuscript name). Named after Dr. R. Florin.

1973. Palaeocycas sp. nov. Hill in Hill & van Konijnenburg 1973:61 (name in list)

Diagnosis

Length of megasporophyll head (including segments) about 2.5 cm, width 1.2 cm to about 2.5 cm. Head (when oval) longer than broad. Margin divided into segments 1.5 to 6 mm long except for 4-10 mm next to the stalk where it is entire. Each segment about 1 mm broad at its base (range 0.5 to 2.0 mm), gradually tapering from the base or width through basal 2 or 3 mm uniform and then tapering. Point of segment acute or rounded.

Surface of head showing more or less strong median ridges; ridges slightly wavy, set close together and occasionally fusing laterally. These ridges give rise to others which each run (without fusing or waviness) into a marginal segment and along its mid-line.

Substance of head moderately thin. Cuticle 2 to 10 μm

thick (periclinal wall measured in folds). Epidermal cells polygonal with strongly rounded corners: isodiametric or elongated up to 4-6 (occasionally more) times longer than broad, often round or oval. Anticlinal walls straight, thickened at the corners of the cells, prominent on the inner surface of the cuticle and making its total thickness up to about 20 μm. Periclinal walls flat or slightly convex, a proportion of them showing a marked longitudinal thin strip or thin areas, minutely and densely pitted and or granular (pits < 1 μm wide), occasionally showing faint longitudinal striae.

Epidermal cells of (presumed) upper cuticle larger than those of the lower, more uniformly cutinised and therefore cuticle appearing thicker than lower, longitudinal thin strips and thin areas more marked, cells with a greater tendency to be in files, proportion of elongated cells greater. Orientation of elongated cells longitudinal on the head and along the marginal segments. Trichomes and stomata absent.

Epidermal cells of lower cuticle irregularly arranged or in short files, orientation of elongated cells variable. Stomata scattered unevenly, 5 to 20 per mm square, orientation variable, surrounded by 7 to 9 (rarely 10) subsidiary cells. Subsidiary cells sometimes showing striae which run towards the stomatal pit. Encircling cells up to 13, present in a complete or incomplete ring. Stomatal pit up to about 30 μm wide, oval or circular or irregular in outline. Guard-cells sunken, their outer (dorsal) walls thickened, thickenings crescent-shaped (poles not seen).

Trichomes unevenly distributed, up to 100 per mm square. Trichome base an oval or circular thin-walled cell having a

thickened centre, periclinal wall typically overlapping neighbouring cells. Central thickened part of trichome base papilla-like, bearing an oval or circular scar. Scar a hole or thin area [free part of trichome unknown].

Hypodermal cells present beneath both upper and lower epidermis, thinly and incompletely cutinised, polygonal, more or less isodiametric or elongated longitudinally.

Stalk of megasporophyll longitudinally striate, substance thick, at least 4 cm long. Width 2 or 3 mm, up to 5 mm where the bulges occur, expanding near the head to more than 5 mm. Bulges produced at intervals of 5 to 10 mm, at least 4 in a row, rows sub-opposite. Bulge in surface view (to be figured elsewhere) showing a round scar less than 0.5 mm across, surrounded by an oval collar about 1 mm wide. In side-view bulges peg-like or wedge-shaped.

Cuticle of stalk 2 to 10 μm thick. Epidermal cells like those of upper cuticle of the head, though tending to be more elongated and nearly all longitudinally orientated. Stomata lacking. Trichome-bases rare, not overlapping neighbouring cells. Hypodermal cells like those of head.

Ovule 10 mm long, 5 mm broad, substance thick. Cuticle of integument 2 to 10 μm thick, cell outlines polygonal, more or less isodiametric with rounded corners. Anticlinal walls prominent, straight or slightly waved. Periclinal walls slightly convex, showing one or more irregular thin areas. Stomata, trichomes and cutinised hypodermals lacking. Cuticle of nucellus (or lining the integument) delicate, showing elongated straight-walled cells. Cell-outlines delicately though distinctly marked. [Megaspore membrane and details of micropyle not seen].

Alvinia florinii is rare. The eight specimens so far known came from the claystone at about 5 or 6 m below the top of the main plant bed. The holotype, specimen no. 4, figured in Pl. 13, shows the head and stalk with one row of bulges seen in side view, and also the ovule. Of the other specimens no. 1A is a stalk showing two rows of bulges alternating sub-oppositely (to be figured elsewhere) and no. 8, collected by Ms. M. Jones, shows the bulges in surface view. The other specimens are all detached heads. They are of variable size and show varied development of the ridges. I suspect that the ridges which run directly into the segments represent veins, whilst the median ones look more like post-mortem wrinkles. The segments are either straight and point radially from the centre of the head or they are somewhat curved towards the stalk. Occasionally they fork once.

The oval body shown in Pl.13 is the only organ so far found which looks like an ovule and is so-termed in the diagnosis. It looks suitably placed for attachment to a bulge and the width of its base is also suitable. However, Pl. 13 shows that it is separated from the nearest bulge by a gap of some mm , possibly owing to slumping more or less contemporary with burial (such as is often seen at Hasty Bank). However it may well not belong at all.

The ovule itself is incompletely known and I macerated only its distal half. If it was normally developed I would expect its distal half to show a micropyle and some of the megaspore, and that it does not leads me to suspect that it was abortive. A collapsed megaspore may well therefore be

present in the unmacerated basal half. (Such abortive seeds are frequently seen in living Cycas).

The poorly preserved outer cuticle of the ovule (Pl. 15 fig. 3) is of the general character of a cycad integument, and the inner one (to be figured elsewhere) of a nucellus.

COMPARISON

Amongst living plants the only organ which is at all similar to Alvinia is the megasporophyll of Cycas L. The gross form of Alvinia is almost exactly matched by C. taiwaniana Carruthers (Carruthers 1893:331; Yamamoto 1928:3-7, fig.2) and its cuticle by C. revoluta Thunberg (Pls. 14-16). Alvinia, however, is smaller than the megasporophyll of any living species, the substance of its head seems thinner, and it also differs from all the living species in having the stomata and trichomes strictly limited to the lower surface of the head, and stomata lacking from the stalk. In Cycas the stomata and trichomes occur on both surfaces of the head, and at least in C. revoluta and C. circinalis L. the stalk has abundant stomata.

As the smaller size of Alvinia may be explained by its having been immature or abortive the securely known differences from the megasporophyll of Cycas are in the distribution of the stomata and trichomes and also the thinness of its substance. Had merely one of these characters differed, for example the stomata, I would have assigned the new fossil to Cycas, but taking them together I am reluctant to do so. In combination the differences seem to me fundamental, as they indicate that Alvinia was very much more like a leaf than the fleshy megasporophyll of Cycas.

Moreover the Zamia-like leaf Pseudoctenis lanei, if rightly attributed to Alvinia, differs considerably from the leaf of Cycas.

The following fossil megasporophylls have been described as Cycas-like though their resemblance to Cycas is much more remote than that of Alvinia, and in most cases their cuticle is unknown:

Archaeocycas Mamay (Mamay 1973)

Phasmatocycas Mamay (Mamay 1973)

Dioonitocarpidium Lilienstern (Lilienstern 1928; Kräusel 1949, 1953)

Propalmophyllum Lignier (Lignier 1895)

Behuninia joannei Chandler (Chandler 1966)

Two other fossil genera, however, are rather like Alvinia (and Cycas). Those species of Cycadospadix considered below resemble Alvinia in their gross form, and C. hennocquei (Pomel) Schimper (Schimper 1872) as figured by Saporta 1879:193 is especially similar. However, the supposed seed-scars of C. hennocquei have never been convincingly figured and the ovules have not been seen attached. Its cuticle, like that of C. moraenus (Pomel) Schimper (Schimper 1872), is as yet unstudied.

This lack of knowledge of the cuticle is my chief reason for separating Alvinia from Cycadospadix, as several species originally assigned to Cycadospadix have in fact been shown to have bennettitalean cuticles, for example C. dactylota Harris (Harris 1932b), Haitingeria (Cycadospadix) Krasserii (Schuster) Kräusel and C. pasinianus Zigno (Carpentier 1938). However, as Palaeocycas integer (Nathorst) Florin, originally placed in Cycadospadix, has a cycad-like

Character	PALAEOCYCAS	ALVINIA	CYCAS
substance of mega-sporophyll head	robust	rather thin	robust. In C. taiwan-iana rather thin.
margin of head	entire	segmented	entire or segmented
distribution of stomata	on both upper and lower surfaces of the head	limited to the lower surface of the head	on both upper and lower surfaces of the head and also on the stalk
subsidiary cells	thickened to form a raised ring of cuticle which forms a rampart around the top of the stomatal pit	thickened next to the pit, not forming a rampart	thickened next to the pit, not forming a rampart
trichomes	lacking	present on the lower surface of the head	present on both upper and lower surfaces of the head
hypodermal cells	not cutinised	cutinised	cutinised
(leaves)	entire	(segmented)	segmented

Table 7. Comparison of generic differences between Palaeocycas Florin, Alvinia gen. nov. and Cycas L.

cuticle it seems possible that C. hennocquei and C. moraeanus might also be cycadalean. For this reason Florin (1933) created the genus Bennettitolepis for Harris's C. dactylota, and C. pasianus was later placed in it. This leaves the position of C. moraeanus and C. hennocquei open. Clearly if they prove on the basis of their cuticles to be bennettitalean then Bennettitolepis would become unnecessary and Cycadospadix could be emended to replace it, as proposed prematurely by Harris 1932b. Equally if their cuticles resemble Alvinia then Alvinia could be dropped in favour of Cycadospadix and the bennettitalean species transferred to Bennettitolepis. I believe, however, that Cycadospadix might usefully be reserved as a form genus for organs looking like Cycas megasporophylls and bennettitalean scale-leaves, but whose cuticles are unknown through poor preservation or because they are as yet unstudied. It is in this sense that I here think of C. moraeanus and C. hennocquei.

Palaeocycas integer (Nathorst) Florin (Florin 1933) is in many of its characters similar to Alvinia, resembling it in gross-form though the head is entire. Like Alvinia its stalk shows bulges but there is no evidence that these bore scars and the ovule, even a presumed one, is unknown. The differences from Alvinia which I consider generic are shown in table 7/ p.136. The chief differences of Palaeocycas from both Cycas and Alvinia are shown by its leaves and the thickening of the stomatal pit which is much more like that seen in the living Stangeria and the fossils Ctenis and Ctenozamites.

The leaf of Alvinia florinii

Alvinia florinii occurs in association at Hasty Bank

with several species of leaves and leafy shoots. There is no close agreement in form and cuticle with any of these other than the Cycadales and pteridosperms of which the following are associated at two sample horizons in section 1:

1: 520-530 cm

Nilssonia kendalliae (abundant)
Pseudoctenis oleosa (rare)
P. lanei (very common)
Ctenozamites cycadea (very rare)
Ctenis kaneharai (rare)
Pachypteris papillosa (abundant)

1:560-570 cm

Nilssonia tenuinervis (rare)
Pseudoctenis lanei (rare)
Pachypteris papillosa (abundant)

The only leaves associated at both horizons are Pseudoctenis lanei Thomas and Pachypteris papillosa (Thomas et Bose) Harris. Unless our ideas are wrong Pachypteris papillosa is a Corystospermaceae-like pteridosperm. Its female fructification is unknown but I would expect it to be different from Alvinia, perhaps more like Umkomaasia Thomas.

On grounds of association in the field the most likely leaf of Alvinia is therefore Pseudoctenis lanei. I should stress, however, that the association is not intimate: the two organs have not been found intermingled on exactly the same bedding planes.

The Cycas-like leaf Paracycas cteis Harris is clearly a potential candidate for a Cycas-like sporophyll such as Alvinia, and like Pseudoctenis lanei it occurs in the claystone of Hasty Bank. However it is very rare and was not found at the same sample horizons as Alvinia.

Of the associated leaves listed above Pseudoctenis lanei has the most similar cuticle to Alvinia and P. oleosa

a somewhat less similar cuticle (Pls. 14, 15, 17-20). In both species the cuticles agree with Alvinia in being thick, in the shape of their epidermal cells, their prominent anticlinal walls and also in having pitting, striae, thin strips and thin areas on their periclinal walls. All three species have stomata sunken in rounded thickened pits surrounded by more or less uniform subsidiary cells. However these leaves also show differences from A. florinii. Neither species shows cutinised hypodermal cells like those of Alvinia, even in their rachises. Unlike Alvinia most of their stomata have gaps in the thickening of the pit, being thickened on only two sides (Pls. 18 fig. 2, 20 fig. 1). Nevertheless a few of the stomata are nearly always thickened uniformly as seen in Alvinia (Pls. 14 figs. 3-5, 18 fig. 4, 20 fig. 3).

Harris (1932a; 1964) suggests that in P. lanei the subsidiary cells are sunken below encircling cells and that these latter cells actually form most of the thickened wall of the stomatal pit (there is some doubt as to whether this interpretation is correct). Though this may seem like a great difference from Alvinia it is unlikely to be fundamental; the stomatal pit in the leaf of living Cycas circinalis is formed from subsidiary cells alone whilst in its megasporophyll the pit is often composed of both subsidiary cells and encircling cells.

An important point of agreement between Alvinia and P. lanei rather than P. oleosa is their trichome-bases (Pl. 17). Those of P. lanei pinnae agree almost exactly with the ones seen on the stalk of A. florinii whilst P. oleosa lacks trichomes. Secondly, though Alvinia

yields some indefinite resinous matter on maceration it lacks the rounded resinous cell-casts which are typical of P. oleosa (Pl. 19 fig. 3), and in this also its resemblance to P. lanei is closer. On the other hand A. florinii agrees more closely with P. oleosa in lacking solid papillae on its epidermal cells whilst P. lanei characteristically has them on a proportion of its cells (Pl. 18 figs. 1,2). This, however, is unlikely to be important as the male cone Androstrobus prisma Thomas et Harris, securely attributed to Pseudoctenis lanei by Thomas and Harris (1960) also lacks such papillae. In fact the trichome-bases and papillae of P. lanei pinnae may often look very similar to one another, the trichome-bases of V.28300, for example, differing from the papillae only in having an oval thin area or scar. Similarly the trichome bases of Alvinia (Pl. 14 fig. 2) may also resemble the papillae of P. lanei (Pl. 18 fig. 2).

None of the other species listed above shows any close agreement with Alvinia. The Nilssonia species have very much more delicate cuticles, their stomata are scarcely sunken and other details also differ. The only similarity is in their trichome-bases which though essentially like those of Alvinia are flatter. Ctenis kaneharai lacks trichomes and differs in various other details, particularly the different surface markings on its cuticle and its nearly exposed stomata whose subsidiary cells have different thickenings. Ctenozamites cycadea and Pachypteris papillosa resemble A. florinii in having thick cuticles but in other respects are different, especially in their stomata: the subsidiary cells of C. cycadea are thickened into a rampart around the top of the pit and in P. papillosa they are

papillose.

Though it does not occur in association at the same sample-horizons as A. florinii the leaf Paracycas cteis deserves consideration as like Alvinia it is essentially Cycas-like. Its single-veined pinnae resemble the segments of Alvinia more closely than do the many-veined pinnae of Pseudoctenis. Paracycas however is very different in many of its cuticular characters from Alvinia though in most of these, for example the epidermal cells, the differences are no greater than between the leaf and megasporophyll of Cycas (compare Harris 1964 p. 66 with this work Pl. 16). Indeed its stomata, though showing thickened projections on the subsidiary cells unlike Alvinia, are nevertheless more like Alvinia than their equivalent (a canopy of encircling cells) in leaves of Cycas. The differences between Alvinia and Paracycas which are greater than those between the Cycas leaf and its megasporophyll are in the very much thinner cuticle of P. cteis compared with that of A. florinii and in its lack of cutinised hypodermal cells. Like Nilssonia the trichome-bases of P. cteis are flatter than those of Alvinia. It seems odd that such a thinly cutinised leaf as P. cteis could bear such a thickly cutinised sporophyll as Alvinia.

The comparisons given above suggest that on grounds of association and agreement in cuticle structure Pseudoctenis lanei is the most likely leaf belonging to Alvinia florinii. As Alvinia is rare, known only from two horizons, the association is inevitably rather weak. The evidence would

be stronger if the two organs were found together at several horizons and in different localities amongst associates which are otherwise different. Though the agreement in cuticle structure seems to me impressive it is not perfect, and is less perfect than that between Androstrobus prisma (the male cone) and P. lanei. It is nevertheless much closer than between the megasporophyll and leaf of Cycas, and as Alvinia seems fundamentally more leaf-like than the megasporophyll of Cycas this greater similarity seems natural. Despite this I do not feel the present evidence for P. lanei is strong enough to reject Paracycas cteis as the possible leaf of Alvinia, especially when the rather great differences between Cycas leaves and megasporophylls are considered. For this reason I offer two reconstructions which I think possible, Pseudoctenis lanei + Alvinia florinii which I regard as more likely on the present evidence to be correct and Paracycas cteis + A. florinii which I think is less likely correct. A hope for further progress may lie in finding organs structurally intermediate between the leaf and the megasporophyll, like the "prophylls" of living Cycas.

Speculations on the morphology of Alvinia florinii

Alvinia florinii is a Cycas-like megasporophyll differing from Cycas chiefly in the distribution of its stomata and trichomes. This gives it a much more leaf-like appearance than the megasporophyll of Cycas and in a general way supports the suggestion based on living cycads that leaf-like megasporophylls are primitive (Chamberlain 1935:100-103). A similar suggestion based on fossil evidence is that the Cycas megasporophyll could have evolved from

fertile leaves of taeniopterid Carboniferous pteridosperms, such as Spermopteris Cridland et Morris (Cridland & Morris 1960), via an intermediate such as Archaeocycas Mamay. However there is no question of anything more than a hint from these fossils about the general way in which the megasporophyll might have evolved, as they are all incompletely known and there are tremendous gaps of time between them. In fact the Rhaetic megasporophyll Palaeocycas is less leaf-like than the geologically younger Middle Jurassic Alvinia. The chief new fact is that in Palaeocycas and Alvinia, considered together, we have every individual cuticular character shown by the vegetative parts of the Cycas revoluta megasporophyll.

If we accept the reconstruction Alvinia florinii + Androstrobus prisma + Pseudoctenis lanei the consequences are similar to those noted above for Androstrobus major + Pseudoctenis oleosa. The plant so reconstructed combines characters of living cycad genera now quite separate from one another. The fossil leaf and the male cone (Androstrobus prisma) show some resemblance to living Zamia (Zamiaceae) whilst the megasporophyll is like living Cycas (Cycadaceae). The pollen is different from any living cycad (van Konijnenburg 1971). This suggests that the Mesozoic cycads were diverse compared with living ones and can not be classified in extant families.

The reconstruction with Pseudoctenis lanei is also consistent with the idea that the Cycas leaf may have evolved by a reduction in the number of veins per pinnae. This is supported by earlier fossils such as Bjuvia + Palaeocycas (Trias : Rhaetic) and Archaeocycas

(Permian) in which entire many-veined (taeniopterid) leaves and megasporophylls are typical, and also by the Triassic Leptocycas Delevoryas et Hope (Delevoryas & Hope 1971) and the Carboniferous Allonilssonia grand'euryi (Saporta et Marion) Pant et Mehra (Thomas 1930) which had segmented leaves rather like Pseudoctenis and Nilssonia and are said to have cycadean cuticles.

Genus Pteroma Harris 1964: 170

Pteroma thomasii Harris

Association with Pachypteris papillosa (Thomas et Bose) Harris (Fig. 23/ p.113)

Pteroma thomasii is known only from Hasty Bank. Its cuticle has been shown by Harris (1964:175) to agree somewhat with the leaf Pachypteris papillosa and the two organs have previously been found in association, though probably on only one bedding plane (Harris 1964: 173). Harris thus concluded that these organs belonged to the same plant (1964:175-178).

The quantitative data (Fig. 23/ p.113) strengthens the evidence of association. P. thomasii is repeatedly associated with Pachypteris papillosa and Nilssonia kendalliae at several horizons in section 2. As the cuticle of N. kendalliae is unlike that of Pteroma thomasii this new evidence reinforces the conclusions of Harris.

The quantitative data also confirms the association of Pachypteris papillosa with the axis which probably belonged to it (Figs. 9-11/ p.56-58; Harris 1964:136).

Genus Allicospermum Harris
(Pl. 10, figs. 4 - 8; Pl. 11, fig. 2. Figs.9-11/ p.56 -58)

Allicospermum spp.

DISCUSSION

The genus Allicospermum was established by Harris (1935) for isolated seeds whose cuticles observed in the light microscope conform to a common gymnosperm kind seen in cycads, Ginkgo and many conifers. Together with isolated seed stones such seeds are frequent at Hasty Bank. In the siltstone of section 1, for example, oval seed stones, 7-9 mm broad and 10-12 mm long, are associated abundantly with the leaf Nilssonia syllis Harris (Fig. 23/ p.113).

Light microscopy offers little hope of further progress in classifying Allicospermum seeds at the generic or family level. The megaspore membrane (Pl. 11, fig. 2) shows some variation though rarely sufficient to satisfactorily distinguish the gymnosperm families which produced these seeds (Harris 1935 ; Coulter & Chamberlain 1917:9-12; Thomson 1905). However, study of a Hasty Bank seed by scanning electron microscopy (Pl. 10, figs. 4-8) shows the complex architecture of the megaspore membrane, revealing a suite of characters which are invisible in the light microscope. SEM comparisons of these isolated seeds with ones attached in fructifications might well therefore prove to be of taxonomic value, and as seeds are widely distributed, of stratigraphic value. Zimmermann and Taylor(1970) have partially demonstrated this value of SEM in a brief comparative survey of seeds from fructifications of Palaeozoic age.

B E N N E T T I T A L E S

Fig. 26

Fig. 26. Distribution and abundances of Bennettitales and Ginkgoales at Hasty Bank

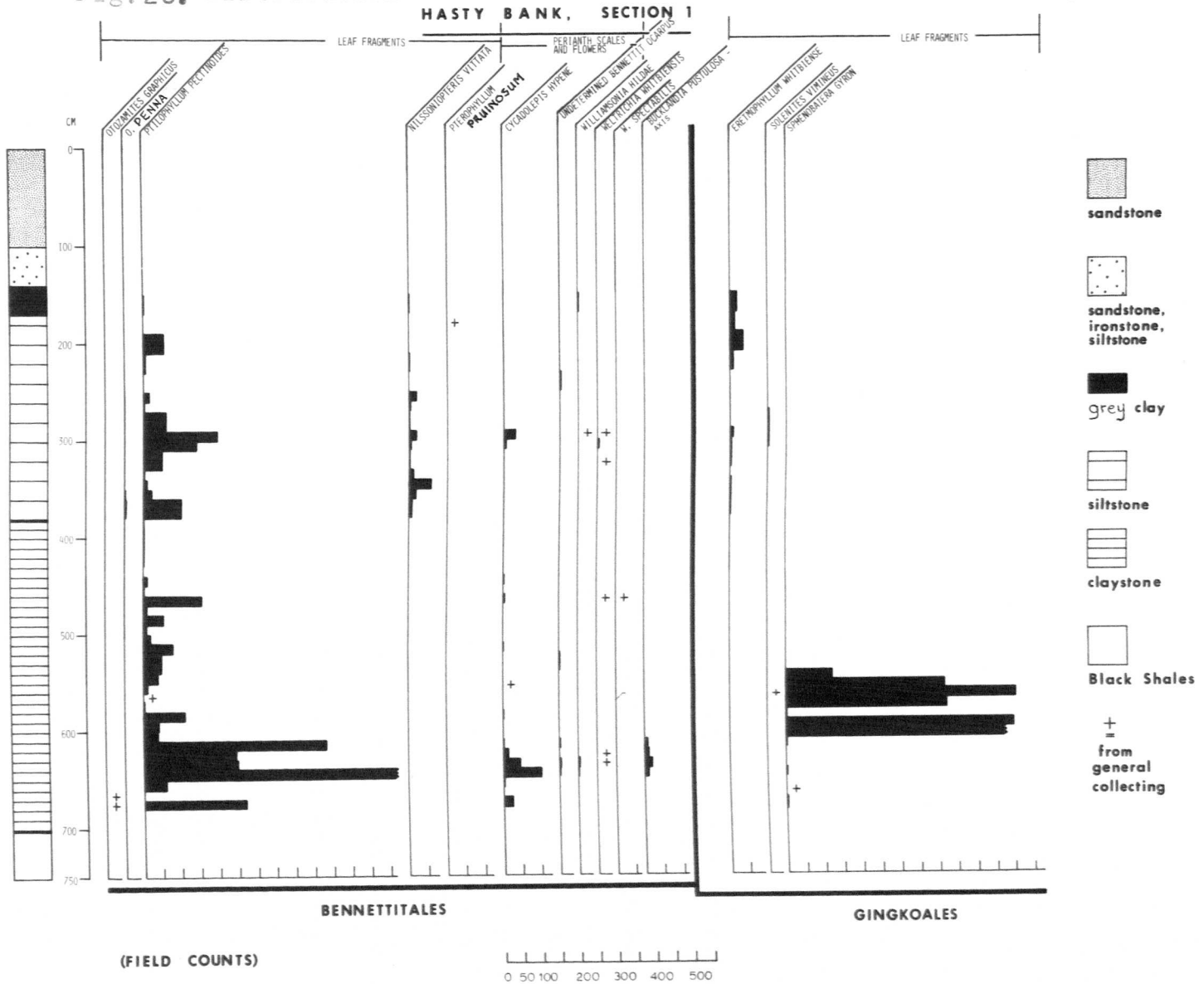


Fig. 26

Fig. 27.

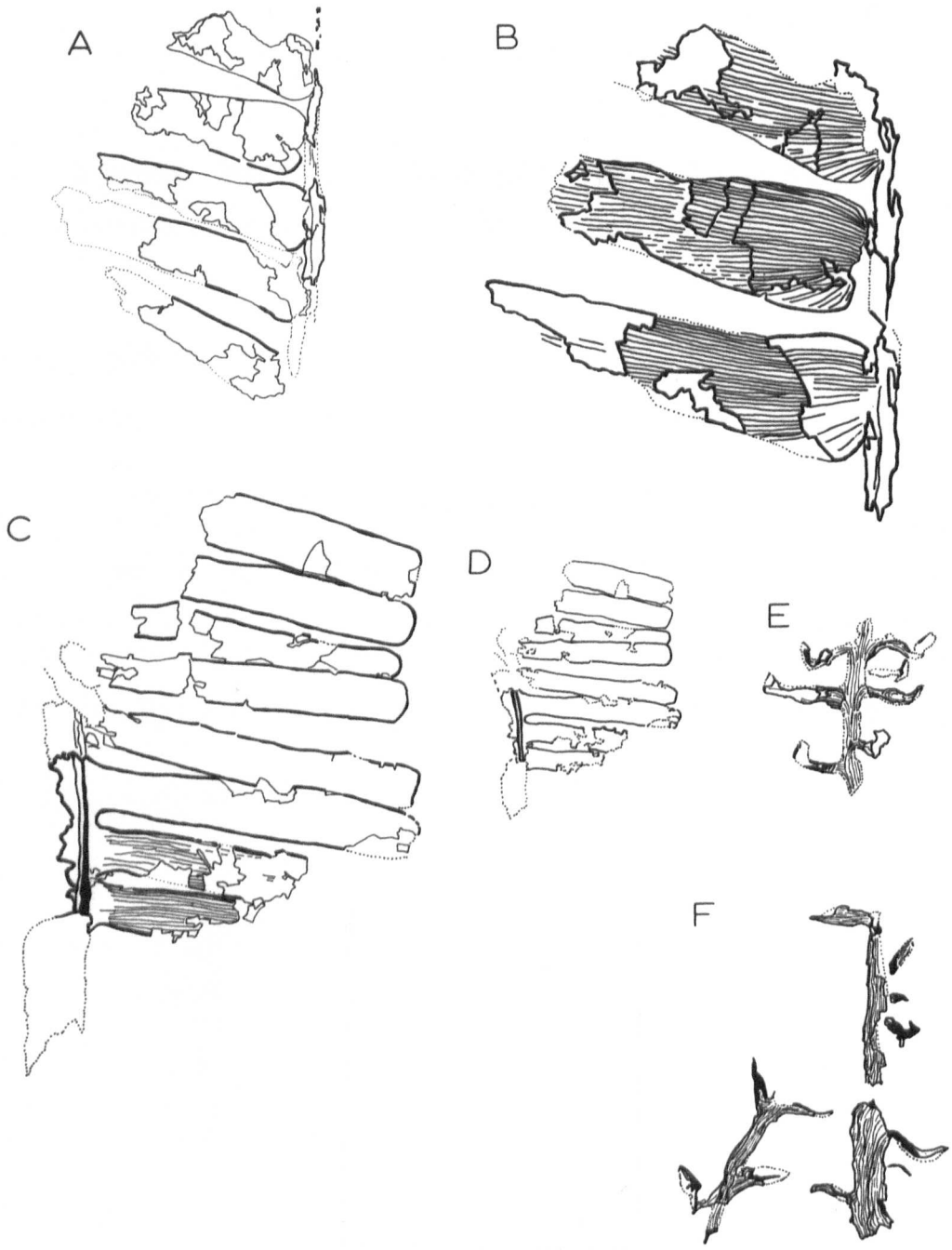


Fig. 27.

Fig.27. Zamites johannae sp. nov., Pterophyllum pruinosum sp. nov., Beania cf. gracilis.

A,B. Zamites johannae sp. nov. (manuscript name)
Holotype, from section S2.
A, x1. B, showing venation, x2.

C,D. Pterophyllum pruinosum sp. nov.
(manuscript name).
Holotype, specimen no. 2 (Part) from
section 1: 190-210 cm. C, x2,
showing venation of the lower pinnae.
D, x1.

E,F. Beania cf. gracilis, from section S2,
x1.5.
E, specimen no. 8
F, specimen no. 7.

All the specimens are from Hasty Bank.

Genus Zamites Brongniart 1828 emend. Harris, 1969

Zamites johannae sp. nov. (manuscript name)
(Pl. 21. Fig 27/ A,B). p.148

The only hand specimen of this species so far known is the holotype, which was collected from section S2 claystone. It is broken into two fragments of which one is figured here (Fig. 27/A,B). p.148

The species is named after Dr. Mrs. Johanna H.A. van Konijnenburg-van Cittert.

DIAGNOSIS [Leaf as a whole unknown (the only known fragment being from the middle region)]. Rachis stout, longitudinally striate. Pinnae straight, arising at angles of 60°-80° to the rachis. Pinna length at least 35 mm, width greatest just above the base (8-10 mm), [apex unknown]. Base of pinna rounded, somewhat overlapping the rachis, width where attached to rachis about half the greatest width. Margins of pinna flat and entire, usually tapering symmetrically from the widest part though base occasionally expanded at the upper or lower margin and therefore slightly asymmetrical. Veins forming well-marked ridges, diverging from the pinna base but nearly parallel in the distal region; forking occasionally, concentration 30-40 per cm.

Upper cuticle about 2-3 µm thick (measured in folds), showing uniform more or less rectangular cells which form longitudinal rows. Anticlinal walls strongly sinuous. Sinuosities thick and typically rather indistinctly marked, often mushroom-shaped. Periclinal wall flat, surface minutely granular. [Papillae and stomata lacking; trichomes lacking except for a few at the margin].

Lower cuticle about 1-2 µm thick, no marginal zone

distinguishable. Stomata occurring in bands about 150-275 μm wide between the veins, separated by strips 60-120 μm wide occurring over them. Stomatal bands slightly sunken but rarely flanked by longitudinal compression folds. Epidermal cells of stomatal bands irregularly rectangular, square, or polygonal; orientation variable though often transverse, rarely in ditinct rows. Anticlinal walls of epidermal cells strongly sinuous. Sinuosities less deeply incised than in cells of upper cuticle, thin and distinct, often mushroom-shaped. Periclinal wall flat, surface granular, central part typically thickened and raised to form a weak papilla.

Epidermal cells of vein strips like those of stomatal bands but uniformly square or rectangular and forming longitudinal rows.

Stomata about 90 per mm square, disposed in short rows in the stomatal bands, usually 3-4 rows per band; orientation transverse or nearly so. Subsidiary cells on the surface or slightly sunken, not overhung by neighbouring cells; smaller than epidermal cells or about the same size, outline semicircular, V- or U-shaped, rarely sinuous; surface distinctly thickened and bearing a single thick-walled papilla. Arrangement of subsidiary cell papillae in the stomata variable; typically arching towards each other over the guard-cells, often meeting at or near their tips; occasionally pointing straight upwards. Guard cells showing well-developed crescent-shaped thickenings along most of their length, slightly sunken, typically 25-40 μm long, aperture 10-18 μm long.

Trichome bases of one kind only; occasional in the stomatal bands, lacking over the veins; consisting of a round or oval cell with a thick periclinal wall which often

overlaps neighbouring cells (presumably originally bulging). Top of trichome base showing a large circular or oval scar seen as a thin area or hole (free part of trichome unknown).

DESCRIPTION. On maceration the pinnae yielded resinous matter which sometimes occurs as large rounded cell-casts 30-100 μm wide. The resin adheres to the cuticles, chiefly the upper. It is a common feature of the Yorkshire Bennettitalean leaves though never constant for a species and therefore of no taxonomic importance. In the Yorkshire Cycadalean leaves, however, such resin is of limited occurrence, fairly constant for a species and therefore taxonomically useful; it is almost diagnostic for Pseudoctenis oleosa.

The pinnae are either quite separate as shown in Fig. 27/A,B, or they may slightly overlap one another. p.148

DISCUSSION and COMPARISON WITH OTHER SPECIES.

The other Yorkshire species of Zamites are Z.quiniae Harris (Harris 1969:8) and Z.gigas (L & H) Morris (Harris 1969: 4). Whilst the gross form of Z. johannae is similar to Z. quiniae its cuticle is different from both of these other species. It is the only one which shows subsidiary cell papillae and subdued papillae on the ordinary epidermal cells of the lower cuticle. Unlike both Z. gigas and Z. quiniae the lower cuticle of Z. johannae lacks a specialised margin. In certain other characters, however, its cuticle is rather similar to Z. quiniae, though the stomata of Z. johannae are more regularly arranged.

Zamites gigas is distinguished by the shape of its pinnae which do not taper from just above the base and its cuticle which shows four kinds of trichomes rather than just one; Z. gigas also has sunken rather than exposed stomata and

differs in other details.

The most similar cuticle to Z. johannae known to me is that of Dictyozamites hawellii Seward (Harris 1969:87), a leaf which is quite different in form from Zamites as it has anastomosing veins.

The similarity of Z. johannae to Z. quiniae in gross form is interesting in relation to the generic boundary between Zamites and Otozamites. Harris has emphasised that this boundary is sometimes difficult to apply in practice (1969: 2,3,11). He defines the pinna base of Zamites as symmetrical and that of Otozamites as asymmetrical. However, in his diagnosis and discussion of Z. quiniae the pinna bases are said to be symmetrical whereas the figures (and specimens) actually show several which to me look asymmetrical (Harris 1969: t.fig. 3 B, C). The pinna bases of Z. johannae are similar. In both species however the expansion is unlike that of Otozamites where it typically occurs consistently on the distal side of the pinna base.

Since Z. johannae occasionally shows asymmetrical pinna bases it could conceivably be an extreme Zamites-like fragment from an otherwise typical species of Otozamites. The fact that the species is based on a single possibly extreme specimen may thus be misleading and further material is clearly required. However, whilst the form of Z. johannae is matched in some atypical species of Otozamites its cuticle is different at least from Yorkshire species. O. leckenbyi for example is similar in form though smaller and it has strongly protected stomata. The most similar species in cuticle is O. thomasi Harris (Harris 1969:21) but unlike Z. johannae it lacks subsidiary cell papillae. Thus even if subsequent study shows that Z. johannae should be transferred

to Otozamites it is clearly new, at least to Yorkshire.

Dispersed cuticles similar in almost every detail to Z. johannae occur abundantly in the Hasty Bank main leaf coal. They differ chiefly in their better preservation. In some of them rounded trichomes are frequent and the epidermal cell papillae are sometimes scarcely developed. The cell outlines of the lower cuticle tend to be broader than in the holotype and are more heavily thickened near the margin. Two of the fragments show a pointed pinna apex which is asymmetrical (like Otozamites!). Vein concentration 40 per cm, like Z. johannae.

Of the few species from other regions whose cuticles are known none seems to be at all similar to Z. johannae.

Genus Pterophyllum Brongniart 1828 emend. Harris 1969:92

Pterophyllum pruinosum sp. nov. (manuscript name)
(Fig. 27/C,D; Pl. 22 fig. 3; Pl. 23)

Pterophyllum pruinosum, as described here, is represented by three specimens. Two are fragments of the leaf and one is an isolated pinna. They all came from one horizon in the siltstone, at 1-2 m below the top of the main plant bed.

The species is distinguished from all others of the genus occurring in Yorkshire by its densely papillose lower surface.

DIAGNOSIS. [Middle region of leaf known only]. Rachis glabrous, 2 mm wide, grooved along the presumed upper surface [but not showing transverse wrinkles]. Pinnae 20 mm to at least 30 mm long and up to 2.5-5 mm wide, straight, attached at angles of 70°-80°(? - 120°) to upper surface of rachis near its edge. Pinna base somewhat expanded, 3-4 mm wide. Margins of pinna flat and entire, narrowing symmetrically just above the expanded base and then gradually expanding again, becoming parallel distally. Pinna apex obtusely rounded, either scarcely lobed or distinctly bilobed; lobes when present rounded, equal or unequal, occurring to either side of an apical notch.

Veins delicately though distinctly marked, concentration typically 45 per cm (range observed 32-60); parallel (forking not clearly seen).

Substance of lamina thin.

Upper cuticle about 2 μm thick (measured in folds). Epidermal cells rectangular or polygonal, typically 2-6 times as long as broad, orientated longitudinally and forming

longitudinal rows. [Cells over veins either longer than those between and veins therefore obvious, or about the same and veins obscure]. Anticlinal walls sometimes straight but typically irregularly undulating or slightly sinuous (amplitude about 1-5 μm), flanked to either side by an irregular thickening or by ridges running on to the periclinal wall. Periclinal wall flat, showing irregular thin areas, often pitted and granular. Cells just near margin with thicker walls than elsewhere, periclinal wall showing a number of elongated thick areas or strips.

Lower cuticle about 2 μm thick. Epidermal cells square or polygonal, isodiametric or about twice as long as broad, corners rounded; orientation irregular though tending to form rows especially over the veins. Anticlinal walls slightly undulating or sinuous (amplitude like upper cuticle), irregularly thickened to either side. Periclinal wall showing irregular thin areas, often finely pitted and granular; typically bulging strongly into a conspicuous hollow papilla. Lateral wall of papilla thickened, penetrated by simple pits; wall at top either thin or surrounding a circular hole (therefore possibly a trichome base rather than a papilla). Stomata scattered, orientation variable though dominantly transverse, occasionally forming short rows, not sunken or scarcely so. Subsidiary cells about the same size as the epidermal cells, outline typically semi-circular (sometimes rectangular or polygonal), straight or scarcely sinuous; [surface neither thickened nor papillose].

Guard cells slightly sunken, irregularly thickened next to the aperture, crescent-shaped thickening of dorsal wall broad; poles elongated and somewhat thickened. Length of guard-cells about 40 μm (range 33-60), dorsal thickenings

24-35 μm; stomatal aperture typically 20 μm (range 9-24).

Marginal region narrow, 2-3 cells broad, resembling margin of upper cuticle.

DESCRIPTION and DISCUSSION. The pinnae. The attachment of most of the pinnae to the rachis has been torn during burial and probably because of this they often overlap. Where not torn they are separated from each other by 1-2 mm (Pl. 22, fig. 3).

The pinnae of the holotype look as if they are attached at angles of up to 120° to the rachis (Fig. 27/C, D and Pl. 22 fig. 2). However the rather short fragments of rachis are unhelpful in orientating the specimens and thus I may well have illustrated the holotype upside down. If so the angle of attachment of the pinnae is about 80° or less in all the specimens. Better specimens are required to resolve this uncertainty.

The lobes at the ends of the pinnae were not formed by wear or curling of the pinnae during burial, nor by cleavage of the specimen during collecting. This is shown by the cuticle which is intact at the pinna apex where the upper and lower cuticles may be seen to join.

In every pinna of the holotype the lobes are scarcely developed and irregular whereas every pinna of specimen 1 shows two well developed ones. Whilst this difference seems large it can hardly be regarded as of taxonomic significance. The two specimens yielded almost identical cuticles and also agree in other characters of gross form. Presumably the development of lobing was variable, possibly between different parts of the same leaf.

The cuticle. There is also some variation between the specimens in the details of their cuticles. The proportion of

papillose cells is greater in specimen 1 (about $\frac{9}{10}$) than in the others (about $\frac{7}{10}$). The sinuosities of the epidermal cells, however, are least developed in specimen 1 and strongest in specimen 3, the detached pinna.

Occasional epidermal cells in the lower cuticle of specimen 3 show a thickened and distinctly scalariform or perforate periclinal wall. These cells are probably trichome bases like the one illustrated by Harris for P. thomasii (1969: Fig. 44C). Considered with the strongly developed sinuosities they make it possible that this specimen represents a different species. However in other characters its cuticle agrees so fully with the others that I identify it with them.

Papillae. That the thick lateral walls of the papillae are not merely compression folds is shown by the pits as they penetrate right through the wall and presumably are original. The dense covering of papillae on the lower surface of the leaf doubtless gave it a velvety (pruinose) appearance in life, like many modern flower petals.

COMPARISON.

The other Yorkshire species of Pterophyllum are P. thomasii Harris (Harris 1969:93), P. fossum Harris (sensu Harris 1969:97) and P. cycadites Harris & Rest (Harris 1969:100).

Pterophyllum cycadites differs from P. pruinosum in its usually narrower pinnae which except at the base are of uniform width rather than gradually expanding; they end in a pointed apex rather than a rounded one. P. fossum differs in its hairy rather than glabrous rachis, which bears narrower pinnae and its pinnae, which are grooved rather than flat.

The pinna apices however may resemble P. pruinosum in sometimes having lobes (Harris 1969:Fig. 45I). Pterophyllum thomasii when it has straight pinnae is the closest in form to P. pruinosum, though its pinnae are of uniform width over most of their length and they taper distally to an acute apex, quite unlike P. pruinosum.

The cuticle of none of these other species is specially like P. pruinosum. They all lack the dense covering of papillae (or trichomes) on the lower cuticle and also differ in other details. P. fossum is the closest, though the broad specialised margin of its lower cuticle is quite different from P. pruinosum; the cells of its upper cuticle are also shorter than in P. pruinosum. The trichome bases of P. fossum are broader in relation to the size of the epidermal cells and never occur on more than about $\frac{1}{10}$ of the cells.

Of the comparable dispersed cuticles, V.29482, from the Birk Brow quarry Coal, is rather similar to P. pruinosum (Harris 1952a:625, t.fig. 6D; 623, t. fig. 5G). Harris originally included it in P. fossum (1952a) but later regarded the determination as doubtful and excluded it (1969:100). Unlike the other material of P. fossum but like P. pruinosum the cells of its upper cuticle are rather elongated. Its lower cuticle lacks a specialised marginal region and the subsidiary cells are large, like P. pruinosum. However, papillae like those of P. pruinosum are entirely lacking and I thus leave it unde termined.

V.29493 is a dispersed cuticle from Sandsend alum pit B; it is labelled P. fossum. It has somewhat similar trichomes (or papillae) to those of P. pruinosum but they are scarce (about $\frac{1}{10}$ of the cells). In other details the cuticle is

more or less typical of P. fossum.

Of the numerous species of Pterophyllum described from the Mesozoic of other regions none that I know is exactly similar to P. pruinosum. P. filicoides (Schlotheim) Thomas is similar in gross form but has a quite different cuticle which is amphistomatic and it also shows sac-like trichomes (Barnard 1970:28, Fig. 2A-I, Fig. 3F-G, Pls. 4 Fig. 1 and 5 figs. 2,4.) Certain other species have rather similar cuticles, for example P. cf. ptilum Harris (Swedish material of Lundblad 1950:64, Pl. 1x fig. 3) and P. xiphipterum Harris (Harris 1932b:69). None of these, however, closely resembles P. pruinosum in form. The most similar species in both form and cuticle seems to be P. subaequale Hartz (sensu Harris 1932b: 74-79, figs. 39-41, Pl. 6 figs. 13 and 14; Harris 1932a:96, Fig. 38 A-C, Pl. 9). P. subaequale in this sense encompasses the variable gross form of P. pruinosum and the cuticles may sometimes be very similar though none of the photographs shows exactly similar papillae. Though P. subaequale always shows transverse wrinkles on the rachis whereas P. pruinosum lacks them this need not be a specific character: it probably depends on conditions of burial (see Harris 1969: 122 and 1973: 6 for discussion of such wrinkling).

There is thus the possibility that P. pruinosum is merely a synonym of P. subaequale and re-examination of the slides and specimens of P. subaequale is called for to clarify this. V.15821a, prepared from Swedish material, has much more sinuous anticlinal walls and very few papillae (or trichomes) compared with the Yorkshire material.

ASSOCIATIONS BETWEEN DETACHED BENNETTITALEAN ORGANS

The "Williamsonia" plant: Williamsonia hildae Harris(female flower) + Weltrichia whitbiensis (Nathorst) Harris (male flower) + Cycadolepis hypene Harris (perianth scales) + Ptilophyllum pectinoides (Phillips) Phillips (leaf) + Bucklandia pustulosa Harris (stem).

Harris has attributed these organs to the same plant and gives an excellent restoration (1969:Fig. 59C: 137-139). The evidence for linking the organs is organic continuity seen occasionally between C. hypene with B. pustulosa and P. pectinoides, and also from the strong association of these organs both with one another and with the flowers. This association is seen repeatedly in several localities. There is also supporting evidence from the occurrence of foliar organs somewhat intermediate in gross form between the perianth scale C. hypene and the leaf P. pectinoides (Harris 1969:115). However, there is no special support from agreement in cuticular characters.

The quantitative data from Hasty Bank overwhelmingly supports Harris's evidence of association (Figs. 26/p.147; 9-11/p.56-58). Frequently when P. pectinoides is very abundant the perianth scales and often the flowers are seen, and sometimes also the stems (Fig.26). There is consistent quantitative agreement in that the scales and flowers are at their commonest where the leaf P. pectinoides is also at its most abundant. No other Bennettitalean leaf is associated so consistently with the flowers.

I can not imagine how these organs could become so impressively associated through sorting by density or size or other agencies during deposition. The association

surely indicates that the organs originally belonged together on plants which became fragmented during or before burial. This is at least partially confirmed from the rare discoveries of organic continuity between some of the organs.

Other bennettitalean reproductive organs at Hasty Bank also show associations, though weakly, notably the suite of organs Otozamites penna Harris + Cycadolepis spheniscus Harris + Weltrichia spectabilis (Nathorst) Harris. In certain other localities these organs show strong association, but with Otozamites gramineus (Phillips) Phillips instead of O. penna. From work currently in progress this seems consistent, as there is evidence to suspect that O. penna and O. gramineus represent a single species.

"TAXAD"

Genus Marskea Florin 1958

Marskea thomasiana Florin

DISCUSSION OF NAME

Florin (1958:303) gave the following three differences between Marskea thomasiana and Taxus jurassica. Marskea thomasiana has undulating cell walls in the lower cuticle as well as the upper whereas in T. jurassica they are confined to the upper cuticle. The upper cuticle of M. thomasiana is mottled whereas that of T. jurassica is not, and the cells near the margin of both upper and lower cuticles show median cuticular ridges, unlike T. jurassica.

Many of the Hasty Bank leaves of Marskea thomasiana in fact show fairly straight cell walls, especially near the leaf apex. The development of mottling appears to vary with the preservation, and the development of cuticular ridges varies in specimens which occur intermingled at the same horizons. These facts suggest that M. thomasiana and T. jurassica represent a single species and should be combined. Professor Harris tells me he has reached similar conclusions on material from several other localities and my findings therefore merely confirm his.

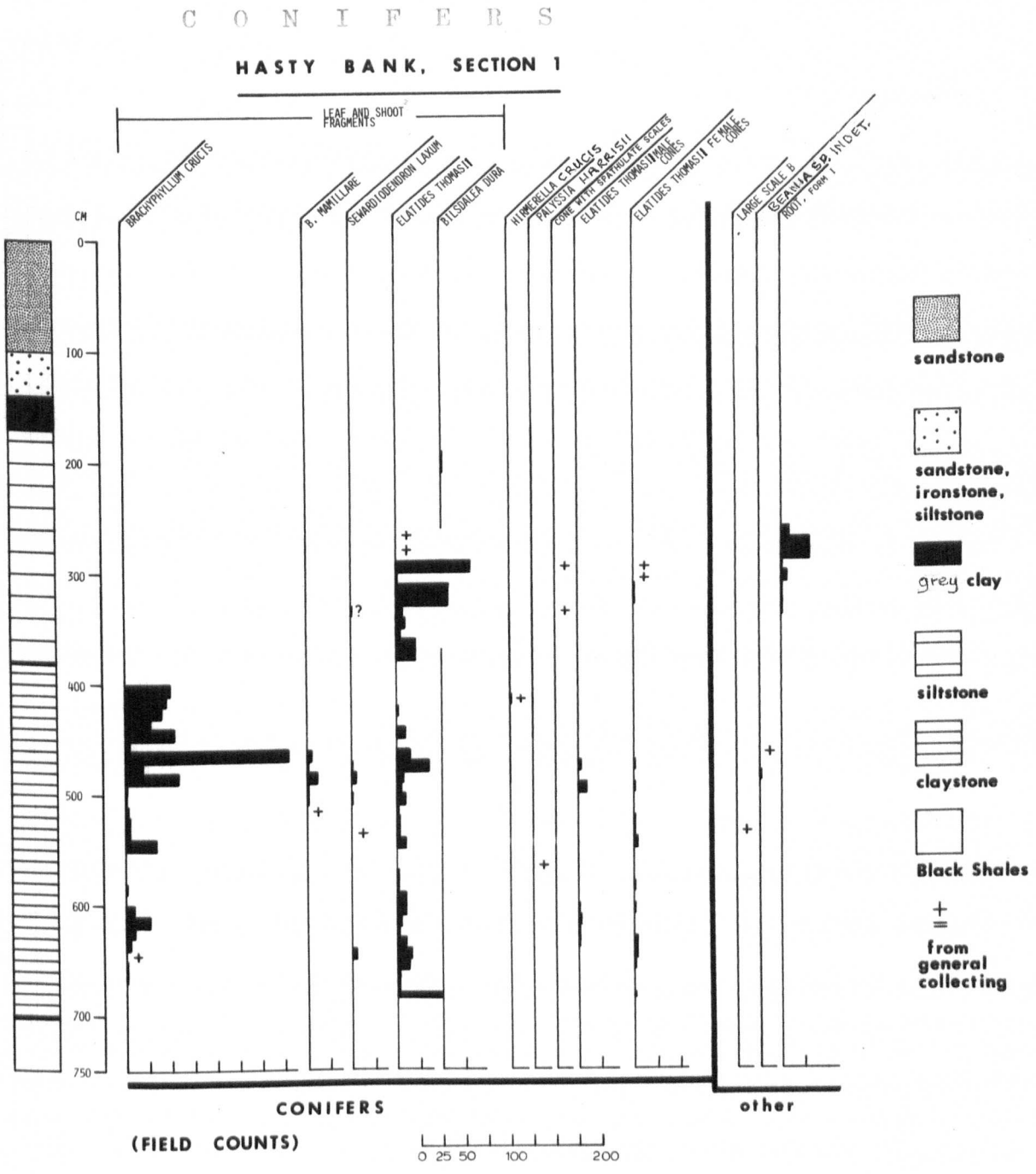


Fig.28.

Distribution and abundances at Hasty Bank of conifers and other, unclassified, plant fossils

STACHYOTAXUS - GROUP

Genus Palissya Endlicher 1847 emend. Florin 1958:267

Notes on Palissya harrisii sp. nov. (manuscript name) (Pls. 24-26; 27, figs. 2,4). Cuticles to be figured elsewhere.

1973 Palissya sp. nov. Hill in Hill & van Konijnenburg 1973:62 (name in list).

Palissya harrisii is known from about 20 fragments of female cones and a dozen or so leafy shoots. It occurs in association with the leafy shoots Sewardiodendron laxum (Phillips) Florin but is here considered morphologically distinct from that species (Hill & van Konijnenburg 1973: 62).

DIAGNOSIS Shoots bearing spirally inserted leaves which are more or less flattened into one plane, [branching unknown]. Axes of shoots up to 3 mm broad, longitudinally striated. Leaves inserted at angles of 30° to 90° to the axis, bifacial, lanceolate, 10-15 mm long and about 1.5 to 2.5 mm broad; usually straight but sometimes slightly curved forwards or backwards, showing a single midrib; substance thick though fragile. Leaf base decurrent for several mm on the shoot axis, more or less twisted; contracted but scarcely petiolate, width where it departs from the axis about $\frac{1}{6}$ to $\frac{1}{2}$ the greatest width. Leaf margins entire, gradually expanding through about 5-7 mm from the base and then gradually contracting towards the apex; in middle region of leaf sometimes parallel. Leaf apex contracting sharply to an acute or obtuse point, sometimes acuminate.

[Leaf on maceration sometimes yielding a good deal of internal parenchyma and abundant small resinous cell-casts

about 10-20 μm in diameter]. Cuticle of leaf thin about 1-2 μm (measured in folds). Presumed upper cuticle and most of lower showing fairly uniform polygonal isodiametric or rectangular cells, occasionally more than twice as long as broad, orientation longitudinal (cells of lower cuticle more often isodiametric than those of upper cuticle). Anticlinal walls straight or sometimes rounded. Periclinal wall flat, mottled; densely and minutely pitted; sometimes showing longitudinal striae. Lower cuticle showing stomatal bands about 0.2 mm wide, presumably one occurring to either side of the midrib. Epidermal cells of stomatal bands each bearing a low papilla which is thick-walled and more or less hemispherical though often irregular in shape and position on the cell. (Details of stomatal bands often obscured by adhering internal tissues).

Stomata scattered in the stomatal bands fairly densely; probably monocyclic (though this was not seen clearly). Stomatal apparatus oval, orientated longitudinally, slightly overhung by papillae from about 5 subsidiary cells. Guard cells very thinly cutinised, 30-40 μm long.

Female cones probably upright, each borne singly at the end of a leafy shoot; cylindrical; up to 35-45 mm or more in length, 10-15 mm broad.Cone axis robust, longitudinally striated, 1-2 mm wide. Cone-scales inserted in a close spiral at angles of 30°-70° to the axis (phyllotaxis obscure); either pointing straight out from the cone axis or sometimes bent backwards near their bases and then bending upwards. Bract-like portion of cone-scale flattened, broadly lanceolate, about 10 mm long, greatest width about 3 mm; substance thin, margins entire. Distal part of bract turned upwards, expanded and broad-lanceolate, either tapering evenly to an obtusely

pointed apex or apex broad-acuminate. Base of bract contracted, decurrent on cone axis.

Ovuliferous portion of cone-scale an elongated ridge lying on top of the bract and taking up the proximal $\frac{1}{2}$ to $\frac{2}{3}$ of its length; proximal 2 mm sterile, distally fertile. Fertile part bearing 4, 6 or 8 ovules (usually 8) in opposite pairs. Ovules forming two rows, one to either side of the ovuliferous ridge, orthotropous, each surrounded by a distinctly asymmetrical scale-like "aril". "Aril" showing longitudinal striations, expanded part about 1 mm high and 1 mm broad. [Ovules themselves unknown, presumably having been shed before preservation].

Cuticle of cone-scale [incompletely known,] like that of the leaf but stomata not seen.

[Male cone unknown, pollen unknown].

DESCRIPTION The following are the better specimens

no. B1. Cone at end of a strongly curved leafy shoot; cone scales straight (Pls.24, 25)

no. B2. Distal portion of bract scale (to be figured elsewhere)

no. B6. Cone-scales curved backwards, arils separated by matrix; leaf cuticles

no. B9. Leaf cuticles

no. B16. Cone (Pl. 26)

no. B18. Cone and detached shoots; leaf cuticles.

no. A8b. Shoot morphology (Pl. 27, fig. 4); leaf cuticles.

DISCUSSION

The free parts of the arils are separated by the matrix

both from one another and from the underlying bract, and were therefore presumably separate in life. Florin suggests that the elongated ovuliferous ridge of Palissya was partially separate from the top of the bract (1958:271; 1944: 505), but this was not clearly seen in the Hasty Bank material. The ovuliferous ridge looks as if it is completely fused to the bract. However, the extent of fusion was not easily investigated because the coal is fragmentary and ordinary degaging is thus difficult. Araldite-embedding and serial grinding might overcome this technical problem.

The stomata are usually poorly preserved and obscured by mineral particles. Often the whole apparatus has disappeared, leaving only an oval hole 30-120 µm long.

Attribution of the shoots to the cones. The cones and shoots occur in intimate association, usually side by side on the same blocks of matrix. There is also agreement in cuticular structure between the cone-scales and the leaves, mentioned above in the diagnosis. This evidence supports the attribution of the shoots to the cones. An attempt was made to go further by preparing cuticles from the poorly preserved leaves which occur on the cone axis of specimen B1, but the preparation was unsuccessful.

DISTRIBUTION

P. harrisii is restricted to the claystone. Apart from an isolated occurrence in section 1 (Fig.28/ p.164) it appears to occur only in sections S1 and S2 where it is locally abundant.

COMPARISON Two other species of Palissya are known from coning material. These are P. sphenolepis (Braun) Nathorst from the Lias of Sweden and Germany, and P. bartrumii Edwards from the Upper Mesozoic of New Zealand. Several

other species of Palissya have been described from foliage of similar gross form to P. harrisii though their cones are unknown.

P. bartrumii Edwards (Edwards 1934:100, pl.V figs. 5,6). The cones of this species are longer and the cone-scales more loosely arranged than those of P. harrisii though this difference may merely reflect the relative maturity of the cones. The cone-scales of P. bartrumii sometimes have a greater number of ovules though often they have a similar number to those of P. harrisii. They are also thicker near their bases. The general resemblance of P. bartrumii to the Northern hemisphere species is thus strong but as its cuticle is not preserved it can not be fully compared with them. Its foliage is unknown.

P. sphenolepis (Braun) Nathorst (Florin 1958:267-276; Pls. 1,2 figs 1-3. Florin 1944: pl. CLXXXIII/IV figs. 20-22. Nathorst 1908: Pl. 1 figs. 1-21). Rhaeto-Liassic.

The form and cuticle of P. sphenolepis and P. harrisii are very similar to one another and I therefore thought at first that the British material might be merely a diminutive form of P. sphenolepis. However the differences are constant for the species and there are no intermediate specimens. The cones of P. sphenolepis are larger (up to 100 mm long, at least 15 mm wide) and their cone-scales have 10-12 ovules, whilst the cone of P. harrisii is nearly always less than 15 mm wide and the cone-scale never shows more than 8 ovules. In contrast to this the leaves of P. sphenolepis are narrower (0.7-1.5 mm) than those of P. harrisii (1.5-2.0 mm) and they are more strongly keeled. The leaf cuticles of the two species are essentially similar though the epidermal cells are typically longer in P. sphenolepis.

Other differences are minor and probably reflect variations in the environment of growth and preservation. The cuticle of P. sphenolepis for example is typically strong whereas that of P. harrisii is fragile. However an otherwise typical shoot of P. sphenolepis kept at the British Museum (V.15823) yielded a fragmentary and poorly preserved cuticle which looks similar to P. harrisii.

The leaves of P. sphenolepis are said to spread in all directions (Florin 1958:271) whereas those of P. harrisii are more or less flattened into one plane. I believe this difference must be chiefly interpretive because the leaf arrangement in both species looks very similar.

Comparison with the sterile shoots Sewardiodendron laxum (Phillips) Florin (Florin 1958:303-307, Pls. 25-27; this work: Pl. 27 figs. 1,3).

Palissya harrisii shoots occur in loose association with S. laxum in the claystone of Hasty Bank (Fig. 28, p. 164). Because of this I previously thought they may have belonged to the same plant but now think I was wrong. There are two main differences which seem constant. Firstly the long leaves of S. laxum always narrow gradually from just above the base (about 1 to 2mm above it)whereas in P.harrisii they do not start to narrow until some 5 to 7mm above the base(Pl. 27 figs. 3,4).(The short leaves of S. laxum do sometimes narrow like those of P. harrisii but being short they are different). Secondly the leaf cuticles of P. harrisii can nearly always be prepared successfully by concentration using a centrifuge after maceration (p. 82), and they show epidermal cell papillae in the stomatal region. Sewardiodendron laxum hardly ever yields a cuticle and when it does there are never any epidermal cell papillae. Other differences are in the substance of the leaf, which is relatively thick in

P. harrisii, and also in the shoots which are never dimorphic in P. harrisii but are characteristically so in S. laxum.

I should point out that whilst the difference in leaf shape seems constant it was only seen clearly in the two better-preserved specimens of P. harrisii and the dozen or so better specimens of S. laxum. More specimens are required because this sample is small and may therefore be unrepresentative.

The systematic position of Palissya.

Fossil evidence suggests that the ovuliferous scale of modern conifers was derived by reduction from a fertile shoot borne in the axil of the bract (Florin 1951:347-348 Fig. 42). The ovuliferous ridge of Palissya is much more shoot-like than the ovuliferous scale of any living conifer and may justifiably therefore be regarded as primitive.

The immature female cone of living Cephalotaxus resembles Palissya and may be imagined as a very reduced derivative in which only the basal pair of ovules remains on the cone-scale and in which the "aril" is relatively suppressed. The cone is borne on a strong lateral shoot like P. sphenolepis though this is also relatively reduced. Schweizer 1963: Fig. 14 gives elegant comparative illustrations in which the fossil Stachyotaxus is reasonably regarded as intermediate between Palissya and Cephalotaxus: the female cone of Stachyotaxus resembles Palissya though its cone-scales show only one pair of ovules, like Cephalotaxus. Cephalotaxus is unique amongst living conifers and it is thus tempting to group it with Palissya and Stachyotaxus as Schweizer did (1963:26). However its foliage is quite different from both of these fossil genera. Unlike them its leaves (at least in

C. fortunei Hook.) have a short petiole and they narrow from just above the base (like Sewardiodendron). Its cuticle differs in lacking subsidiary and epidermal cell papillae and the subsidiary cells are more specialised, into terminal and lateral ones of unequal shape (Florin 1931:301-304, pls. 33 figs. 4,5 and 34 figs. 2,3).

The leaf and shoot form of Palissya are most closely matched by the living conifers Cunninghamia lanceolata (Lamb.) Hook. and Sequoia sempervirens (Lamb.) Endl., both of the Taxodiaceae. Their leaves lack petioles and the subsidiary cells of S. sempervirens show thickenings somewhat like the papillae of Palissya. However the organisation of the ovuliferous scales in these species is quite different from Palissya: their ovules are arranged radially whereas in Palissya they are in two linear rows.

Similar comparisons are also possible with Dacrydium of the Podocarpaceae (Florin 1958:274).

These comparisons of Palissya with living conifers have been debated at length by several workers (Schweizer 1963; Florin 1958: 273-276 who also gives earlier references). The evidence, summarised above, suggests that whilst Palissya shows primitive features it is unlikely to be directly ancestral to any one living group and probably represents a blind alley in evolution.

Relationship of Palissya with the fossil conifer Stachyotaxus Nathorst 1886.

The morphology and cuticle of the leafy shoots and female cones of Palissya and Stachyotaxus are remarkably similar to one another, and on this basis Florin proposed the family Palissyaceae for them (Florin 1958:275,276). However though known for Stachyotaxus the male cones of Palissya are unknown

and thus the two genera can not be fully compared. To give a formal family name to such incompletely comparable genera implies the fuller evidence of natural relationship which a botanist would have if these genera lived today, as he or she would thus be enabled to investigate all parts of the plants. I believe there is a case for emphasising our lack of knowledge until more is learnt, and this is done here by referring these fossils to an informal group.

HIRMERELLA - GROUP

Genus Hirmerella (Hoerhammer) Jung 1968

Notes on Hirmerella crucis (Kendall) comb. nov.
(Pls. 28-30).

1947.	Brachyphyllum crucis Kendall (foliage)	Kendall 1947:240. (Holotype. Description of Callovian specimens from Oxford Clay of Wiltshire, England).
1952.	Brachyphyllum crucis Kendall (foliage)	Kendall 1952:590 (Description of Bajocian material from Yorkshire, England and Bathonian from Oxfordshire, England.
1971.	" " " (male cone and pollen)	van Konijnenburg 1971:59 (Description).
1972.	" " " (male cone)	van Konijnenburg-van Cittert 1972: 98, Pl. 1 fig. 3 (illustration).
1973.	" " " (foliage)	Hill & van Konijnenburg-van Cittert 1973:62 (name in list).
1973.	Hirmerella sp. nov. (female cone)	Hill & van Konijnenburg 1973: 62 (name in list)

SHOOTS. Discussion of Hasty Bank material (Pl. 29)

New Hasty Bank specimens show the main shoots and branching, which are to be described by Professor Harris. They also show considerable variation in leaf form. A few unusually long-leaved shoots were seen in which the leaves are awl-shaped and up to 12 times as long as broad. These leaves not only overlap into Pagiophyllum Heer but also

resemble Geinitzia Endlicher in the sense of Harris 1969a:249. Their cuticles however are typical except that they lack the normally scarious margin. These long-leaved shoots occur with the normal ones and since a range of intermediate forms was seen there is no reason to consider them specifically distinct.

This kind of variation in leaf form and the absence of a scarious margin in the long leaves is like that seen in shoots of Hirmerella muensterii (Schenk) Jung (Lewarne & Pallott 1957: 76).

The leaf cuticles are essentially uniform in showing scattered stomata which are never in strongly marked rows and having subsidiary cells which form a thickened ring around the stomatal pit. The subsidiary cells usually show radiating striations and the ordinary epidermal cells are always in well-defined rows. However, there is also considerable variation in most of the characters (cf.Kendall 1947:240). The scarious and microscopically dentate margin occurs near the apex of the short leaves but is lacking from long ones. The cuticle as a whole varies in thickness and the thickened ring around the stomatal pit also varies in thickness. The stomata may be strongly sunken or almost on the surface and the outer surface of their subsidiary cells may bulge but often hardly does so. The encircling cells are typically elongated and form a complete ring but sometimes they are irregularly present and often of irregular shape. The striations and markings on the periclinal walls of the epidermal cells are also usually present but sometimes faintly. Shape of stomata round, oval or slit-like. Anticlinal walls of epidermal cells occasionally interrupted by pits; of variable thickness and sometimes quite thin.

FEMALE CONES (Pls. 28,30. Fig.29/p.177,A-E).

There are six fragmentary specimens of cones and also a few detached cone-scales and bract-scales. All the material mentioned here came from Hasty Bank though Dr. van Konijnenburg-van Cittert tells me she has found detached cone-scales in the Millepore bed.

Preliminary study shows that the cones agree in essential features of gross form with the better-preserved German Hirmerella muensterii (Schenk) Jung (Jung 1968). The cuticles are similar to both H. muensterii and H. airelensis Muir & v. Konijnenburg-van Cittert (Muir & van Konijnenburg 1970:433).

There is no indication that the cone-scales of H. crucis are organised differently from the interpretations given by Hoerhammer (1933) as revised by Jung (1968), but they have not yet been properly studied. Florin (1944: 497-502) has given different interpretations from Hoerhammer and Jung.

Preliminary diagnosis of the female cones.

Cone ovoid, presumably composed of a stalk which bears cone-scales in a complex spiral (stalk not seen), at least 10 mm long and up to about 13 mm wide, probably pendant. Cone-scales overlapping one another, morphology complex, composed of a bract scale which supports an ovuliferous scale on its adaxial surface. Cone-scales fibrous and probably deciduous at maturity.

Bract scale about 7-12 mm long, broad-lanceolate, width gradually expanding from the base, tapering sharply in the distal part to an obtuse point which is turned downwards towards the tip of the cone; substance fairly thin; showing a thickened midrib flanked on the adaxial surface by two

Fig. 29.

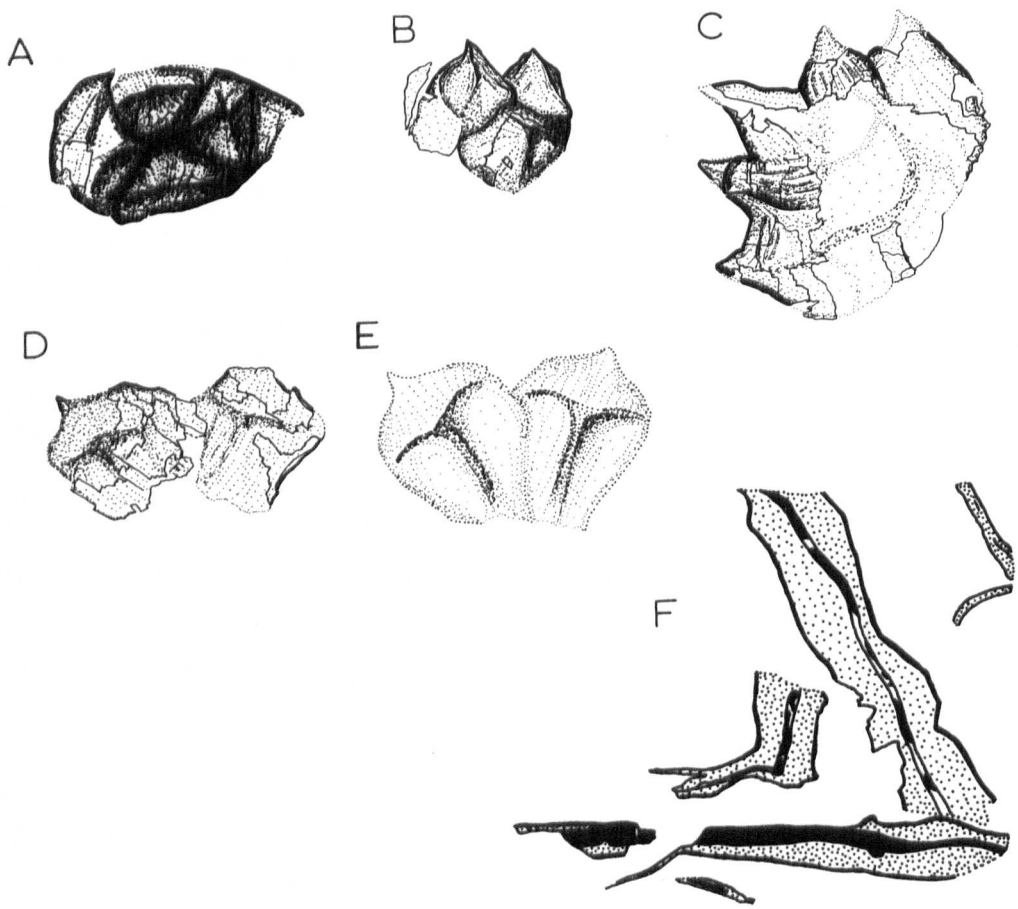


Fig. 29.

Fig. 29

Hirmerella crucis (Kendall) comb. nov.; Root, form 1.

A-E. Hirmerella crucis.

Sketches of isolated cone-scales, A-C ovuliferous scales, D and E bract scales. All x 3.

A, specimen no. 3a; B, no. 5; C, no. 7 (drawn from Part and Counterpart); D, no. 1 (Part). E is a restoration of no. 1, based partly on sketches made in the field and partly on sketch D.

F. Root, form 1

Drawn freehand from block no. 1.

x 0.5.

All the specimens are from Hasty Bank.

longitudinal depressions [which probably represent impressions of ovules]; longitudinally striated, margins entire. Greatest width of bract scale much nearer the point than the base; width of base about half the greatest width.

Ovuliferous scale smooth, about 4-8 mm long and 5-10 mm broad (detached ones larger than those seen attached), upper surface produced into 5 more or less leaf-like lobes, substance thick. Lobes equal; either 2,3 or 4-faceted and pyramidal, or rounded and conical or cigar-shaped; apex of lobe obtusely pointed or a ridge, margins entire and not scarious. Lobes arranged either all in an arc near the free end of the scale or some in this position and some nearer the base of the scale.

Inner surface of ovuliferous scale presumably bearing two longitudinal pockets which surrounded the ovules (this was not seen clearly). Ovules two per scale. [Position of attachment of ovules unknown].

Cuticle from presumed basal part of bract scale thin, about 2 μm, (fragile) showing more or less uniform square, rectangular or elongated cells which are rather small compared with the rest of the bract cuticle. Anticlinal walls thin, clearly defined or vague. Periclinal wall showing a single more or less solid and hemispherical papilla. Cuticle presumably from the rest of the bract like that from the upper surface of the ovuliferous scale but stomata fewer and cell walls thinner.

Upper cuticle of ovuliferous scale thick (but fragile), in all essential characters just like cuticles from the leaves but lacking a scarious margin (Pl. 30). The only other differences from the leaf are that the stomata are less densely concentrated per mm^2 and they occur in more

definite files; the epidermal cells are also in more definite files and often are more elongated than in the leaf.

Cuticle presumably from pockets surrounding ovules very thin (1 μm). Cells small, isodiametric and polygonal or elongated. Anticlinal walls thin, sometimes vague.

[Megaspore membrane and integument cuticles unknown].

DISCUSSION. The positions of the various kinds of cuticle on the cone scales have yet to be fully investigated. Where I have added the qualification "presumably" or "presumed" I have merely compared with Hoerhammer's 1933 plates of H. muensterii. As Harris has rightly stated, Hoerhammer's plates were not intended for such comparison (1957:302). Clearly there is a strong case for carefully recorded removal and maceration of individual fragments of coal from these scales.

The cone-scales yielded abundant fibres on maceration and must therefore have been fibrous in life (Harris 1957:302).

I am intrigued by the consistently larger size of detached cone scales compared with those still attached in cones. It suggests to me that the fibrous scales became detached only at maturity and were possibly deciduous as they probably were in H. muensterii (Jung 1968). Intact cones are probably, therefore, abortions.

Attribution of the female cones to the leafy shoots.

The counterpart of specimen no. 3 shows a cone attached to the end of a leafy shoot. This, however, is not certain as the cone counterpart is almost entirely an impression surface so there is no demonstrable organic continuity with the shoot. The main evidence for attribution is from association of the cones with the shoots and the marked agreement in their cuticular details (Figs. 9-11/ p.56-58).

In section 1 the cones are associated with the leafy shoots Brachyphyllum crucis and no other conifer.

The only other Hasty Bank conifer shoots which have similar cuticles and therefore might conceivably belong to these cones are those of Pagiophyllum ordinatum Kendall. However there is no evidence for this from association and the cuticle of P. ordinatum is much less like that of these cones than is that of Brachyphyllum crucis (see Kendall 1948 for details).

About twenty grains of pollen looking like Classopollis multistriatus Burger were seen adhering to the cone-scale cuticles of specimen no. 8. As no other kind of pollen was seen on the cuticles and as these grains are identical to those produced by the male cone this supports the attribution made above (van Konijnenburg-van Cittert 1971:64).

COMPARISON. The other two described European species of Hirmerella are H. muensterii the type species and H. airelensis. Hirmerella crucis is rather similar to both of them.

H. airelensis Muir et van Konijnenburg (Muir & van Konijnenburg 1970:433 pls. 78-80). As described by Muir & van Konijnenburg this species encompasses leaf and male cone material described by Lewarne & Pallot (1957), Harris (1957), Chaloner (1962), Lemoigne (1967) and Wood (1961), and originally attributed by those authors to H. muensterii. The chief differences of H. airelensis from H. muensterii are said by Muir & van Konijnenburg to be as follows. The leaf cuticles of H. airelensis show papillae on their epidermal cells, the bract scale shows similar papillae to those of the leaves and the male cone-scales probably bore only two pollen sacs. H. muensterii is said to lack papillae

from the leaves and bracts, and it looks to have 10-12 pollen sacs (Jung 1968; 62, pl. 17 fig. 30). (The number of pollen sacs had been questioned by Harris 1957:299 and Florin 1944: 488 because Hoerhammer's 1933: Pl.IV figs. 27 and 27a photographs were not clear, but Jung's 1968 photograph appears to confirm Hoerhammer's finding).

Two of these supposed differences are not real ones. Lewarne & Pallot (1957:76) re-examined H. muensterii leaves and showed that they are also papillose: the German ovate leaves "matched the Welsh ones (H. airelensis) in all details". I have prepared cuticles from cone scales of German H. muensterii in the British Museum (V.12064, 1164 and 1165) and can add that they also show papillae. These papillae can in fact be seen with a lens in Hoerhammer's 1933 Pl. V1 fig. 7 and especially Pl. II fig. 19B where they are rather well marked. The only real difference between H. airelensis and H. muensterii therefore seems to be in the number of pollen sacs borne by the male cone scales. The female cone-scales of H. airelensis are incompletely known but probably show 5 or more lobes, just like H. muensterii.

H. crucis differs from both H. muensterii and H. airelensis in its foliage leaves. They show scattered stomata which have only a slight tendency to occur in rows, whilst the rows of H. muensterii and H. airelensis are always strongly marked. This character is quite uniformly seen in the many leaf cuticle preparations of these species at the British Museum. All other characters of H. crucis leaves are shared by H. airelensis, though the proportions of leaves showing them differs; for example the fully developed scarious margin seen typically in H.crucis is seen in rather few leaves of

H. airelensis, where it is usually narrower and more thickened. *H. crucis* leaves typically lack the epidermal cell papillae often seen in both of the other species, but I have seen two leaves from Hasty Bank which show a few papillose cells.

The female cone scales of all three species seem uniform though they have not been uniformly studied and therefore can not be fully compared. *H. muensterii* (and possibly *H. airelensis*) shows a greater number of lobes on the ovuliferous scale (6-10) than *H. crucis* (5). The lobes of *H. crucis* are always more or less equal in size whilst those of *H. muensterii* are usually differentiated into large ones and smaller ones (Jung 1968).

All the species agree in showing epidermal cell papillae on their bract scales.

The male cone scale of *H. crucis* has two pollen sacs (van Konijnenburg 1971:60; 1972: Pl. 1 fig. 3). It is therefore like *H. airelensis* but differs from *H. muensterii* which seems to have 10-12.

These specific differences are compared below:

	H. crucis	*H.airelensis*	*H.muensterii*
Stomata of Leaf	scattered	In strongly marked rows	In strongly marked rows
♂ cone scale	2 pollen sacs	2 pollen sacs	10-12 pollen sacs
Pollen	8-12 equatorial striations	No equatorial striations	8-12 equatorial striations
ovuliferous scale	5 lobes 2 ovules	(?) 5 or more lobes	6-10 lobes 1 or 2 ovules
Range	Bajocian-Callovian (M.& U. Jurassic)	Rhaetic-Lias	Rhaetic-Lias

The comparisons just given show that these three Western European species of Hirmerella are rather similar to one another. Indeed they may possibly represent local varieties of a single natural species but there is no proof. The species seem consistently distinct at least on practical grounds though clearly further comparative study on their cones is required. Hirmerella airelensis occupies a somewhat intermediate position between H. crucis and H. muensterii. Muir & van Konijnenburg (1970:435, Pl. 78 fig. 6) point out that the stomatal rows of the Airel material are weaker than those of H. muensterii and thus they somewhat approach H. crucis. If the male cone scales of H. airelensis were shown to sometimes bear a greater number of pollen sacs there might be a case for combining all three species.

The shoots of all three species are essentially similar in both gross form and cuticle, and all have long-leaved shoots as well as short broad leaved ones. Muir & van Konijnenburg 1970:435 believe the long leaves are "immature" and the broader ones older. This may be true of the Airel specimens but it does not apply to H. muensterii and H. crucis. The long leaves in these species are in fact longer than the broad ones and presumably did not become shorter as they matured.

The Hirmerella -group (Cheirolepidaceae)

Jung (1968:89,t.fig.10) gives an elegant restoration of the Hirmerella plant. A number of further species from other continents probably also bore Hirmerella cones and the group may well have been an important one in Mesozoic times. Its chief features have been summarised by van Konijnenburg 1971:61-62. Two other Yorkshire Jurassic species of leafy shoots which also bore the Hirmerella kind of cone-scales

are Pagiophyllum kurrii Kräusel (=P. connivens Kendall) and P. maculosum Kendall, and these are to be described by Professor Harris.

Genus Brachyphyllum L. & H. ex Brongniart (see also Harris 1969a: 248).

Brachyphyllum mamillare Brongniart

DISCUSSION

Most of the Hasty Bank shoots are of a long-leaved form which is to be described by Professor Harris. The free part of the leaf is typically about twice as long as the breadth of its base and the form of the shoots thus overlaps into the genus Pagiophyllum Heer (see Harris 1969a: 248). Such long-leaved shoots were described by Kendall (1947) under the name B. scalbiensis Kendall. There seems, however, to be no reason to consider them specifically distinct from normal B. mamillare, at any rate at Hasty Bank. I occasionally saw shoots of the normal form, and these are identical to the long-leaved ones in their cuticular details and occur associated with them. The female cone-scales Araucarites phillipsii Carruthers and the male cones are also strongly associated with the shoots at Hasty Bank, and like the shoots they are specifically indistinguishable in their gross-form, cuticles and pollen from the cones of normal B. mamillare (Kendall 1947; Florin 1958).

TAXODIACEAE

Genus Elatides Heer

Elatides thomasii (manuscript name used by Professor Harris).

1973. Elatides sp. nov. Hill & van Konijnenburg 1973:62 (name in list)

The male and female cones of this species are associated at Hasty Bank with the shoots and sometimes occur attached to them (Figs. 28 p.164 and 10,11 pp. 57,58). The cones are usually at their commonest where the shoots are at their most abundant(Fig. 28 p. 164), and only rarely are they found not associated (for example sometimes in section 3).

UNCLASSIFIED ROOTS

Root, form 1. (Fig.29F,p.177)

DESCRIPTION

Root-like organs known from fragments only and showing several orders of branching. Larger roots at least 9 cm long, 1-16 mm wide, branching monopodially, often showing a central strand up to 1-2 mm wide (the presumed stele). Cortex broad, substance often thin (presumably originally soft). Small roots strongly associated with the large ones, about 1-2 mm wide, showing the central strand faintly and branching dichotomously.

Cellular details unknown. No cuticle preserved, so if originally present it was very thin.

DISCUSSION

The stele has sometimes shifted from its normally central position, showing that the cortex probably liquefied before final compression. Though the small roots look like badly preserved Thallites Walton I have attributed them to the larger ones owing to their strong association.

I have determined these axes as roots because they possess a central strand, surrounded by an apparently soft cortex, and they also show root-like branching. Nevertheless they might have been aerial parts of a protostelic plant. They were not seen in position of growth.

Root, form 2 (Pl. 22 fig. 4; Fig.10/) p.57

DESCRIPTION (2 specimens)

Coaly axis about 5 mm wide, bearing a tuft of presumed rootlets. Rootlets richly and dichotomously divided, about 0.5 mm wide, their ends showing oval or conical swellings about 1 mm wide. Substance thin.

Cellular details unknown. No cuticle preserved, so if originally present it was very thin.

DISCUSSION

The swellings are of unknown function. They can be imagined to have been root nodules like those of modern legumes and cycads, though they might have been adhesive pads on aerial tendrils like those of certain vines such as Parthenocissus. I do not know of any other fossil which resembles this root. It was not seen in position of growth.

APPENDIX 1 : DISCUSSION OF THE SAMPLING METHODS

The sampling methods chosen for Hasty Bank were designed to give as detailed a quantitative description of the plant fossil assemblages as practicable. They were also intended to describe vertical changes of those assemblages in considerable detail and lateral changes in less detail. The statistical limits on resolution of the target were determined by the depths and volumes of the samples and the number of them studied.

The depths of the samples ideally could have been thinner, thus providing an even more detailed resolution of vertical changes. Unfortunately, however, the Hasty Bank matrix is friable and individual bedding planes cannot therefore be traced laterally for more than a few cm. A sample depth of 10 cm was the thinnest depth which I could excavate laterally as a unit and even then I was often unable to prevent overlap of 1 or 2 cm into the next sample below. For this reason the abundance represented by each bar in the histograms may be expected to overlap by up to about 20% into the next one below.

Detection of vertical changes is further limited by the possible occurrence of any periodic changes which coincide with the spacing of the samples. Laterally the limit is imposed mainly by the number of sections and ideally more than three sections would have been examined.

THE BULK MACERATION SAMPLES

Abundances from the bulk maceration samples are eminently comparable with each other but only in a limited

way with the channel-samples. Bulk macerations are likely to be less representative than the latter because the assemblage obtained after maceration is a selected one. Only the more robust cuticles survive the treatment and rather few of these are properly determinable in the absence of hand specimens. All cuticular evidence of Filicales and of gymnosperms having poorly characterised cuticles is thus lost.

The extent of fragmentation is also increased during maceration and sieving, thus upsetting the relationship of abundance counts compared to those from equivalent channel-samples.

A further difference of the bulk macerations from the channel-samples was the scales used for estimating abundance.

THE CHANNEL-SAMPLES

Representation of species diversity (Fig.30p.193).

Volume of a sample is the chief limitation on whether it is representative of the range of species present in the target assemblage. The problem is analogous to that of choosing a minimal representative area in quadrat studies on living vegetation (Kershaw 1973: 31-32, 172-175) though vastly complicated by the added dimension of time. The sample volume is composed of a stack of numerous bedding planes and each of these may be regarded as a quadrat area. The height of the stack is represented by the sample depth.

Each of the bedding planes is strewn heterogeneously with its individual assemblage of species. The rate of sedimentation of the bedding planes is likely to vary and thus also the concentration of the species on them. Thus the minimal representative sample area is likely to vary from

bedding plane to bedding plane. Ideally the minimal area should therefore be determined for each bedding plane and the data then combined to give the generalised data for the whole depth of the sample. This however would be an enormous task and is impossible at Hasty Bank owing to the impracticality of exposing large areas of bedding planes.

As an approximation to the ideal a minimal volume can be determined for a sample by extending its area whilst keeping its depth uniform. I did this on the following three horizons which were selected because they represent the range of species diversity at Hasty Bank.

section 2: 620-630 cm : claystone; very diverse assemblage

section C: 50-60 cm : siltstone; moderately diverse

section 1: 380-400 cm : claystone; low diversity.

At each horizon the sample area was increased by stages from about 5 x 5 cm^2 to 50 x 100 cm^2. For each increase in area the number of species seen for the first time was noted and the cumulative number of species finally plotted against sample volume (Fig.30,p.193).

The curve shown in Fig.30 for section 1: 380-400 shows a single break of slope and then levels off, as would be expected from a homogeneous assemblage (Kershaw 1973). The minimal representative volume is reached roughly where the first curve levels off, at about 10,000 cm^3. A sample of area 50 x 50 cm^2 is therefore fully representative of the species diversity at this kind of horizon. 25 x 25 cm^2 is roughly 90% representative and I consider this also adequate.

The other curves each show what seem to be two breaks of slope, doubtless indicating heterogeneity in the sampled assemblage. In each curve the first break occurred when only

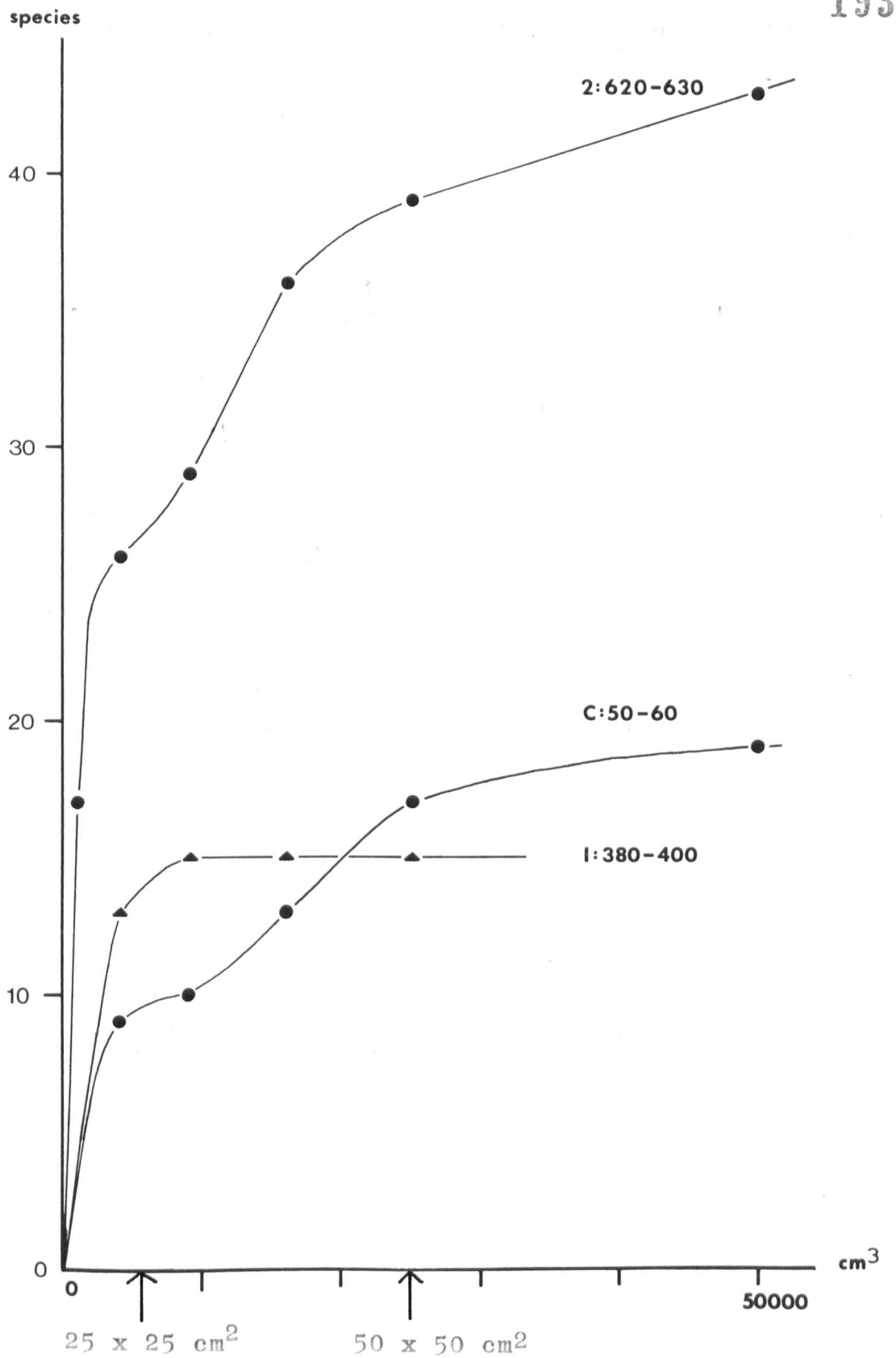


Fig. 30. Cumulative number of species plotted against sample volume. For explanation see p.192..

about half of the total species recorded had been seen, at roughly the 25 x 25 cm^2 area, and I do not consider this to be adequately representative.

I conclude that the samples of area 50 x 50 cm^2 taken at Hasty Bank are likely to be 90% representative of the species diversity whilst at least some of the samples taken in the section 1 claystone and of area 25 x 25 cm^2 are likely to be only 50% representative.

The foregoing discussion assumes that the flattening of the curves at 50,000 cm^3 is progressive and would not be followed by further large increases in slope if the area was increased. Unfortunately this could not be tested as excavating larger areas is limited by the practical difficulty in tracing individual bedding units laterally. A larger area might well overlap fully into the next horizon below and indeed this kind of overlap may be the reason for the breaks in slope seen in Fig.30,p.193.

Counts of species abundance in neighbouring samples

Simple comparisons between counts of species abundance recorded from neighbouring samples were made at the following horizons.

Table	Section:horizon(cm)	Matrix
9,p.204	1 : 170-190	siltstone
10,p.205	1 : 380-400	claystone
11,p.206	1 : 190-210	siltstone
12,p.207	1 : 210-230	siltstone
13,p.208	2 : 620-630	claystone

At each horizon the counts were recorded on two samples taken side by side and each of uniform volume.

These counts are shown in columns 1 and 2 of tables 9 -13/ (appendix 2). For each species the counts from the neighbouring samples were then compared and on this basis the species assigned to one of four groups shown in column 3 of the tables and defined as follows.

	Group	Definition
	A	Species recorded from only one of the two samples
Species recorded from both samples	B	Species for which the two counts differ from each other substantially, by more than 100%
	C	The two counts differ substantially, by 50-100%
	D	The counts agree fairly closely, differing by less than 50%.

(For each pair of counts the percentage difference is based on the smaller count = 100).

The number of species assigned to each group is shown in column 4 of tables 9 - 13, p.204-208.

The chief conclusions I draw from these comparisons are as follows:

1. The counts for only a half or even fewer of the species agree fairly closely in the neighbouring samples, and the majority differ substantially. This is rather disappointing and presumably reflects considerable local heterogeneity of species abundance in the target. Even when relative abundances were calculated the agreement between the samples was scarcely closer.

2. Every species recorded from one sample but not from the one next to it is rare, having a count less than 10. This is interesting in relation to representation of species diversity by the samples. Tables 9, 10 and 11 each show only 30%-60% representation of species in the individual samples compared to the total number of species listed from the pair. However for every reasonably common species (whose counts exceed 10) the representation is 100%.

Practical limitations on representation of species abundance

Weathering

As a result of extensive weathering along joints and bedding planes the Hasty Bank matrix is more or less heavily stained with iron oxides. The staining sometimes also obscures the fossils and may make their determination difficult.

Where a heavily weathered joint passed through a sample the weathered part was ignored and the sample volume simply increased to compensate for it. Weathering of bedding planes however is erratically variable and the extent to which stained specimens can be determined varies with the species. This variation is of a nature which could not readily be quantified and in practice I merely recorded such frustrating notes as "many bedding planes heavily weathered" and "Sagenopteris heavily obscured by weathering."

Block size

As a rule the Hasty Bank matrix fractures, on excavation, into rather small blocks. Thus the estimates of plant fossil fragment size obtained from these blocks must often be smaller than the sizes of the specimens as originally

Table 8.

SPECIES	1 abundance counted	2 abundance estimated on 1-10 scale	3 counts from column 1 calculated to their equivalent on 1-10 scale	4 differences between columns 2 and 3
Pachypteris papillosa	1135	10	9	1
Nilssonia kendalliae	1008	9	9	0
N. tenuinervis	451	8	9	1
Ctenozamites cycadea *	292	6 or 8	8	2
			8	0
Equisetum columnare: rhizome fragments	274	6	8	2
Ptilophyllum pectinoides *	180	5	7	2
Brachyphyllum mamillare	89	4	6	2
E. columnare: fragments of aerial axes	82	4	6	2
Brachyphyllum crucis	71	3 or 4	5	2
			5	1
Elatides thomasii: shoots	20	3	3	0
Cycadolepis hypene *	10	4	3	1
Allicospermum: large	9	2	3	1
Pachypteris papillosa: axis and berets	7	3	3	0
Sagenopteris colpodes	6	2	2	0
Cladophlebis harrisii	5	1	2	1
Allicospermum: small	4	2	2	0
Pseudoctenis/Nilssonia sp.	2	1	1	0
Beania cf. gracilis	2	1	1	0
Eretmophyllum whitbiense	2	1	1	0
E. columnare: upright rhizome	2	1	1	0
E. columnare: rhizome apex	2	1	1	0
E. columnare: diaphragm	2	1	1	0
Brachyphyllum mamillare: male cone	1	1	1	0
Large scale B	1	1	1	0
Undetermined cone	1	1	1	0
Elatides thomasii: female cone	1	1	1	0
Williamsonia hildae	1	1	1	0
E. columnare: cone fragment	1	1	1	0
PACHYPTERIS PAPILLOSA				
black, ca. 1-2 pinnae	678	8	9	1
black, ca. 5-10 cm long	261	8	7	1
brown, ca. 1-2 pinnae	116	5	7	2
black, ca. 10-15 cm long	52	7	5	2
brown, ca. 5-10 cm long	28	2	4	2

Table 8 . Comparison of estimated abundances with ones counted on the same material. The differences between abundances estimated on a 1-10 scale and abundances referred to the same scale but based on counts are shown in column 4.
Horizon - section 2:620-630cm. Sample volume:50x50x10 cm^3.

*: localised within the samples.

deposited. It follows that the abundance counts must often be over-estimates. Block size varies considerably and like the weathering could scarcely be quantified adequately.

Parting

The extent to which a sample could be split depended on the concentration and development of bedding planes in the matrix. This is very variable though as a rule the bedding of the claystone is more concentrated and better developed than in the siltstone. For this reason it is to be expected that abundances recorded for the siltstone would tend to be lower than those from the claystone, other facts being equal.

A further effect of bedding on abundance counts is from the splitting of specimens into Part and Counterpart. In theory this merely doubles the counts. In practice, however, the splitting is often unequal and sometimes the Part may be easy to determine whilst the Counterpart is not. This varies with both the species and the bedding and is difficult to quantify.

Counts of abundance v. estimates (Table 8/p.197)

The validity of representing abundances by estimates rather than counting was assessed at section 2: 620-630 cm (table 8/p.197). This horizon was chosen because its assemblage is one of the most diverse encountered and the abundances should therefore be amongst the most difficult ones to estimate adequately.

A sample 50 x 50 x 10 cm^3 was excavated and the 1-10 scale of table 4 , p.44 , used for estimation of species abundance. The estimates are shown in column 2 of table 8 . Counts were subsequently made on the same material and these are shown in column 1 of the Table.

To facilitate comparison with the estimates the counts were converted to their numerically equivalent points on the 1-10 scale, using table 4 , p. 44. These points are shown in column 3. Column 4 shows the differences between these points and those independently estimated in the field.

The differences do not exceed two points for any of the species. This shows that the abundance when estimated on the scale of ten points is probably a consistently fair representation of that calculated from counting.

On page 195 I concluded that counts made on samples taken side by side often differed substantially, by over 50%. However, when pairs of counts from columns 1 and 2 of table 13/ p.208 were calculated to their equivalent points on the 1-10 scale the differences only exceeded two points for one species. This was Ctenozamites cycadea (Berger) Schenk, a species which had been recorded on the field data sheets as a localised one and therefore subject to fluctuations in abundance in neighbouring samples. Thus although the counts differed substantially the differences in terms of the 1-10 scale did not exceed two points except where this would in any case be expected. As this conclusion is based on examination of a specially diverse assemblage I feel it is reasonable to suggest that it may apply generally at Hasty Bank.

The comparisons given above between counts and estimates may now be summarised:

COUNTS. These have the greatest accuracy, subject only to practical limitations and personal errors. For most species, however, counts on samples excavated side by side differ substantially, by more than 50%. The counts were time-

consuming, taking six weeks per section; I found them exceedingly tedious.

ESTIMATES. These agree well with the counts, within two points on a ten-point scale. Estimates on samples taken side by side also agree well, within two points. They are almost as quick as qualitative collecting, taking only one or at most two weeks per section.

It was for these reasons that after section 1 had been sampled I cheerfully abandoned counting in favour of estimates. There is evidently considerable heterogeneity of species abundance at Hasty Bank, and the masking effects of this on the general trends wanted in relation to deposition and "palaeoecology" must be considerable. The ten-point scale, however, seems admirably suitable because the effects of heterogeneity hardly ever exceed two points.

The validity of quantification at Hasty Bank

Like many other young men I have tried to do something different and new in palaeobotany. My idea was that quantification of the Yorkshire Jurassic Flora might lead to terrific advances in both understanding palaeoecology and reconstructing plants from detached organs. Naturally I would like to paint a glowing success story, though I feel I cannot.

I started out by making detailed counts on the plant fossils. Apart from Hamshaw Thomas's brief (1925) study of Caytonia this was to my knowledge the first attempt to establish quantitatively associations between detached organs and the first in the Mesozoic to attempt to quantify deposition and"palaeoecology." I found, however, that there

were substantial local variations in species abundance as shown for example between counts on samples taken side by side. There were also many practical limitations which may have had marked effects on the counts, of some species more than others.

In relation to general trends in the data, wanted for interpretations on deposition and palaeoecology, the counting thus seemed too accurate for my purposes, scarcely worth the time-consuming and tedious effort involved. For this reason I eventually abandoned counting in favour of an essentially logarithmic scale of ten points, rather like the familiar Domin scale used by ecologists for living vegetation. I used this scale for estimating the abundances and as it was quick and represented major trends rather than the complicating local variations it seemed ideally suited to the problems under consideration.

On the other hand I suggest that the detailed counts were perhaps worthwhile in that they did establish associations securely, supporting those detected previously by other workers from qualitative collecting and also adding a few new ones. However, the ratio of counts of the leaves of a plant to its reproductive organs varied a lot from sample to sample, for example by a factor of ten times. The general relationship that leaves of a plant are more abundant than the associated fructifications, however, seems quite adequately expressed on the scale of ten points. Indeed the logarithmic nature of the scale proved ideally suited to expressing the abundances of both very rare and enormously common species.

I feel the question should be considered whether the same conclusions would or could have been reached by careful

qualitative observation, without actual counting or even without estimating on the ten-point scale: and I admit that I probably could have done so. The chief value of doing the counts was to show that they were not in fact worth the effort involved. Indeed I believe the conclusions on deposition and palaeoecology show that quantifying at all was really useful only for a few species such as Pachypteris papillosa. I could perhaps have quantified more selectively.

Despite this I would on the whole defend the use of a Domin-like scale for estimating abundance. Its use is almost as quick as general collecting and gave a statement on abundance more satisfactory, at any rate to me, than vaguer assessments like "very abundant", "frequent" and "rare". It also provides a basis for comparisons in future with other localities.

I believe that not directly the quantification itself but rather the systematic sampling approach used for it had a positive value in greatly improving the efficiency of my collecting for new and rare species. The detailed recording of precise horizons at which species occurred made it possible to go back and collect repeatedly for further specimens. The rare fern Mariestopesia is just one of many examples which I found supported this claim. It was known originally from a few pinnules collected some fifty years ago at Hasty Bank by Hamshaw Thomas, a man on whose patient collecting much of our knowledge of the Yorkshire Jurassic Flora is based. But his Mariestopesia specimens were never described. They were subsequently lost and the horizons from which they came went unrecorded. Only after almost half a century had lapsed, during which many people collected

at Hasty Bank, was a single specimen rediscovered and described, though its horizon again went unrecorded. However, using a systematic approach I was fortunate enough to locate the productive horizons and, once this was done, to collect large numbers of specimens. Subsequently I was able to show visitors the horizon where I recorded Mariestopesia at its most abundant and after an hour or two of labour it has been found there by all of them.

APPENDIX 2

Tables 9 - 13.

Comparisons between counts of species abundance as recorded from samples excavated side by side.

Table 9.

HB: 1: 170 - 190. 50x50x20 cm^3	1	2	3	4
SPECIES	count from sample volume 1	count from sample volume 2	group (A-D)	number of species in group
Nilssonia syllis		5	A	4
Pterophyllum pruinosum		1	A	
seed stone		3	A	
Ptilophyllum pectinoides		9	A	
			B	0
undetermined cuticle fragments	7	1	C	1
Equisetum columnare - small fragments	102	90	D	5
E. columnare - upright axes	31	36	D	
Eretmophyllum whitbiense	13	17	D	
woody axis	4	5	D	
Caytonia seeds	2	2	D	

Table 9.

Table 10.

HB: 1: 380 - 400. 20x20x20 cm^3	1	2	3	4
SPECIES	count from sample volume 1	count from sample volume 2	group (A-D)	number of species in group
small seed stone	1		A	
Phlebopteris woodwardii	1		A	
Equisetum columnare - rhizome apex	1		A	
E. columnare - upright axes	1?		A	
Ptilophyllum pectinoides		1	A	
Pachypteris papillosa - axis with berets		4	A	9
Fusain		1	A	
Caytonia-like seed		1	A	
E. columnare - sporangiophore head		1	A	
Nilssonia kendalliae	49	9	B	1
			C	0
coaly axis	4	1	D	
Pachypteris papillosa	144	129	D	3
E. columnare - horizontal axes	70	57	D	

Table 10.

Table 11.

HB: 1: 190 - 210. 50x50x20 cm^3	1	2	3	4
SPECIES	count from sample volume 1	count from sample volume 2	group (A-D)	number of species in group
Phlebopteris woodwardii	1		A	
Bilsdalea dura	1		A	
Pterophyllum pruinosum		1	A	
woody axis		2	A	7
Cladophlebis harrisii		2	A	
Pachypteris papillosa		4	A	
Fusain		2	A	
Equisetum columnare - upright axes	82	177	B	
E. columnare - aerial axes	78	5	B	
large seed stones	65	32	B	5
Ptilophyllum pectinoides	54	8	B	
Caytonia seeds	21	5	B	
E. columnare - small fragments	265	429	C	
Eretmophyllum whitbiense	37	57	C	2
Nilssonia syllis	331	359	D	
E. columnare rhizome apex	20	15	D	4
Sagenopteris colpodes	5	3	D	
small seed stones	1	2	D	

Table 11.

Table 12.

HB: 1: 210 - 230. 50x50x20 cm^3	1	2	3	4
SPECIES	count from sample volume 1	count from sample volume 2	group (A-D)	number of species in group
Nilssoniopteris vittata	2		A	
Equisetum columnare - sporangiophore head	1		A	
Cladophlebis "lobifolia"		1	A	5
Ctenis kaneharai		4	A	
undetermined cuticle		1	A	
E. columnare - rhizome apex	11	4	B	2
Ptilophyllum pectinoides	5	21	B	
Caytonia seeds	31	47	C	
Mariestopesia blackii	7	11	C	3
large seed stone	6	12	C	
Sagenopteris colpodes	90	85	D	
Nilssonia syllis	65	69	D	
Eretmophyllum whitbiense	7	9	D	
woody axis	6	5	D	
small seed stone	4	4	D	9
Fusain	3	1	D	
Pachypteris papillosa	1	5	D	
Marattia anglica	1	2	D	
E. columnare - diaphragm	1	3	D	
E. columnare - small fragments	445	not counted	-	
E. columnare - large fragments of rhizome	91	not counted	-	
E. columnare - upright axes	92	not counted	-	
Caytonia fruits	13	not counted separately from seeds	-	

Table 12.

Table 13.

HB: 2: 620 - 630. 50x50x10 SPECIES	1 count from sample volume 1	2 count from sample volume 2	3 group (A-D)	4 number of species in group
Brachyphyllum mamillare - male cone	1		A	
undetermined cone	1		A	
Eretmophyllum whitbiense	2		A	
Araucarites phillipsii		1	A	
Cladophlebis "lobifolia"		1	A	
Equisetum columnare - upright root		1	A	11
Elatides thomasii - male cone		1	A	
Fusain		2	A	
Ctenis kaneharai		8	A	
Pseudoctenis oleosa		3	A	
Nilssonia compta		4	A	
Ctenozamites cycadea	292(localised)	28	B	
E. columnare - fragments of aerial axes	82	174	B	
Cycadolepis hypene	10(localised)	45	B	6
large Allicospermum	9	37	B	
Sagenopteris colpodes	6	16	B	
small Allicospermum	4	18	B	
Nilssonia kendalliae	1008	1737	C	
Nilssonia tenuinervis	451	846	C	
E. columnare - rhizome fragments	274	515	C	
Ptilophyllum pectinoides	180	227	C	
Pseudoctenis/Nilssonia sp.	2	7	C	7
Beania cf. gracilis	2	8	C	
E. columnare - upright rhizomes	2	7	C	
Pachypteris papillosa	1135	1271	D	
Brachyphyllum mamillare	89	68	D	
Brachyphyllum crucis	71	93	D	
Elatides thomasii - shoots	20	20	D	
P. papillosa - axis with berets	7	9	D	
Cladophlebis harrisii	5	5	D	
Phlebopteris woodwardii	1	3	D	
large scale B.	1	1	D	13
Elatides thomasii - female cone	1			
Williamsonia hildae	1	1	D	
E. columnare - cone fragments showing sporangiophore heads	1	2	D	
E. columnare - diaphragm	2	1	D	
E. columnare - rhizome apex	2	2	D	
		1	D	

Table13.

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P L A T E S

PLATE 1.

Plate 1

Botryococcus braunii Kützing (Chlorococcales) from Hasty Bank, preparations made from the lithological unit composed of interbedded ironstone, sandstone and siltstone.

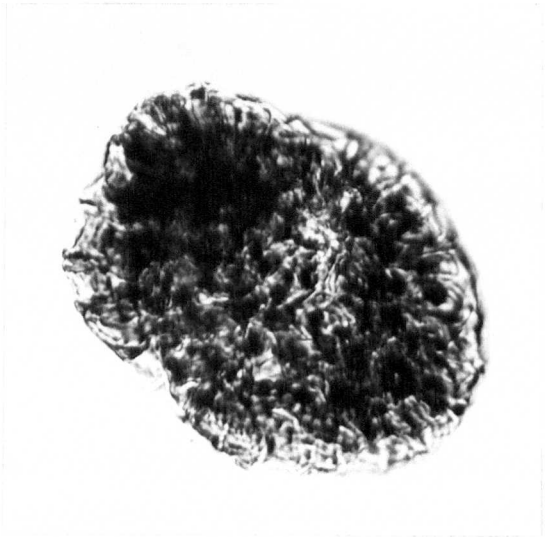
Fig. 1. Compact colony, x 640. Slide 1 specimen marked no. 6.

Fig. 2. Compact colony in which the subcolonies are clearly seen, x 640. Prepared without oxidation, slide 1 specimen marked no. 3.

Fig. 3. Diffuse colony, showing cups, x 640. Slide 2 specimen marked no. 1.

Fig. 4. Colony fragment showing well developed cups, x 640. Slide 3 specimen marked no. 10.

Fig. 5. Colony fragment showing branching structure, x 800. Slide 1 specimen marked no. 9.



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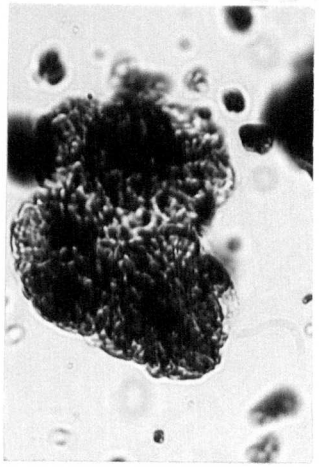

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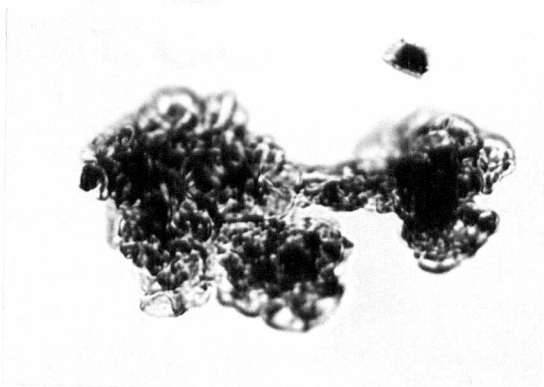

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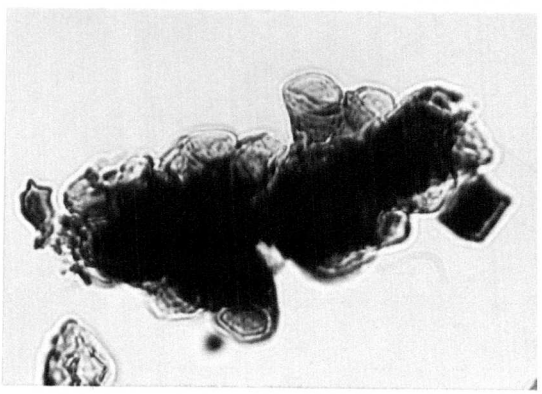

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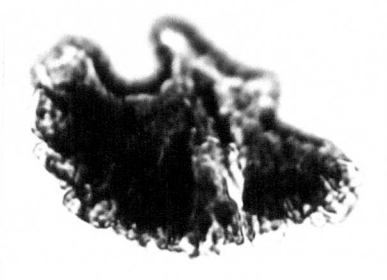

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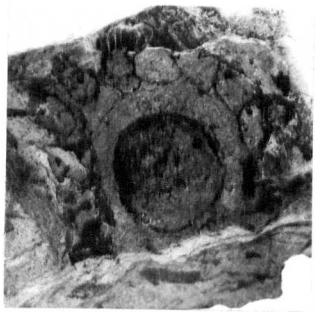
PLATE 2

Plate 2. Equisetum columnare Brongniart. Specimen from section C siltstone showing branching at a node.

Figs. 1,3. Specimen photographed under paraffin. Fig. 2 photographed dry.

Fig. 1, x1.5; fig. 3, x4; fig. 2, x5.



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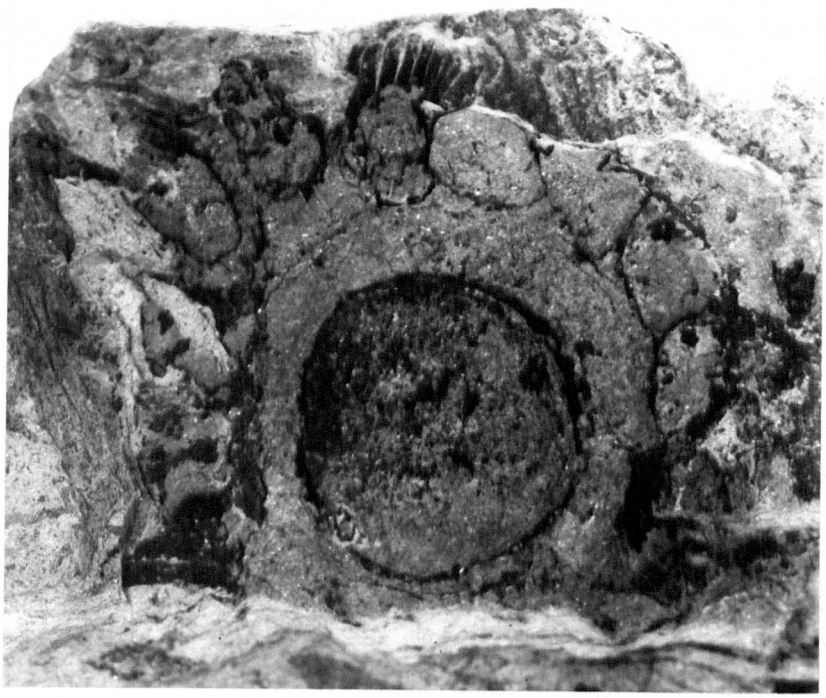

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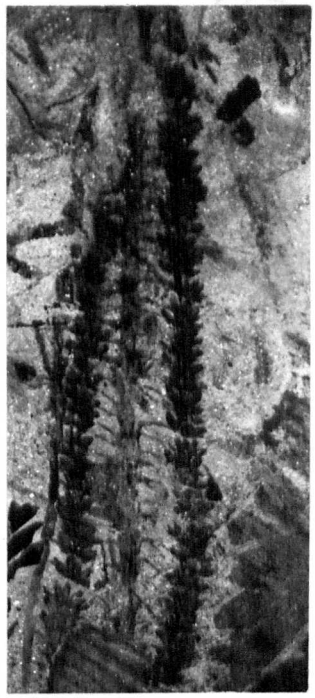
PLATE 3

Plate 3

Mariestopesia blackii gen. et. comb. nov.

Specimen no. 74, from section C siltstone, photographed under paraffin. Fig. 1, x2; fig. 2, x6.

The sori are tilted towards the pinnule apex. On the right of the midrib this tilt is in the opposite direction to the apparently backwards shift of the veins.



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2

PLATE 4

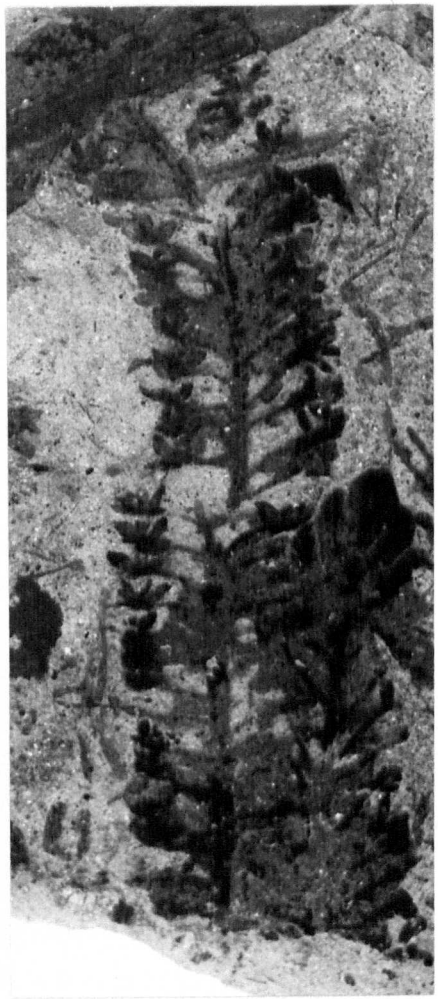
Plate 4

Mariestopesia blackii gen. et comb. nov., photographed under paraffin.

Fig. 1. No. 3 (Part), from section C siltstone, x4.

Fig. 2. No. 3 (Counterpart), x3.5. Sterile pinnule showing the apex and leaf-spot fungi. Note the lobed margin and disappearance of the lamina tissue between the veins.

Fig. 3. No. 121 (Part), from section C claystone, x6. The sori are tilted towards the base of the pinnule.



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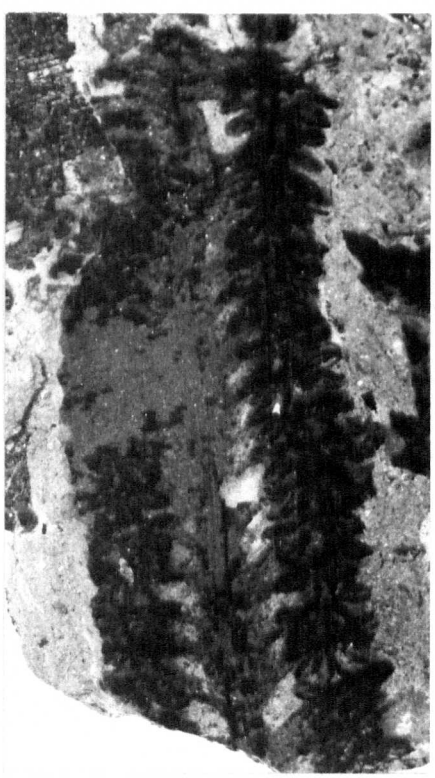

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PLATE 5

Plate 5

Figs. 1 - 3. *Angiopteris crassipes* Wall, from the Kew herbarium (Specimen no. 6711).

Fig. 1. Part of a dried fertile pinnule showing veins and sori, x13.

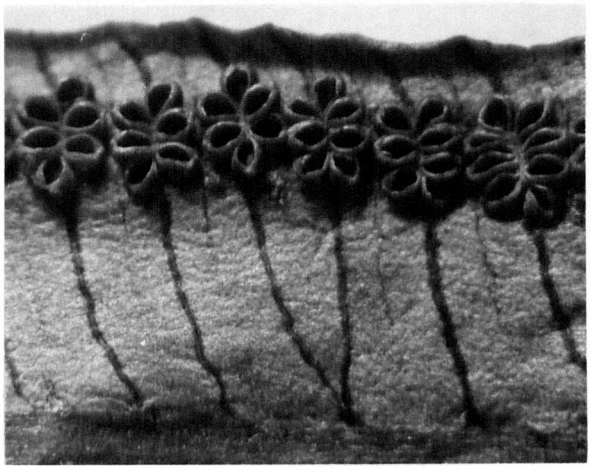
Fig. 2. Rehydrated sori, x20.

Fig. 3. Rehydrated sorus, x60.

Figs. 4 - 5. *Mariestopesia blackii* gen. et comb. nov. from Section C siltstone. Photographed under paraffin.

Fig. 4. No. 107A (Part). Single sorus compressed sideways, x25.

Fig. 5. No. 31. Sori and sporangia, x25.



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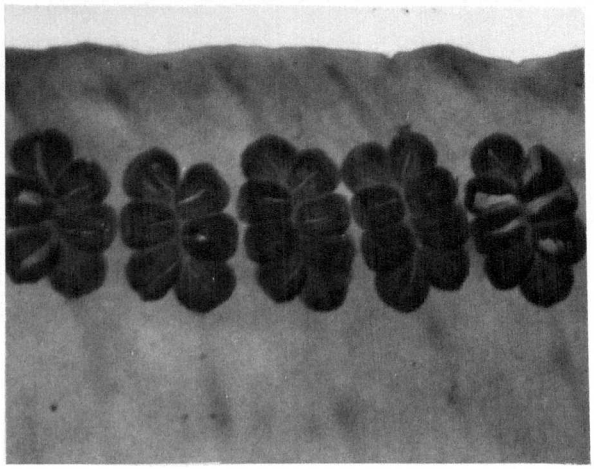

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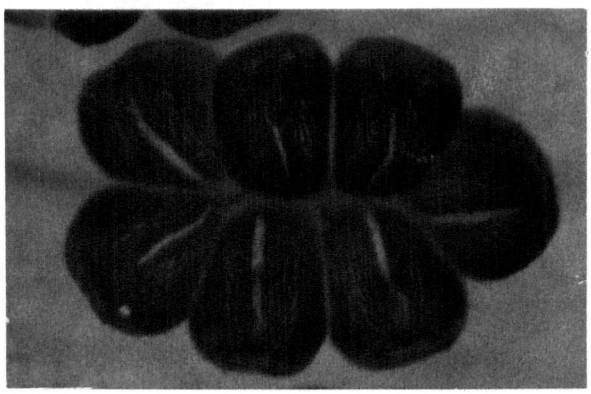

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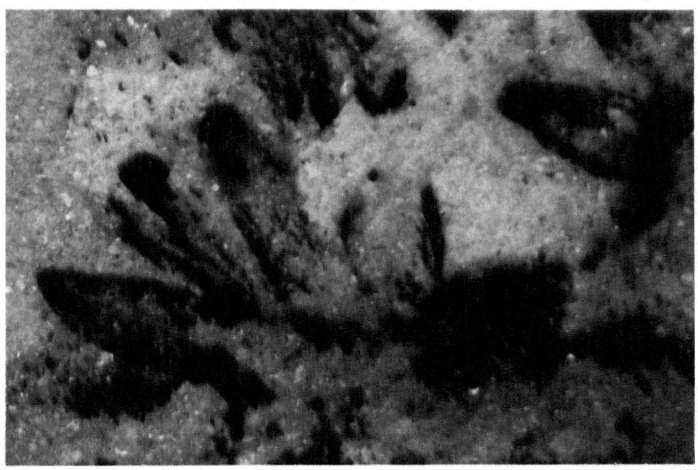

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PLATE 6

Plate 6

Figs. 1 - 7. *Mariestopesia blackii* gen. et comb. nov. Figs. 1,2 photographed by oblique illumination and figs. 3 - 7 by scanning electron microscopy.

Fig. 1. No. 15 (Counterpart) from Section C siltstone, showing impressions of the sori before preparation of the celloidin replica. x20.

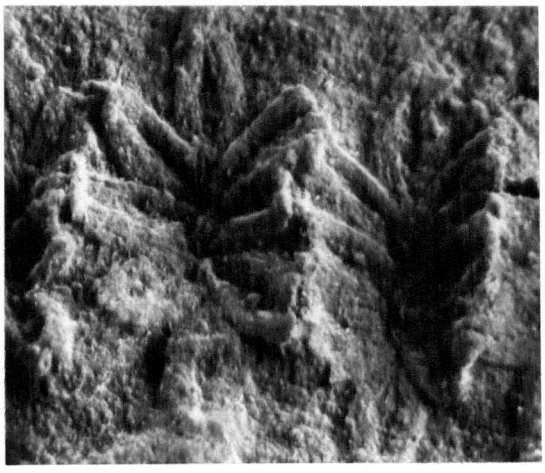
Fig. 2 - 5. No. 15. Celloidin replica showing details of the sori, sporangia and cells of the sporangial wall. Fig. 2, x23; fig. 3, x26; fig. 4, x52; fig.5, x80.

Fig. 6. No. 52, from section D claystone. A compressed sorus, x52. Note the compression lump at the tip of the most complete sporangium.

Fig. 7. Specimen from section C siltstone. Impression surface of the ventral wall of a sporangium, x127. Note the curved tip of the sporangium, shown at the left, and the elongated imprints of the cells of the sporangial wall.

Fig. 8. *Angiopteris evecta* Hoffmann, from a specimen in cultivation at Leeds University. Scanning electron micrograph of a dried sorus, showing sporangia with collapsed thin-walled cells on their dorsal walls, x96. Except for these cells, and the crest of thickened isodiametric cells, the wall is composed of elongated thick-walled cells like those of *Mariestopesia*.

1



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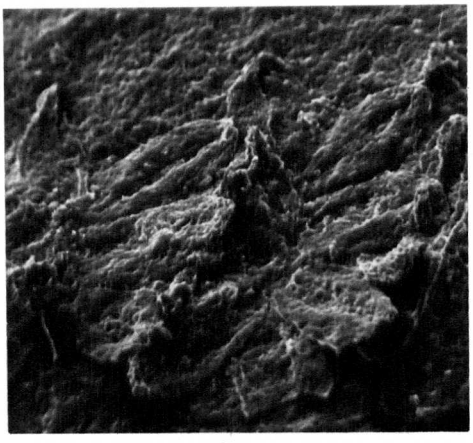

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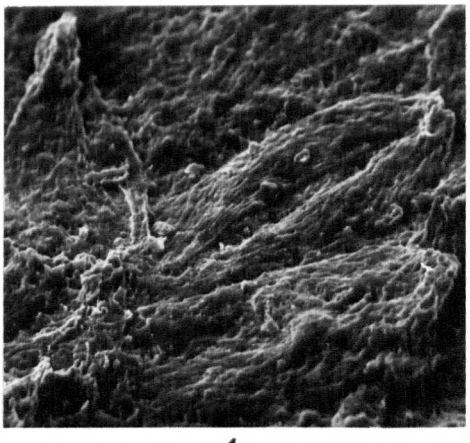

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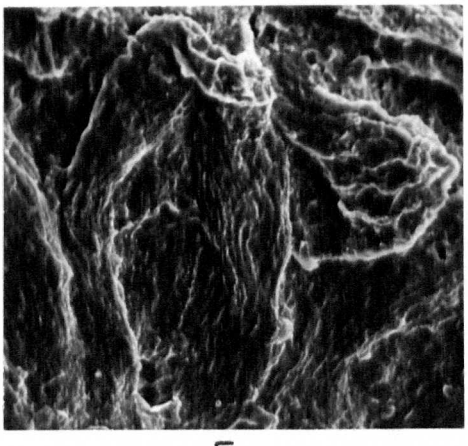

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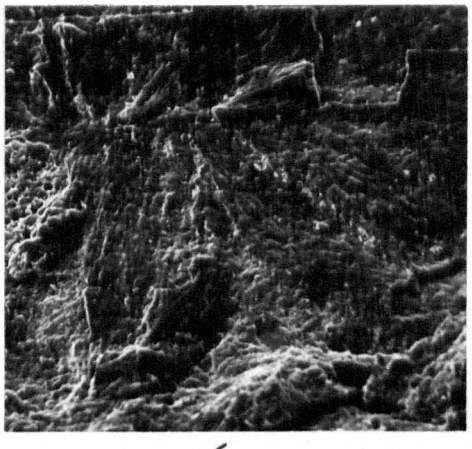

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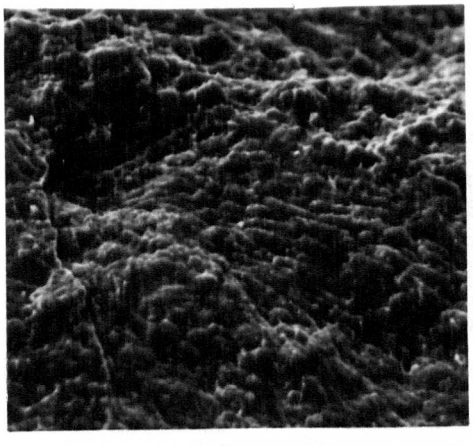

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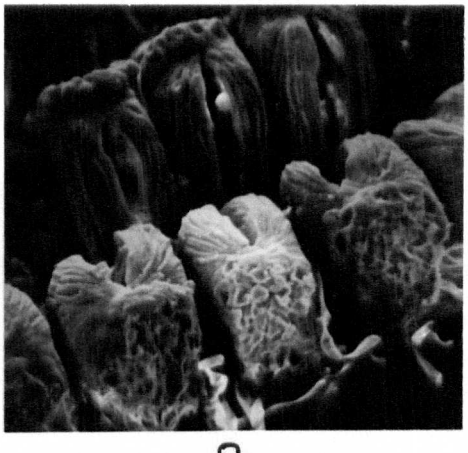


8

PLATE 7

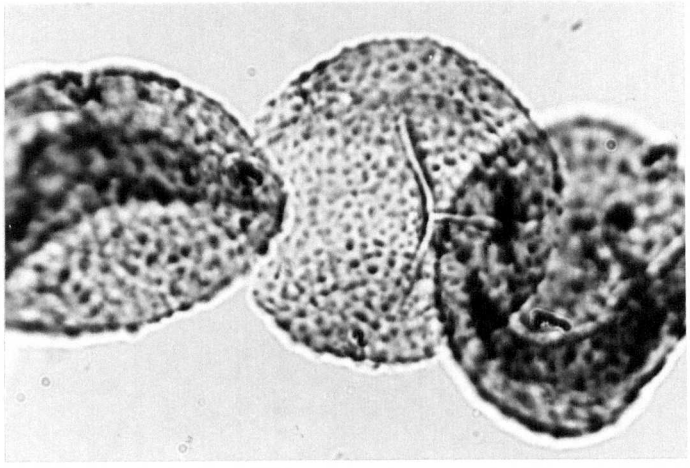
Plate 7

Figs. 1 - 3. Spores prepared from sporangia of *Mariestopesia blackii* gen. et comb. nov., showing the characteristic arcuate folding and variation of the tetrad mark. All x1600.

Fig. 4. Dispersed spore from Hasty Bank having a similar ornament to spores of *M. blackii* but whose tetrad mark, if any, was not seen. x800.

Fig. 5. A dispersed spore very similar to those from the sporangia of *M. blackii*. x1600.

Fig. 6. Spore of *Angiopteris evecta* Hoffmann, prepared by acetolysis of material collected in Samoa by Dr. W.A. Sledge. x800.



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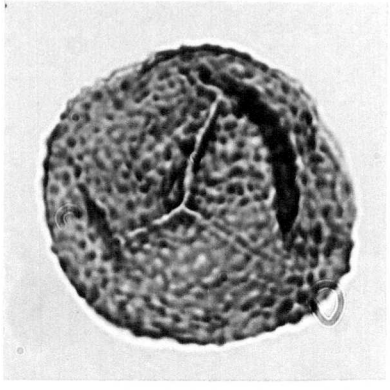

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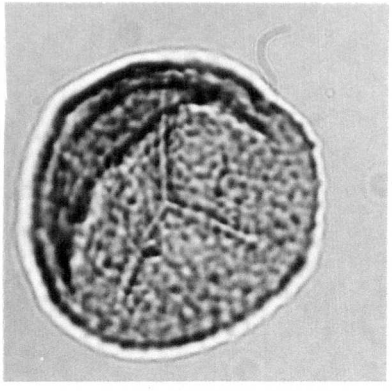

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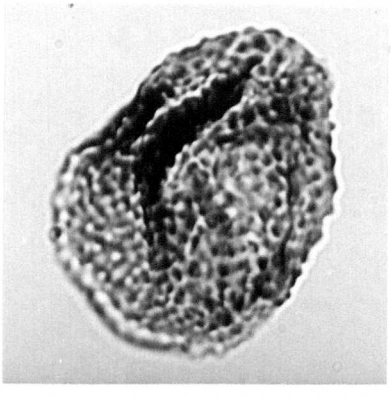

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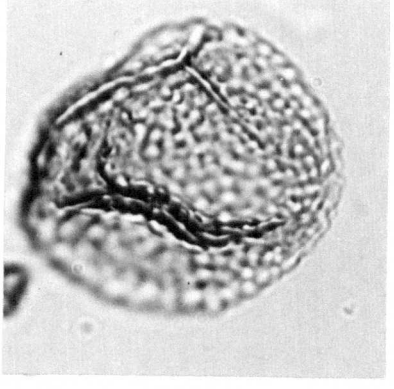

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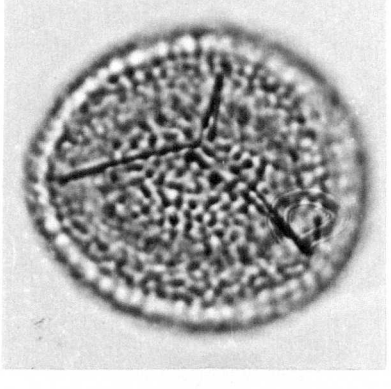


6

PLATE 8

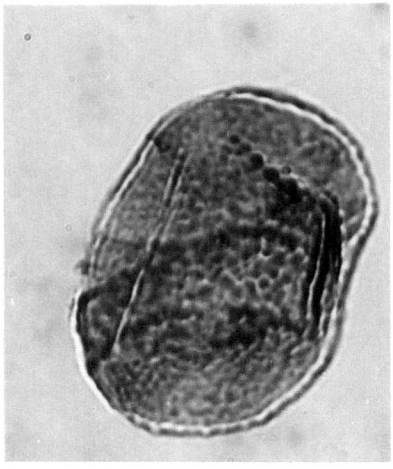
Plate 8

Spores prepared from sporangia of *Marattia anglica* (Thomas) Harris, collected from Hasty Bank.

Fig. 1. Monolaesurate spore, x1200.

Figs. 2,3. Trilaesurate spores. Fig. 2, x1900; fig. 3, x1200.

Fig. 4. Arcuate folding comparable with that of *Mariestopesia* spores. x1200.



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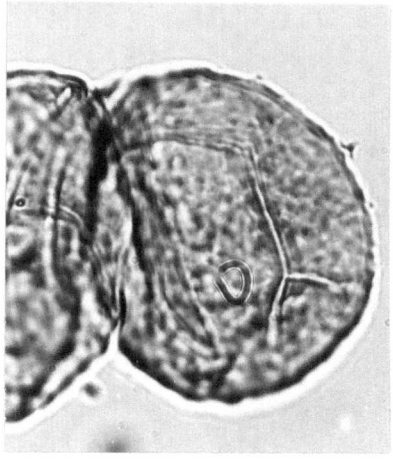

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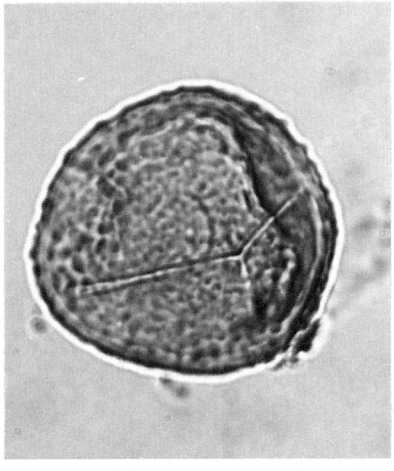

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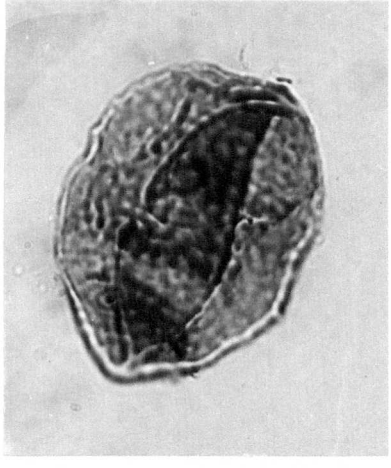


4

PLATE 9

Plate 9

Scanning electron micrographs of spores of *Mariestopesia blackii*/*Marattia anglica* and *Angiopteris evecta*.

Figs. 1,3,4. *Mariestopesia blackii* gen. et comb. nov.

Fig. 1. Showing the tetrad mark, verrucae, and arcuate folding. x3450.

Fig. 3. Detail of tetrad mark, verrucae and rugulae. x5700.

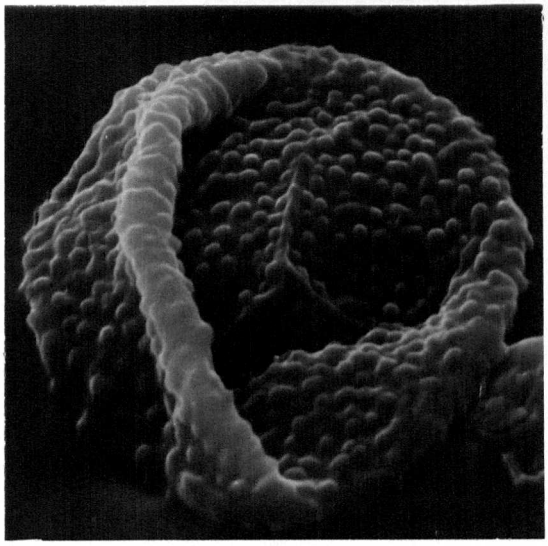
Fig. 4. Small granules seen on the exine of some spores at high magnification. x11,200.

Figs. 2,5. *Angiopteris evecta* Hoffman, acetolysed spores.

Fig. 2. Surrounded by the wrinkled perine. x2000.

Fig. 5. Spore from which the perine has become detached, displaying verrucae on the exine which are like those of *Mariestopesia blackii*. x2000.

Fig.6. *Marattia anglica*(Thomas)Harris
Spore extracted from a Hasty Bank specimen, x 1900. (Background retouched).



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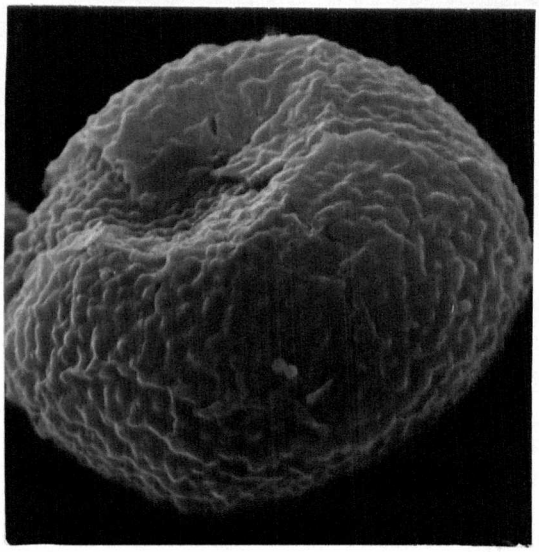

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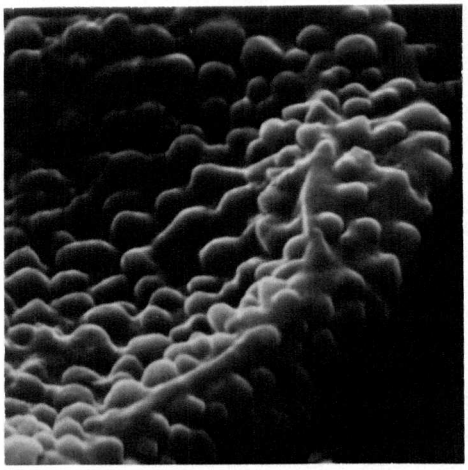

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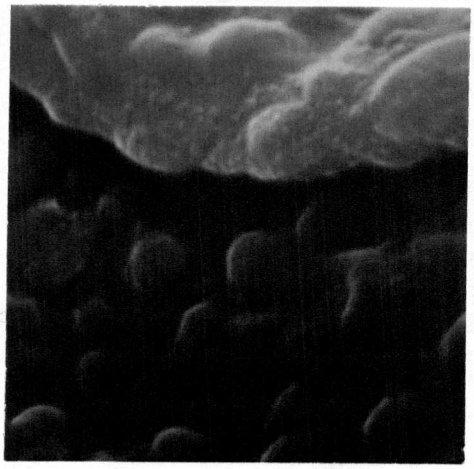

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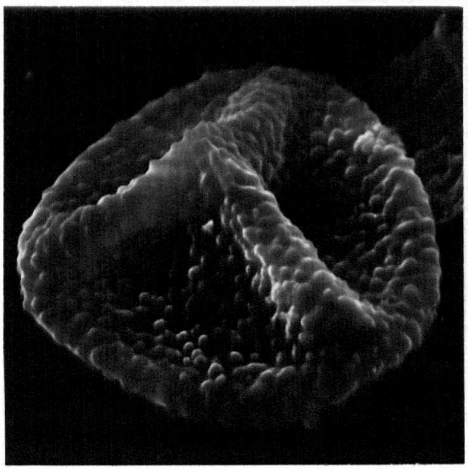

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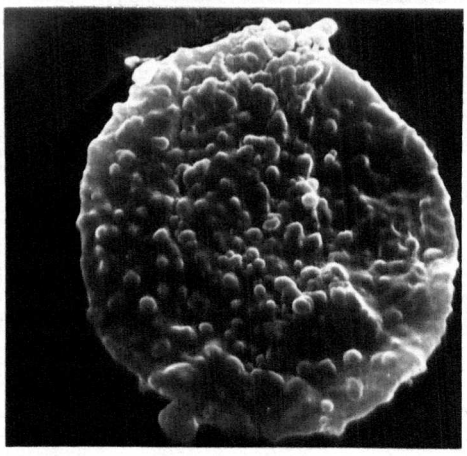


6

PLATE 10

Plate 10

Scanning electron micrographs.

Figs. 1 - 3. *Phlebopteris woodwardii* Leckenby. fusainised material from Section C claystone.

Fig. 1. Veins, distribution of stomata and placenta of sorus, x66. Over the veins there are no stomata and the cells are elongated.

Fig. 2. Details of stomata, x660.

Fig. 3. Spongey mesophyll cells, x approx. 1200.

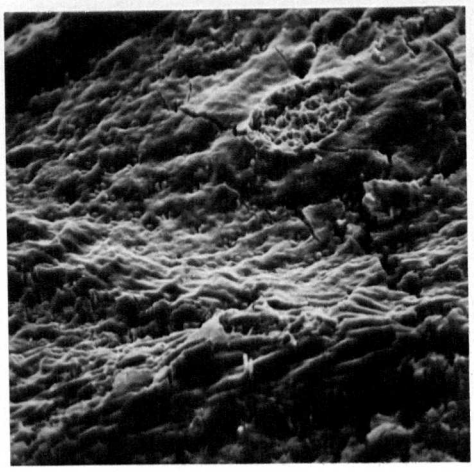
Figs. 4 - 8. *Allicospermum sp.* from Hasty Bank siltstone. Seed membranes. Compare with pl. 11, fig. 2.

Fig. 4. Inner side of nucellus cuticle and megaspore membrane, x500.

Figs. 5,7. ?Outer (sexine) side of megaspore membrane showing branching rods. Fig. 5, x 4800; fig. 7, x5040.

Fig. 6. ?Inner (nexine) side showing pitting, x9920.

Fig. 8. Broken edge, with indication of a tectum on the outer side, x5760.



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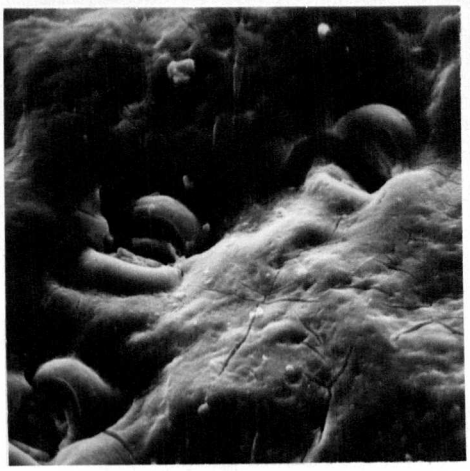

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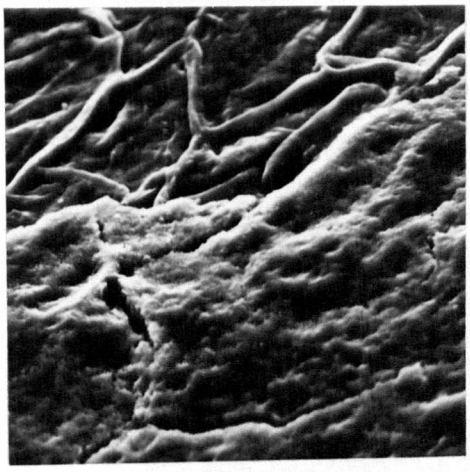

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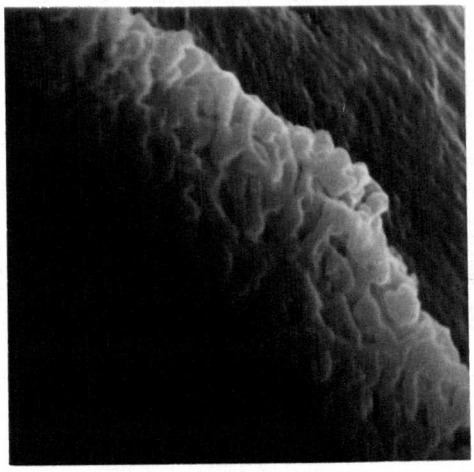

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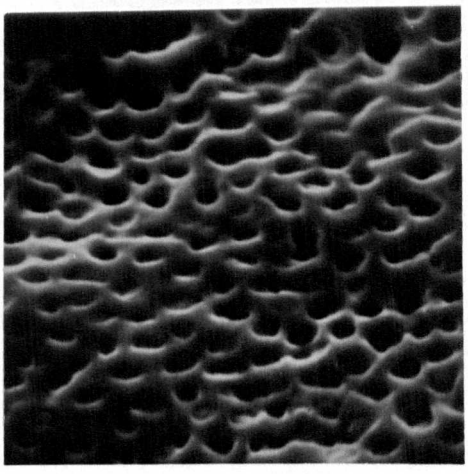

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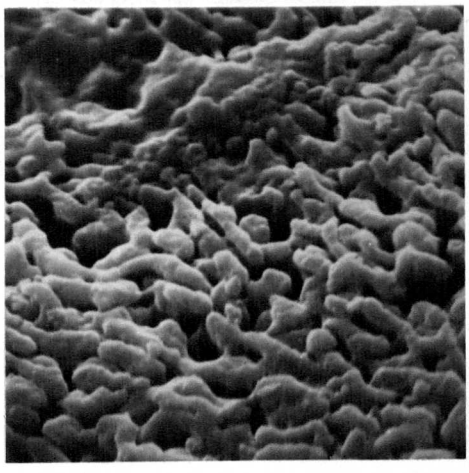

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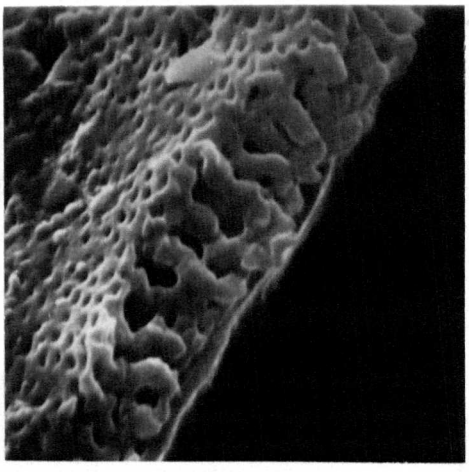


8

PLATE 11

Plate 11

Fig. 1. *Amphorispermum pullum* Harris from the Hasty Bank main leaf coal. x48. The three seeds are stuck together.

Fig. 2. *Allicospermum sp.*, megaspore membrane, from the same specimen as shown in pl. 10, figs. 4-8, x1575.

Figs. 3,5. *Beania cf. gracilis* Harris

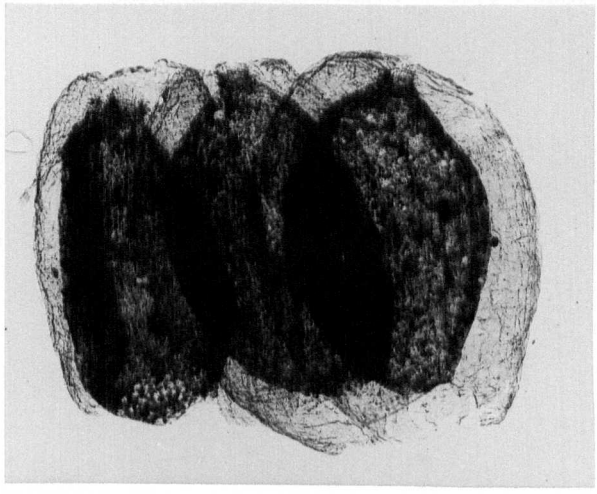
Fig. 3. Cuticle from sporophyll head, showing a possible stoma. x625.

Fig. 5. Cuticle of cone axis. A trichome base is seen at the left. x250.

Figs. 4,6. *Nilssonia tenuinervis* Seward, from section 1, 630-650 cm, slide 1.

Fig. 4. Stomata of syndetocheilic appearance. x480.

Fig. 6. Pair of stomata at bottom left of syndetocheilic appearance, x480.



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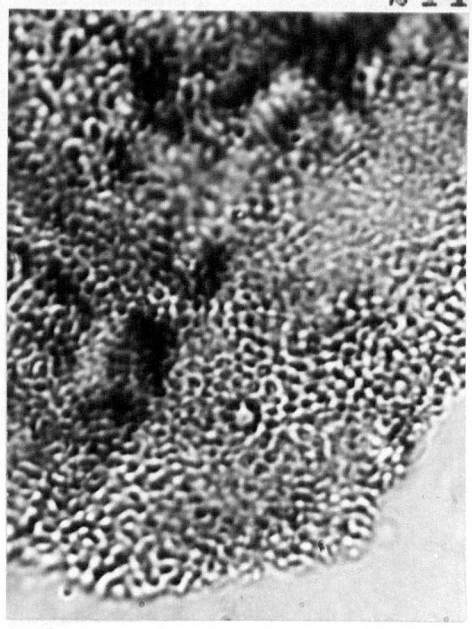

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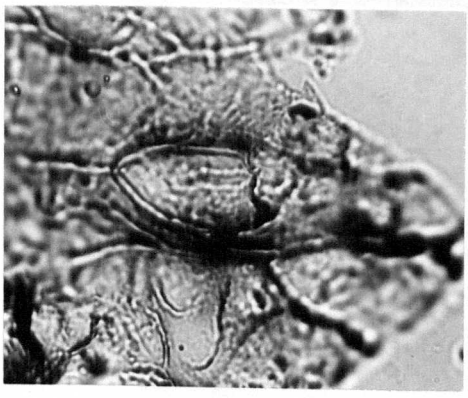

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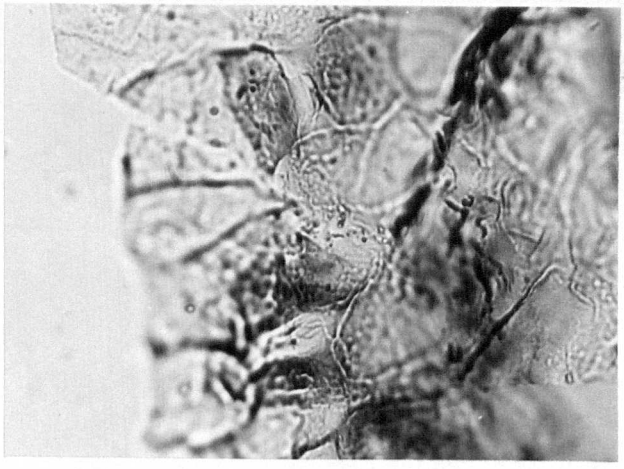

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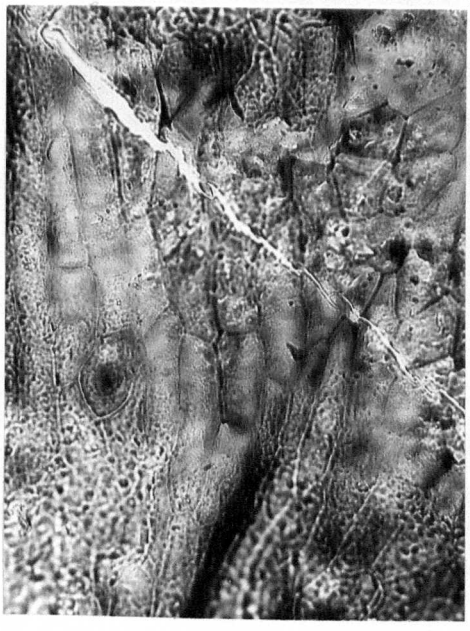

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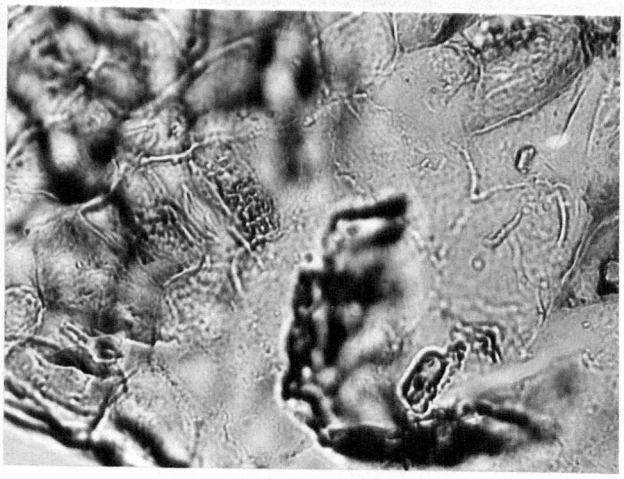


6

PLATE 12

Plate 12

Androstrobus major van Konijnenburg

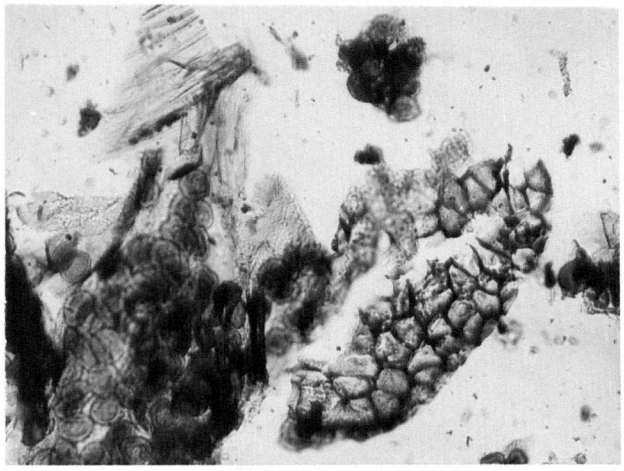
Fig. 1. Fertile scale no. 2, from section 1: 530-540 cm. Pollen mass, cuticle of sporangium wall, and cuticle of the scale (to the right of the photograph). x150

Figs. 2-4. Cuticles from sterile scale no. 5, section 1: 660-670 cm. All x 400.

Fig. 2. Typical stomata and epidermal cells

Fig. 3. Large resinous cell-cast

Fig. 4. A typical stoma



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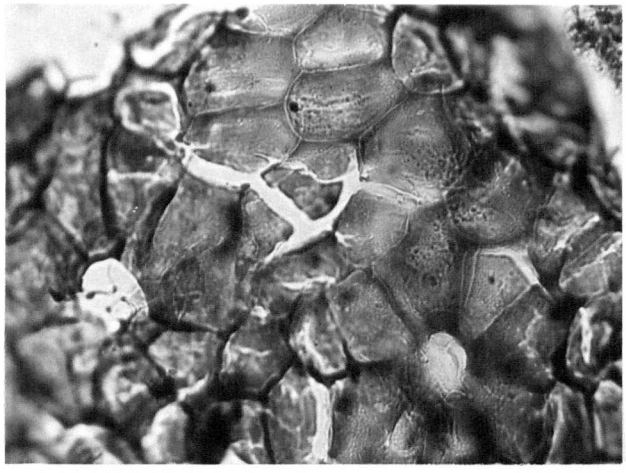

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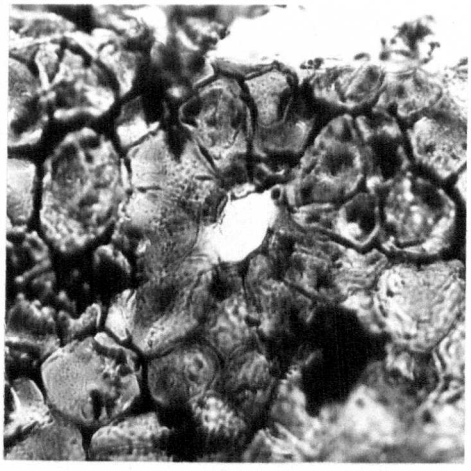


4

PLATE 13

Plate 13

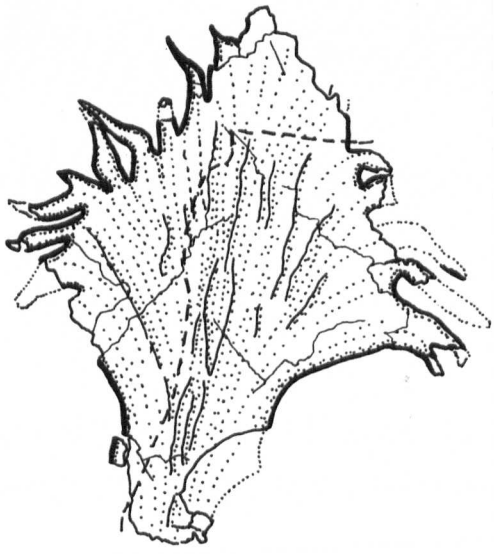
Alvinia florinii gen. et sp. nov. (manuscript name). Holotype (specimen no. 4, photographed under paraffin).

Fig. 1. Part. Expanded head of megasporophyll, showing segmented margin. x 3.

Fig. 2. Counterpart. Megasporophyll stalk showing one ovule

(though not organically connected) and three bulges to which other ovules presumably were attached. x 3.

Fig. 3. Camera lucida drawing of Part and Counterpart, for comparison with the photographs. The specimen was drawn before removal of the distal half of the ovule for preparation of cuticles.



1

3

2

PLATE 14

Plate 14

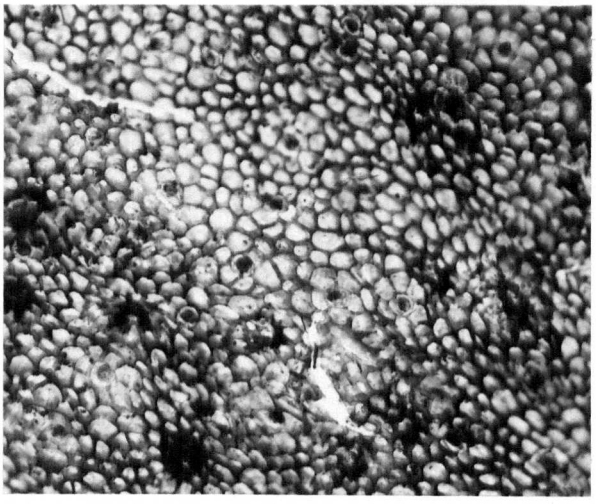
Alvinia florinii gen. et sp. nov.
Lower cuticle of sporophyll head.
Figs. 1-5 are from preparations of specimens 1-5 and Fig. 6 is from specimen 6.

Fig. 1. x 100

Fig. 2. Trichome bases and ordinary epidermal cell-outlines. x 300. Slide 2.

Figs. 3-5. Typical stoma at high focus (fig. 3) and low focus (figs. 4,5). Slide 1. Figs. 3,4, x 300. Fig. 5, x 875.

Fig. 6. Trichome base seen sideways at the margin. x 1200.



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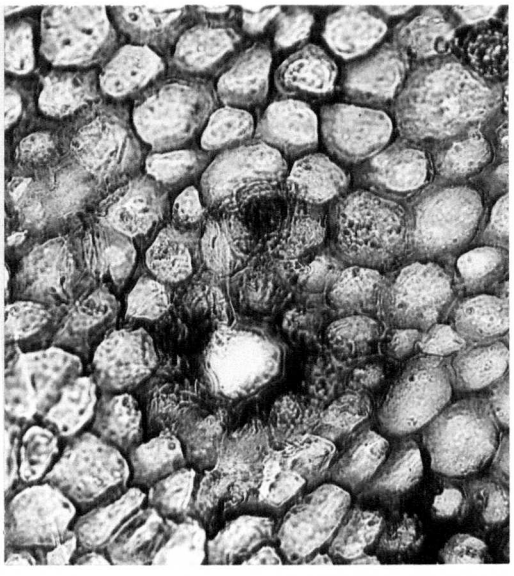

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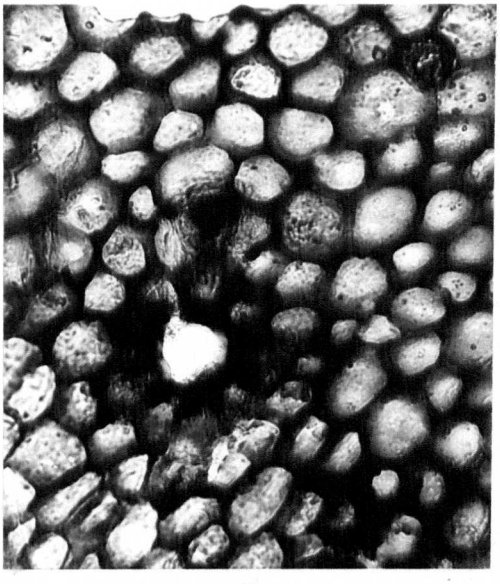

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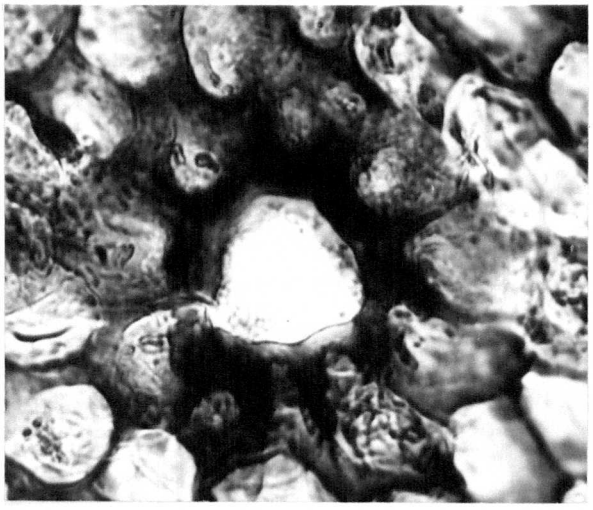

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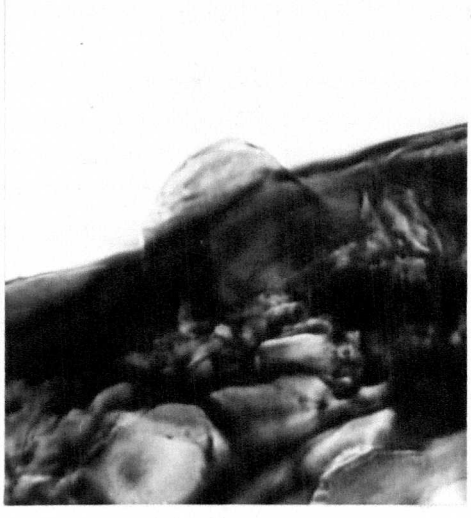


6

PLATE 15

Plate 15

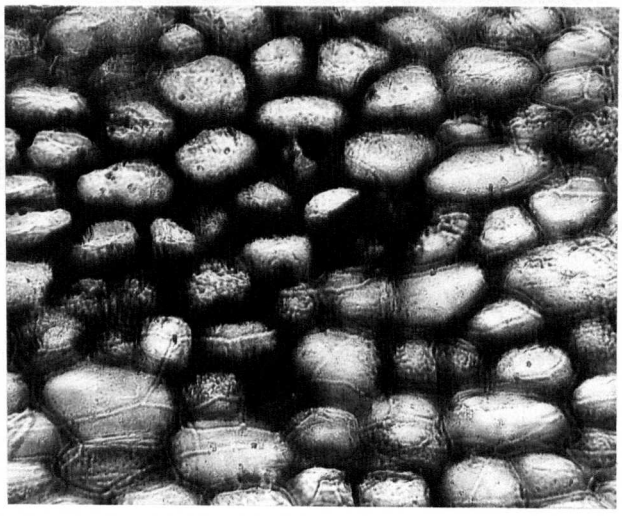
Alvinia florinii gen. et sp. nov.

Cuticles from sporophyll head.

Fig. 1. Hypodermal cell-outlines, x 250. Slide 2, prepared from specimens 1-5.

Fig. 2. Upper cuticle showing thin strips in the periclinal walls of the epidermal cells. Specimen no. 6. x 250.

Fig. 3. Outer cuticle of the integument, prepared from the distal half of the ovule of the holotype. x 480.



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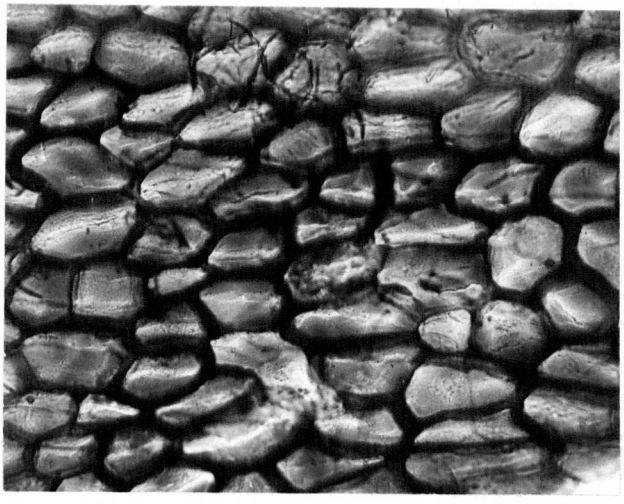

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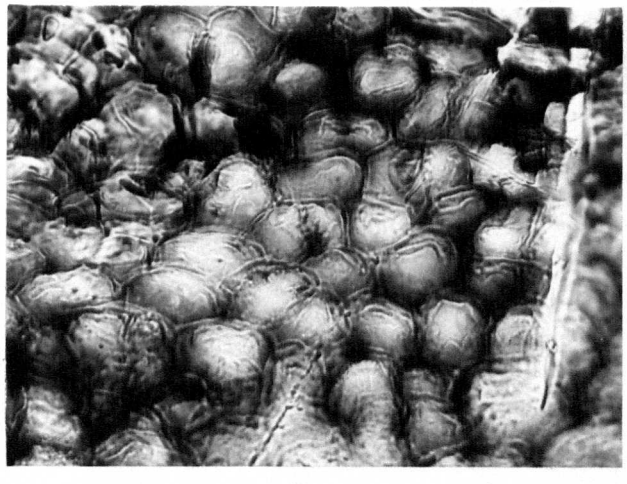


3

PLATE 16

Plate 16

Cycas revoluta Thunberg

Fig. 1, leaf cuticle; figs. 2-5, cuticle from head of megasporophyll.

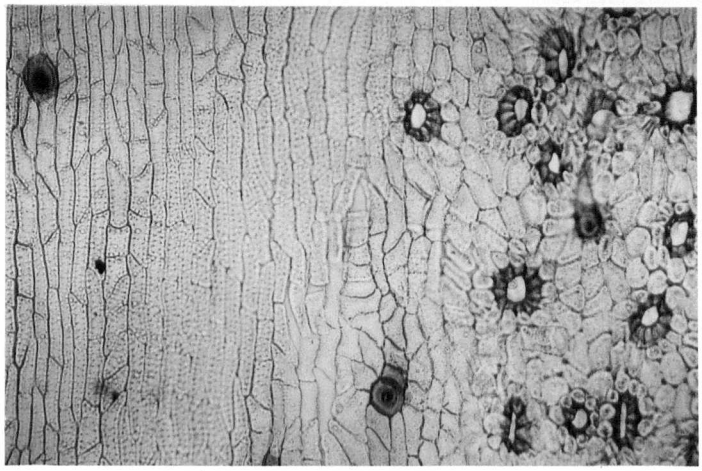
Fig. 1. Cuticle of leaf pinna, x 100. Stomata are lacking over the midrib, shown at the left.

Figs. 2-5. Cuticle from head of megasporophyll.

Fig. 2. Lower cuticle, x 100

Figs. 3,4 Typical stomata showing subsidiary cell striations. x 400.

Fig. 5. Hypodermal cell-outlines and a trichome base. x 400.



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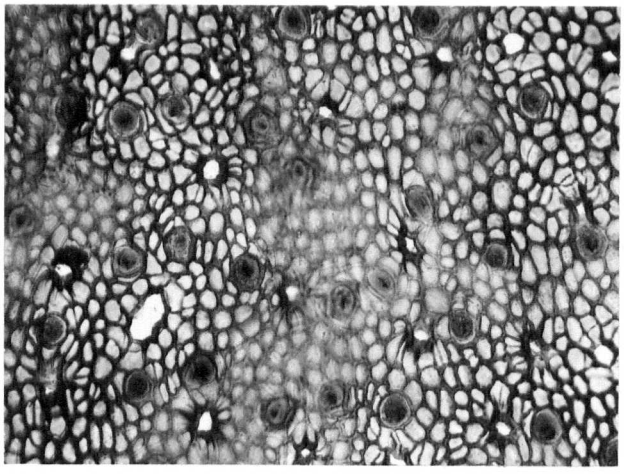

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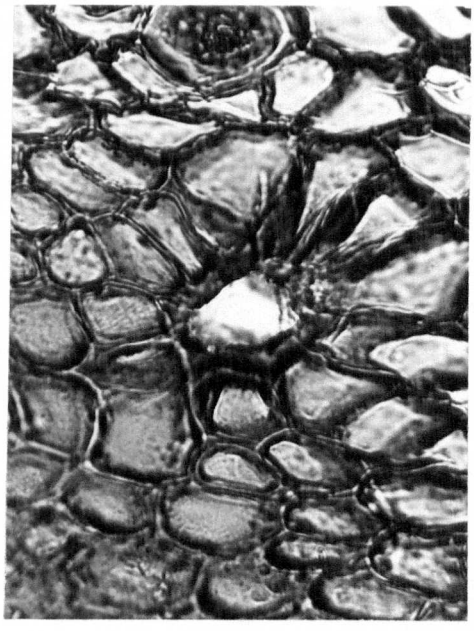

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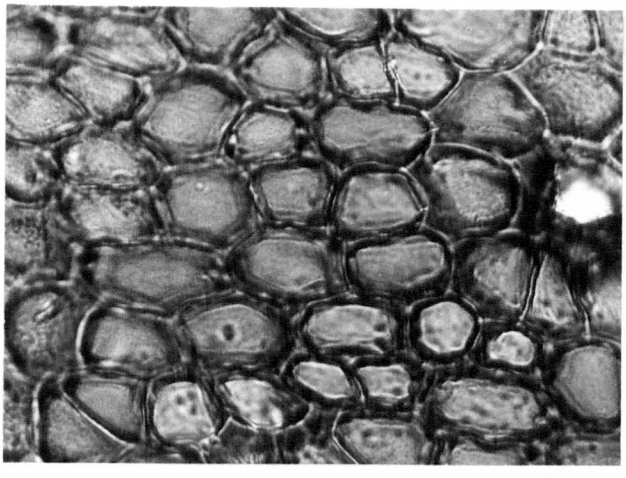

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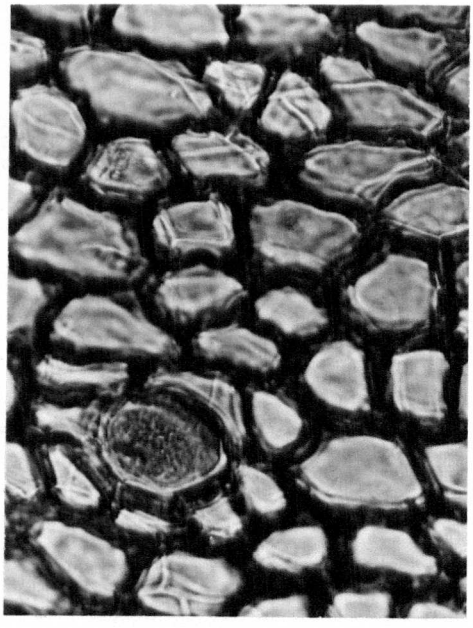


5

PLATE 17

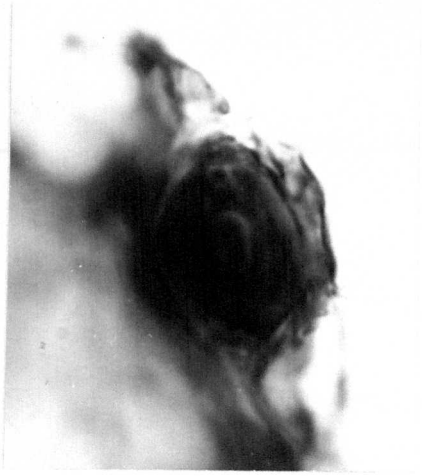
Plate 17

Trichome bases of *Alvinia florinii* gen. et sp. nov. and *Pseudoctenis lanei* Thomas.

Fig. 1. *Alvinia florinii*. Stalk cuticle of holotype.

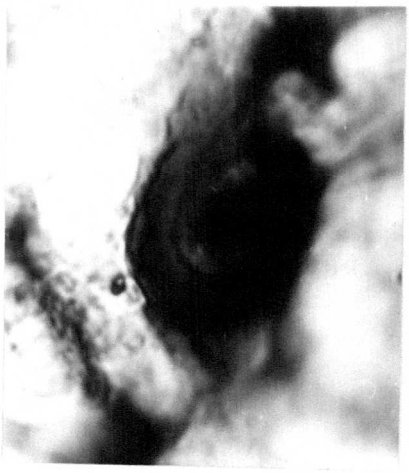
Figs. 2,3. *Pseudoctenis lanei*. Leaf pinna cuticle of V.28300.

All x 1500.



1

2



3

PLATE 18

Plate 18

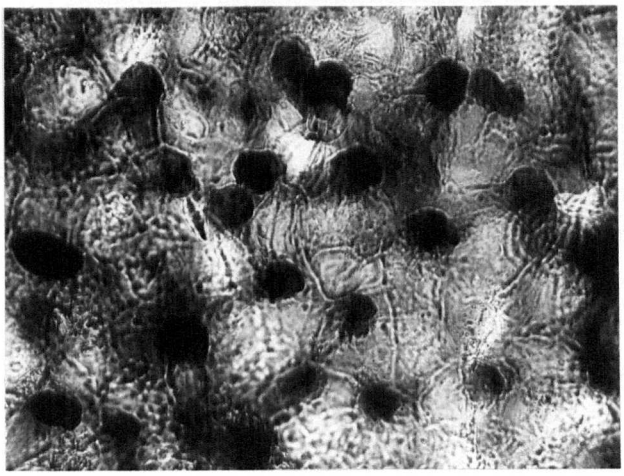
Pseudoctenis lanei Thomas. Cuticles of leaf pinnae.

Fig. 1. Strongly developed papillae on the lower cuticle of specimen no. 1. x 310.

Fig. 2. Weakly developed papillae on the lower cuticle of specimen no. 3, from section 1:530-550 cm. x 312.

Fig. 3. Upper cuticle of specimen no. 4, from section 1:510-530 cm. x 312.

Fig. 4. An unusual stoma, rather similar to typical stomata of *Alvinia florinii*. x 312.



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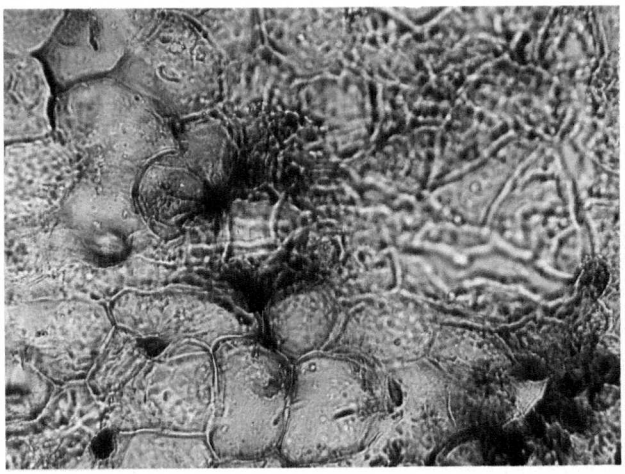

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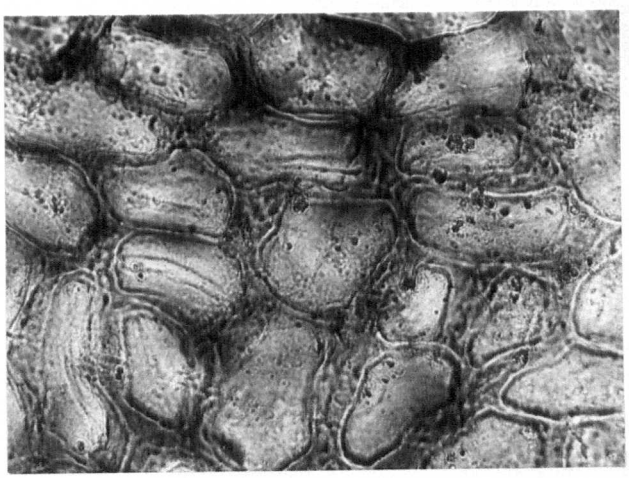

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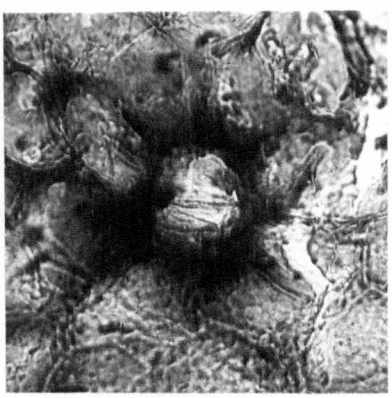


4

PLATE 19

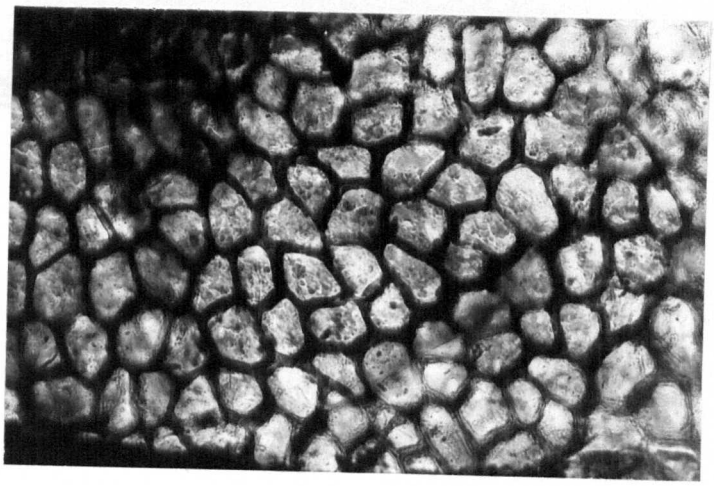
Plate 19

Pseudoctenis oleosa Harris. Cuticles of leaf pinnae. Resinous cell-casts.

Fig. 1. Upper cuticle of a leaf pinna which lacks large resinous cell-casts. Specimen from section 2:620-630 cm. x 400.

Fig. 2. Upper cuticle showing a few small resinous cell-casts. Specimen no. 2 from section 1:610-630 cm.

Fig. 3. Lower cuticle showing typical development of large resinous cell-casts. Specimen no. 6 from section 1:610-630 cm. x 100.



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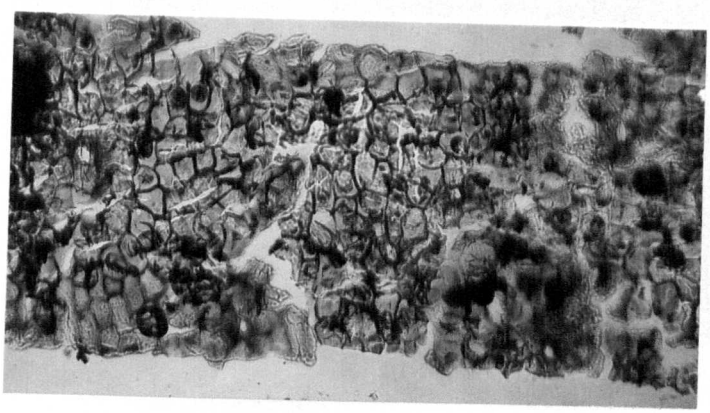


3

PLATE 20

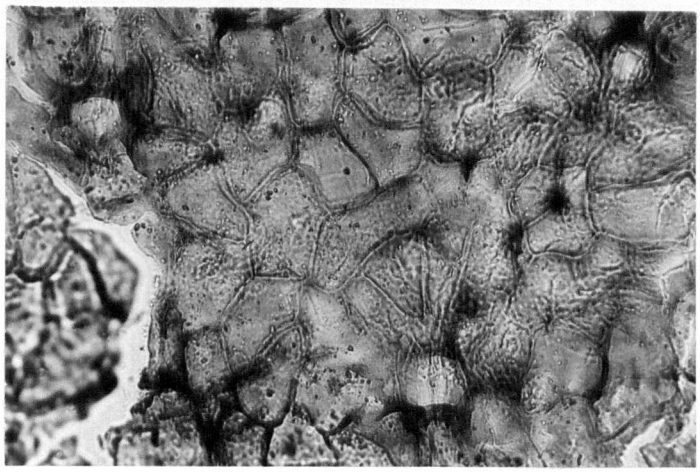
Plate 20

Pseudoctenis oleosa Harris. Lower cuticles of leaf pinnae.

Fig. 1. Cuticle typical of the species except that resinous cell-casts are lacking. Specimen no. 3 from section 1:610-630 cm. x 250.

Fig. 2. Unusual stoma, resembling typical stomata of *Alvinia florinii* and *Androstrobus major*. Specimen from section 2:620-630 cm. x 312.

Fig. 3. Unusual stoma, resembling typical stomata of *Alvinia florinii* and *Androstrobus major*. Specimen no. 6, from section 1:610-630 cm. x 312.



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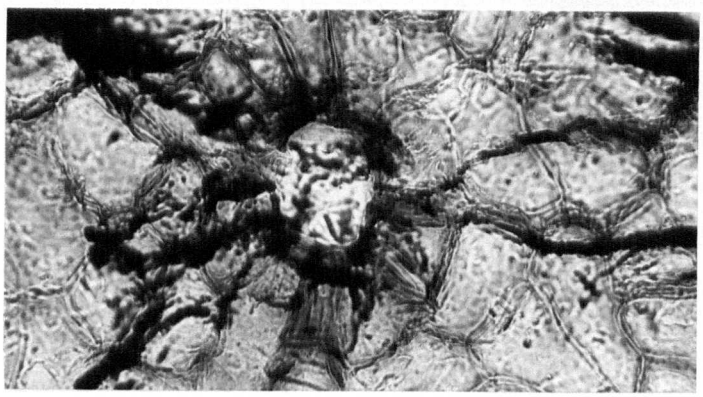

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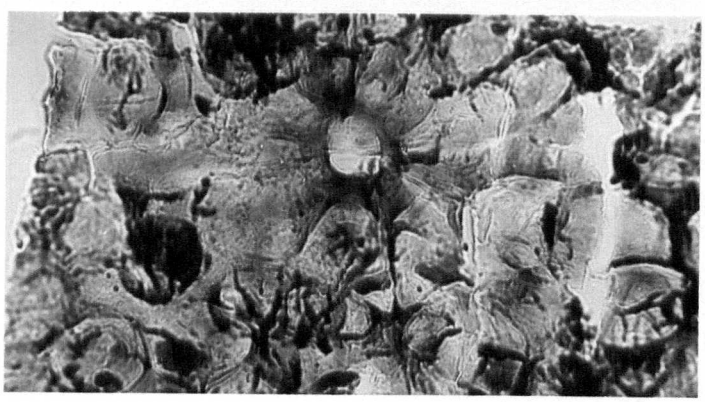


3

PLATE 21

Plate 21

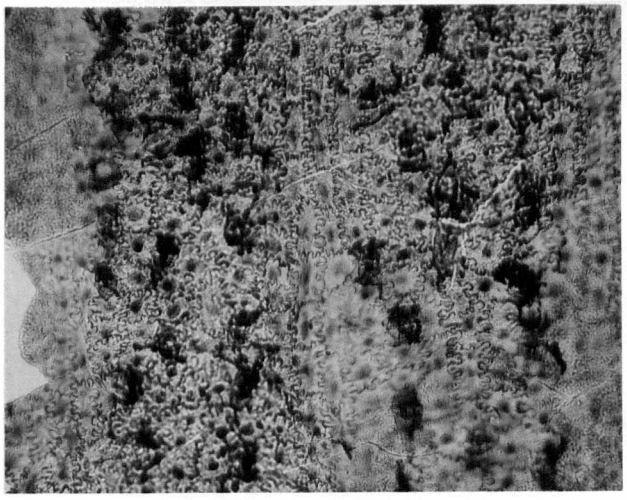
Zamites johannae sp. nov.

Lower cuticle of a pinna from the holotype, slide 1.

Fig. 1. x 100

Figs. 2,4. Stoma and details of epidermal cells. Fig. 2, x 400; fig. 4. x 800.

Fig. 3. Stomata and trichome base, x 400.



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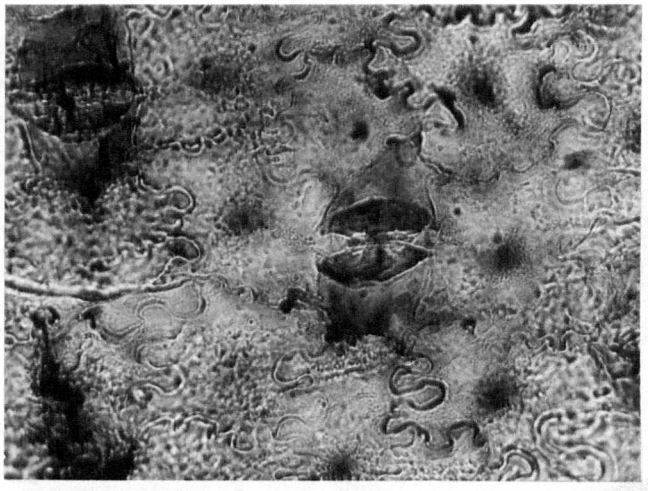

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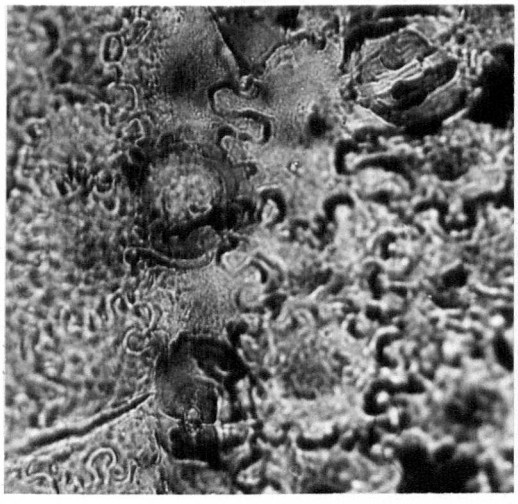

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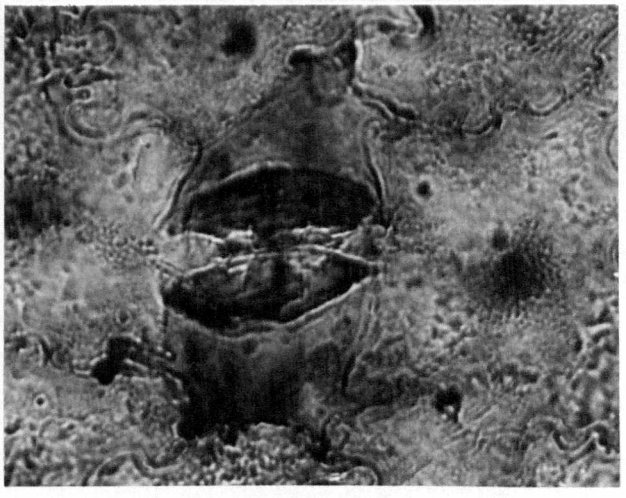


4

PLATE 22

Plate 22

Cycadolepis sp. indet., Pterophyllum sp. nov., Root (form 2)

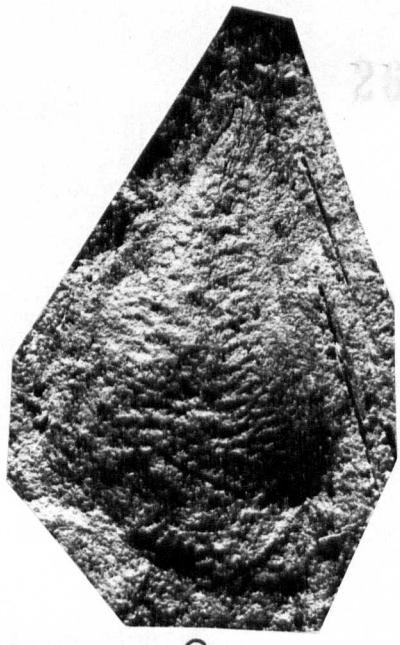
Figs. 1,2. Cycadolepis sp. indet. (syn. Cycadolepis sp. (hairy) of Hill & van Konijnenburg 1973:62). Specimen from section C siltstone, Mariestopesia blackii block no. 102. x 6.

Fig. 3. Pterophyllum pruinosum sp. nov. Holotype (no. 2). Part; from section 1:190-210 cm. x 3.

Fig. 4. Root, form 2. Showing swellings. Specimen no. 1 (Part) from section 2: 60-80 cm. x 2.

Figs. 1,3,4 photographed under paraffin, Fig. 2 dry.

1



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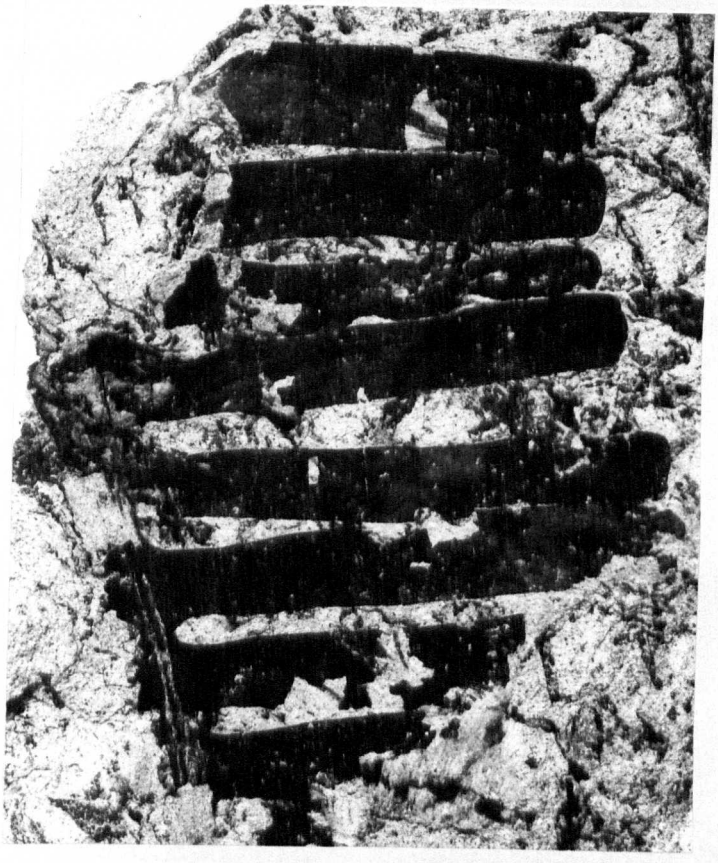

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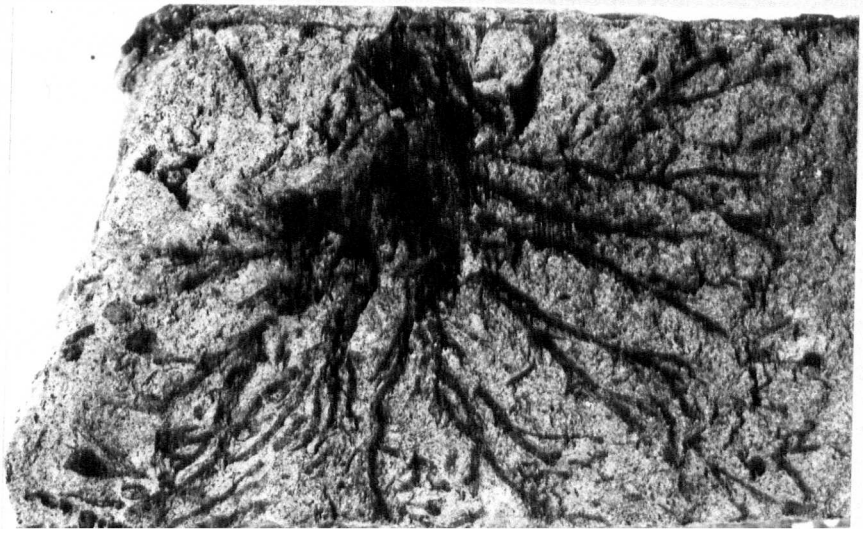


PLATE 23

Plate 23

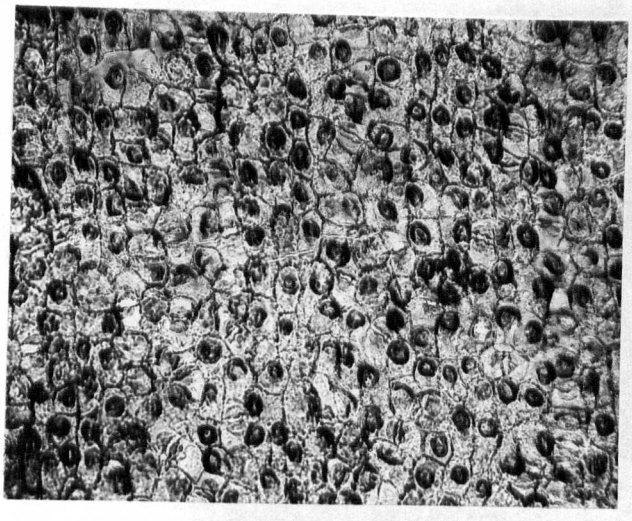
Pterophyllum pruinosum sp. nov.

Fig. 1. Specimen no. 3, from section 1: 170-190 cm. Upper cuticle. x 125.

Fig. 2. Specimen no. 1, from section C ca. 100 cm, slide 2. Lower cuticle. x 100.

Figs. 3,4. Specimen no. 1, slide 1. Typical stomata. x 625.

1



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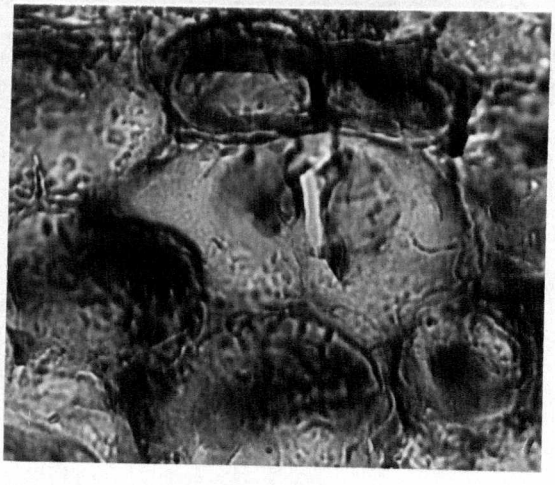


4

PLATE 24

Palissya harrisii sp. nov. (manuscript name).

Holotype; specimen no. B1 (Part), from section S1 claystone

x 2.

Photographed under paraffin.

PLATE 25

Plate 25

Palissya harrisii sp. nov., holotype.

Specimen no. B1, from section S1 claystone.

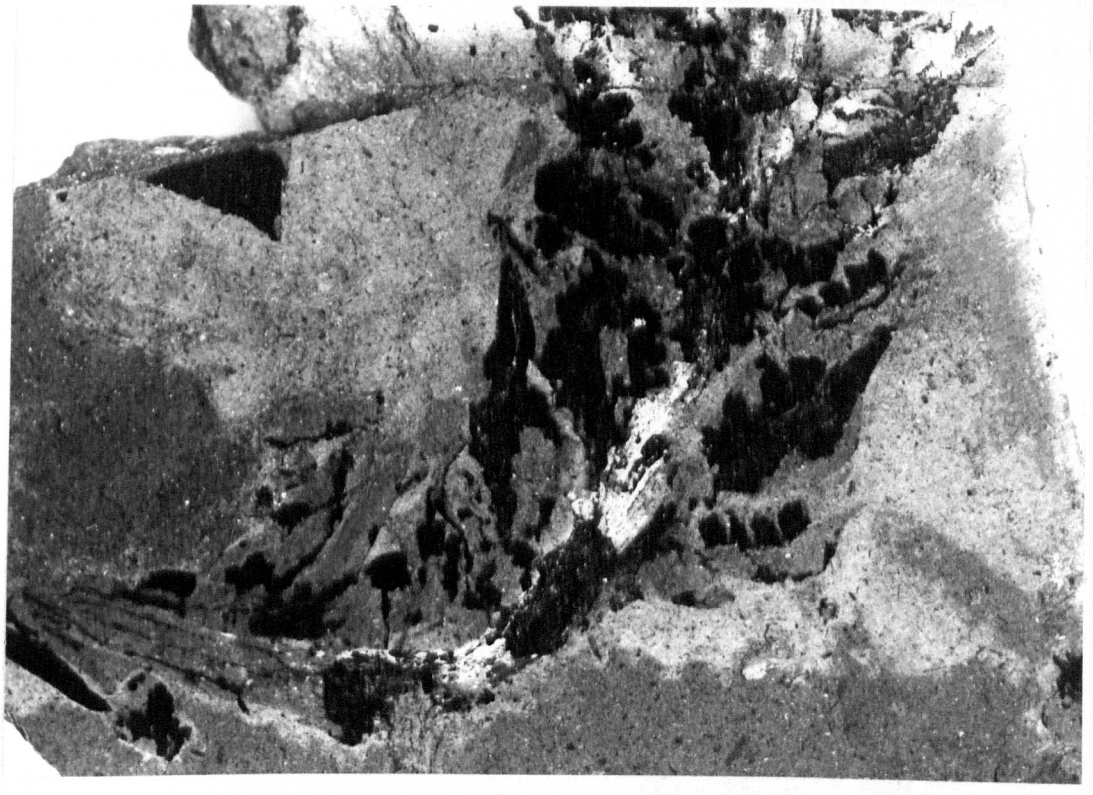
x 5.

Photographed under paraffin.

Fig. 1. Part

Fig. 2. Counterpart. The negative was inverted for printing to enable direct comparison of the print with fig. 1.

1



2

PLATE 26

Plate 26

Palissya harrisii sp. nov.

Specimen no. B16 (Part) from section S2 claystone, photographed under paraffin. Fig. 1, x 4. Fig. 2, x 2.

A foliage shoot of *P. harrisii* is seen on the left of Fig. 2.

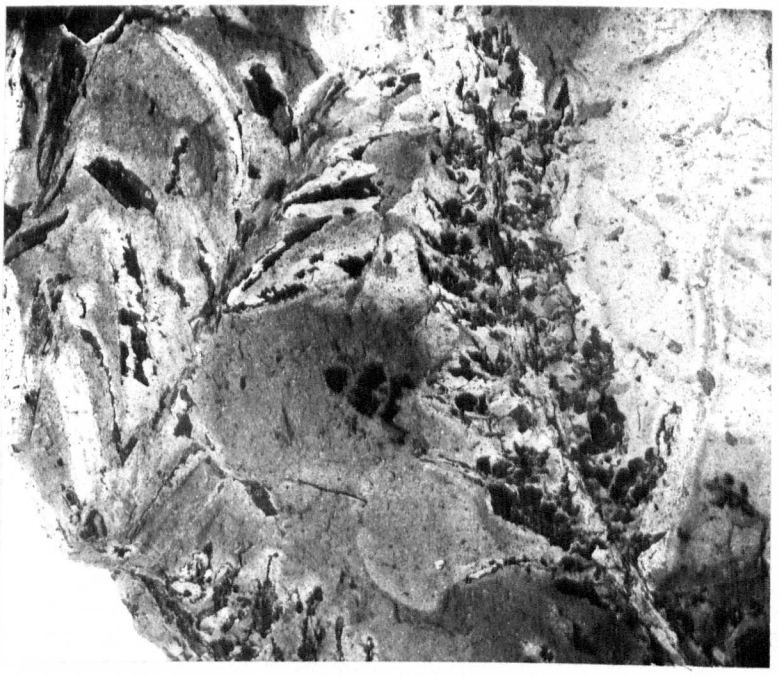


PLATE 27

Plate 27

Foliage shoots of Palissya harrisii sp. nov. and Sewardiodendron laxum (Phillips) Florin, from sections S1 and S2 claystone. All x 2. Photographed under paraffin.

Figs. 1,3. Sewardiodendron laxum

Fig. 1. No. A7, from section S1; form with short leaves.

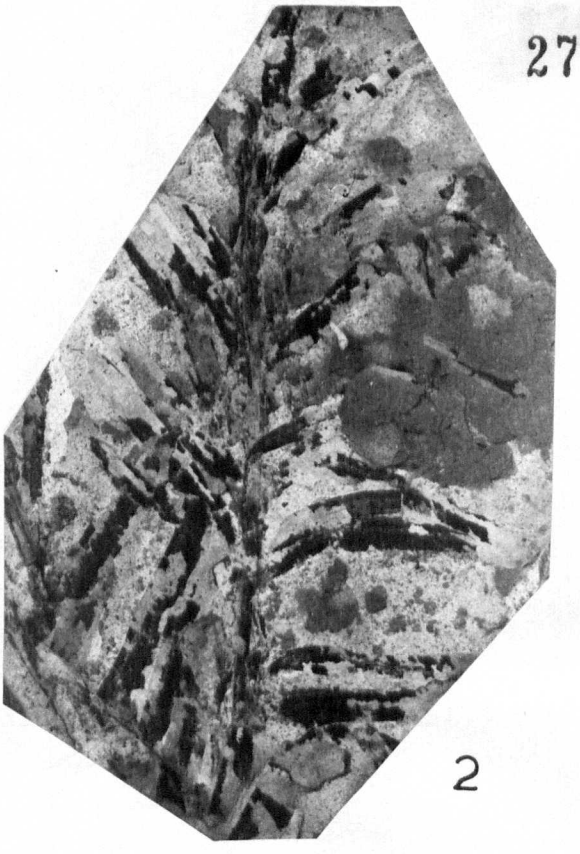
Fig. 3. No. A3 (Counterpart), from section S2

Figs. 2,4. Palissya harrisii

Fig. 2. No. A2 (Part), from section S2

Fig. 4. No. A8b, from section S2.

1



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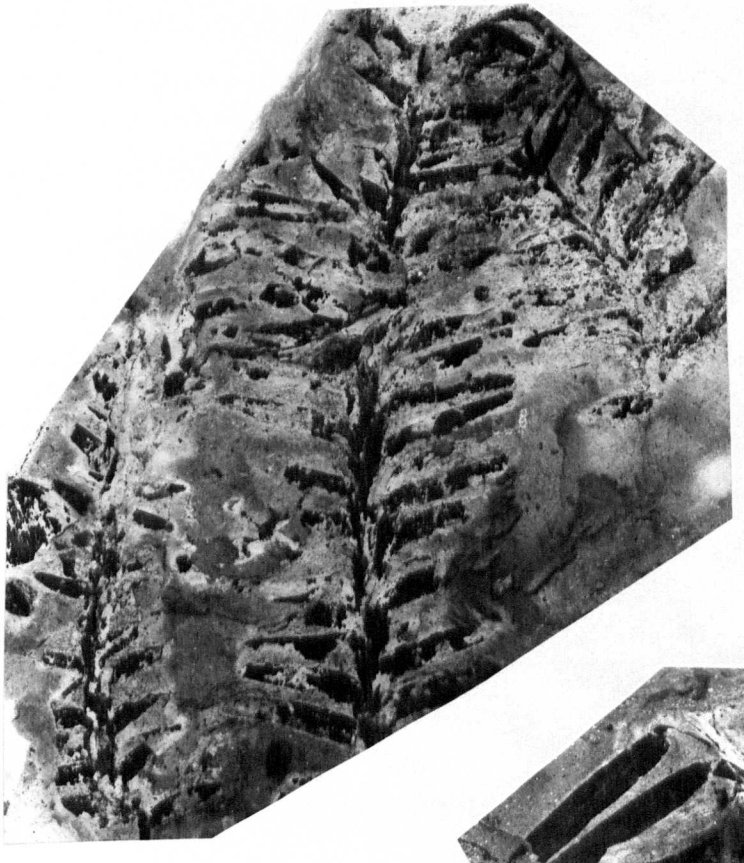

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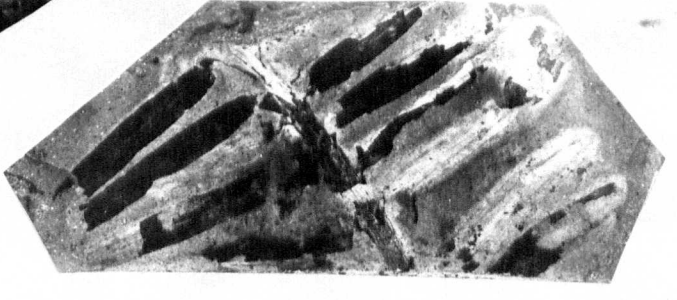


4

PLATE 28

Plate 28

Hirmerella crucis (Kendall)comb. nov. (manuscript name), female cone.

Specimen no. 8, from section S1 claystone, photographed under paraffin. x 4.

Fig. 1. Counterpart

Fig. 2. Part

1

2

PLATE 29

Plate 29

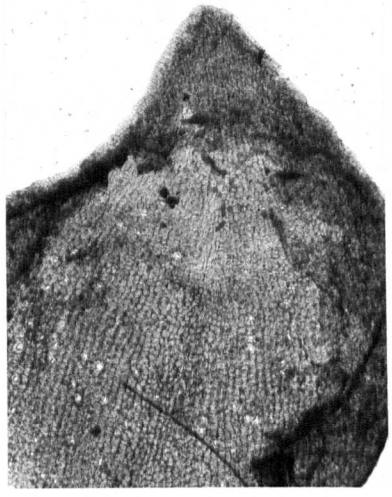
Hirmerella crucis (Kendall) comb. nov., leaf cuticles.

Fig. 1. A leaf, from slide V.29524

Figs. 2,3. Scarious margin of a leaf. Slide V.29524.

Figs. 4-9. Stomata and ordinary epidermal cell-outlines, illustrating their range of variation. Figs. 4-5:V.29526, figs. 6-9: V.29524.

Figs. 1,2, x 126. Figs. 3-5,9, x 320. Figs. 6-8, x 500.



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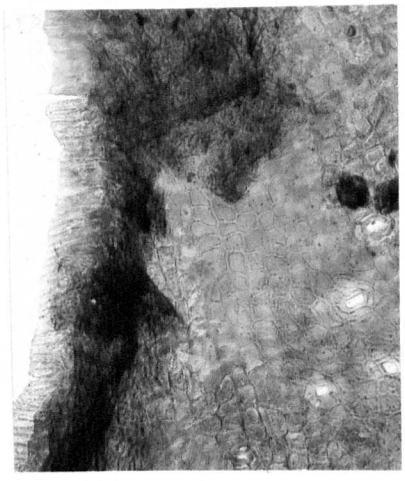

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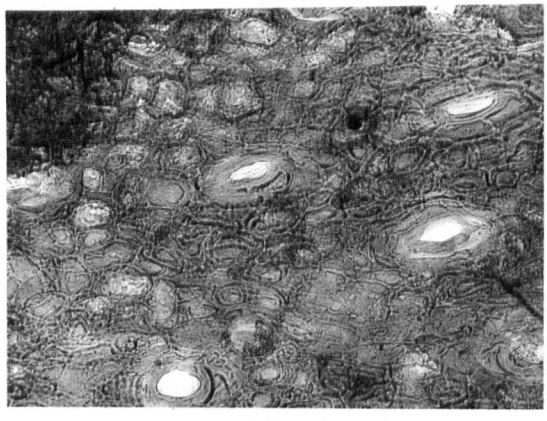
3



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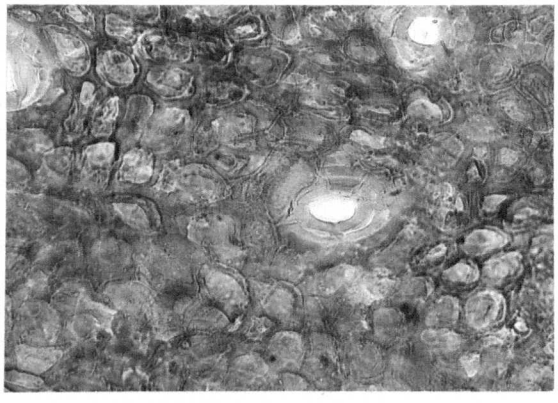

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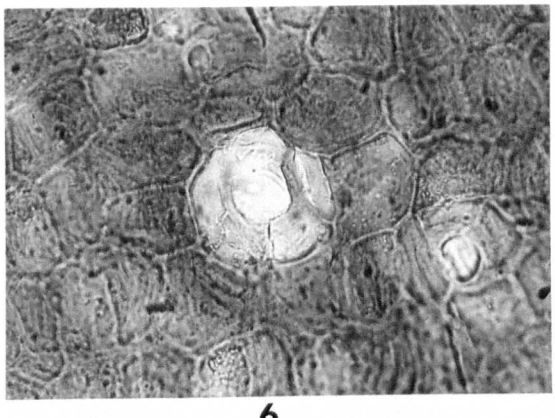

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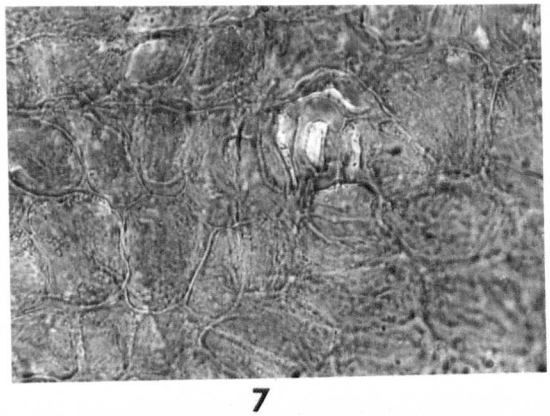

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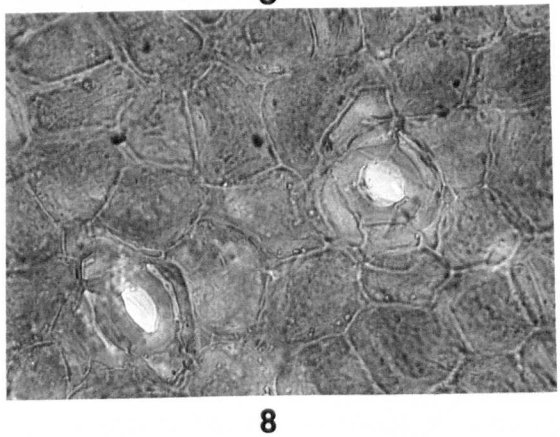

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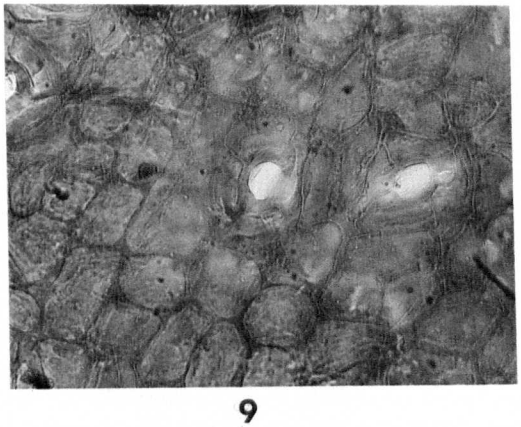


9

PLATE 30

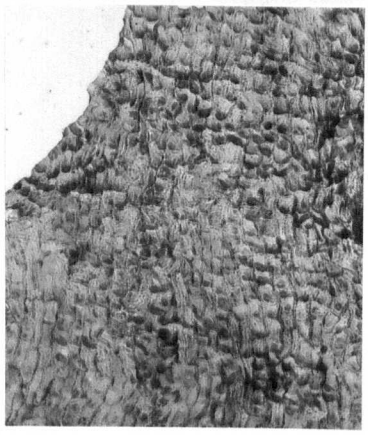
Plate 30

Cone-scale cuticles of *Hirmerella muensterii* (Schenk) Jung and *H. crucis* (Kendall) comb. nov.

Figs. 1,2. *Hirmerella muensterii*
Bract-scale cuticle showing papillae, x 126. Prepared from BMNH specimens, registered nos. 1164+1165.

Figs. 3-9. *Hirmerella crucis*
Fig. 3. Bract-scale cuticle showing papillae. Specimen no. 1. x 126.

Figs. 4-9. Ovuliferous-scale cuticles, showing stomata and ordinary epidermal cell-outlines.
Figs. 4,6, specimen no. 1.
Figs. 5,7-9, specimen no. 2.
(Figs. 3-5 are at x 126 and figs. 6-9 at x 320).



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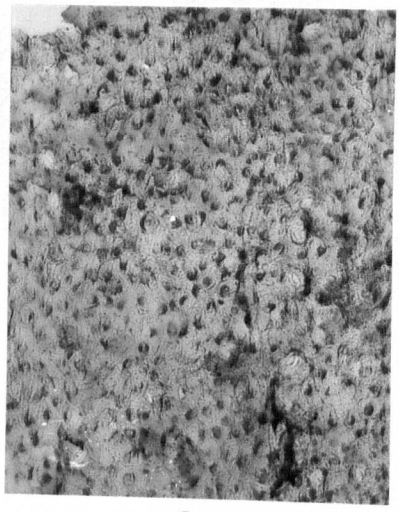

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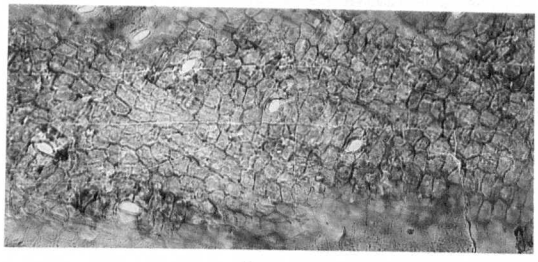

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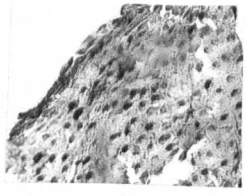

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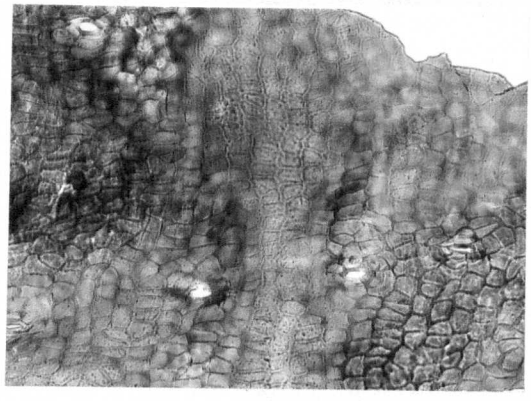

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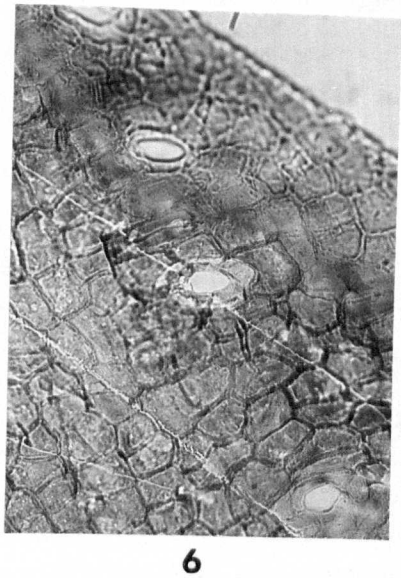

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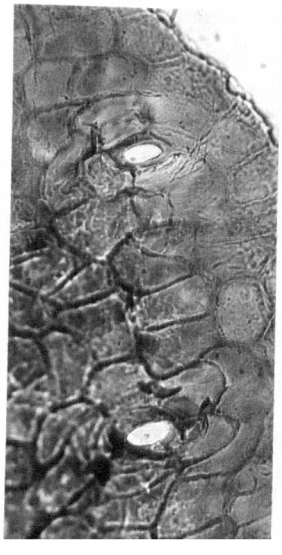

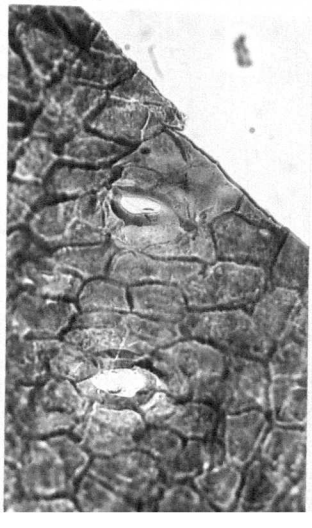

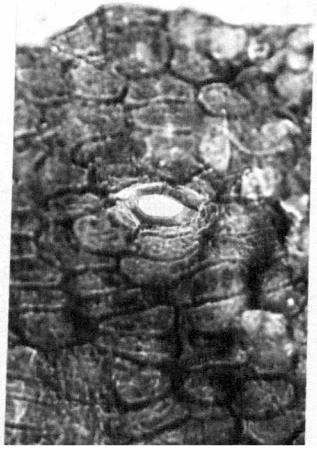

ex PhD thesis of Hill,1974.

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FURTHER PLANT FOSSILS FROM THE HASTY BANK LOCALITY

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A further eight species of plant fossils are recorded from the Middle Jurassic Hasty Bank locality (NZ 568 038), thus adding to the previous list of Hill and van Konijnenburg (1973).

Species marked * were found from bulk maceration (Harris, 1926) of a sandy 5cm thick coal which is rich in fragments of plant fossil material. The coal lies 21 metres above the base of the lenticular sandstones (see fig. 1 of Hill & van Konijnenburg, 1973) and its present outcrop extends for more than 34 metres. It is of interest because only a few of the species so far recorded are shared with the somewhat older main plant bed, and presumed mangrove-like species are lacking.

SPECIES LIST

All identifications have been supported where possible by preparations of cuticles. Because detached leaves were identified only when both upper and lower cuticles agree perfectly with species known more fully from elsewhere, a number of undetermined fragments, mostly of Bennettitales, are left unrecorded.

The current name and literature reference are followed by an estimate of abundance according to the following scale:—

(1) Less than 5 specimens known at time of press
(2) 5 — 100 specimens known (or seen during fieldwork)
(3) 100 — 500 specimens
(4) 500 or more specimens
(5) Many thousands of specimens seen

All the specimens and preparations are lodged with the palaeobotanical collections of the British Museum (Natural History).

ALGAE

CHLOROCOCCALES

Botryococcus braunii Kützing See Harris, 1938; Traverse, 1955. (2)

PTERIDOPHYTA

**Triletes areolatus* Harris Megaspore; see Harris, 1961, 61-63. (2)

GYMNOSPERMS

UNCLASSIFIED

**Amphorispermum pullum* Harris Seed; see Harris, 1964, 28-30. (2)

CAYTONIALES

Sagenopteris colpodes Harris Axis with attached bud scales; see Harris, 1971. (1)

CYCADALES

Pseudoctenis herriesii Harris Leaf; see Harris, 1964, 72-76. (1)

BENNETTITALES

**Ptilophyllum hirsutum* Thomas & Bancroft Detached leaflets; see Harris, 1969, 61-64. (3)

Cycadolepis spheniscus Harris Perianth scale; see Harris, 1969, 104-106. (1)

Bucklandia pustulosa Harris Axis; see Harris, 1969 173-174. (2)

CONIFER (unclassified)

Pagiophyllum ordinatum Kendall Detached leaves; see Kendall, 1948; Harris, vol. V in preparation. (2)

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SPECIES OF PLANT FOSSILS COLLECTED FROM THE MIDDLE JURASSIC PLANT BED AT HASTY BANK, YORKSHIRE

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The Yorkshire Jurassic flora became first known scientifically almost 150 years ago, and soon came to be a world standard for the Middle Jurassic. Knowledge of the flora is based mainly on about eight major plant beds which were formed 150 million years ago in a large fresh-water delta. The delta sediments now form the solid rocks of the "Deltaic Series", which is divided into 4 units by marine incursions (Hemingway, 1949). Like the similar locality at Roseberry Topping, the Hasty Bank plant bed occurs at the base of the lowest unit ("Lower Deltaic") and its age is lower Bajocian.

The exposure at Hasty Bank was made by alum workers in the 19th century, but its discovery as a major plant fossil locality (by Dr. M. Black in 1927) was relatively recent. The bed is remarkable for its unusually extensive exposure (over 100 metres long and 7 metres thick) which gives evidence of the conditions of deposition, the wealth of its flora (70 species) and for the presence of some marine microfossils amongst the terrestrial plant fragments. Since whole plants were usually fragmented before being preserved as fossils, the special interest of Hasty Bank to palaeobotanists is the presence of reproductive organs, associated with the more common leaves and shoots. When evidence of association is strengthened by agreement in structure (cuticles) the plants can be partially reconstructed and more learnt about their classification than is possible merely from isolated fragments.

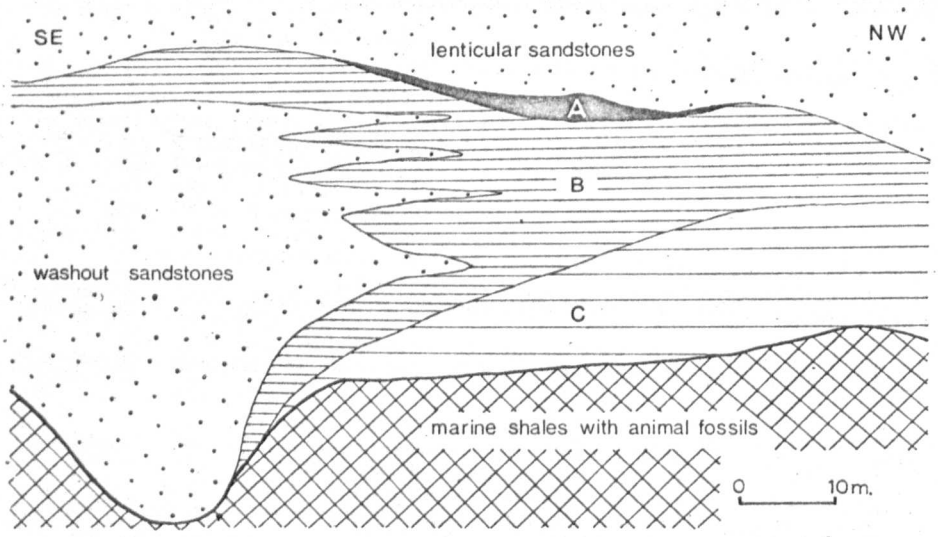

Fig. 1. Diagram of the Hasty Bank exposure (038 568) and its geology. Vertical scale exaggerated 4 × horizontal.
Fragments of fossil plants are abundant in the dark clay (A) the siltstone (B) and claystones (C). These three rock types form the main plant bed.

DEPOSITIONAL ENVIRONMENTS (fig. 1)

The main bed (Ordnance Survey ref. NZ 038 568) consists of three rock types, one of which (the siltstone) was probably the slow part of a river channel (Hill, unpublished). Immediately to the south-east of the siltstone, the parent channel is represented by a sandstone-filled "washout" (an erosive river channel—see Black, 1928).

The occurrence of some marine algal microfossils in the lower (claystone) part of the bed (Muir, 1964) may indicate that it was sometimes flooded by sea water. On evidence of structure and widespread association with these microfossils Harris (1964) has suggested that one of the commonest species (*Pachypteris papillosa*) was a mangrove-like plant of tidal channels.

The Flora

Like other rich Jurassic floras, that at Hasty Bank is composed mainly of forms which cannot be assigned to living genera and shows no convincing evidence for the presence of Angiosperms (flowering plants). Many species are referred to extinct and apparently isolated groups (e.g. Caytoniales and Bennettitales), though others show characters of certain living plant groups but not of any one modern genus (e.g. *Nilssonia kendalli*). In only three cases are the fossils so like living species that they have been given the same generic name (*Marattia*, *Dicksonia* and *Equisetum*).

Two specially interesting recent discoveries are known only from Hasty Bank. One is a primitive eusporangiate fern (van Cittert, 1966) which appears to be intermediate between older genera and the living *Angiopteris* (Hill, *in* MS). The other is a cone, *Hastystrobus muirii* (van Konijnenburg, 1971, 1972) which produced the pollen *Eucommiidites*. *Eucommiidites* is widespread in Jurassic rocks and because it superficially resembles the pollen of certain Angiosperms was at first thought to be evidence that Angiosperms existed in the Jurassic. However, this evidence is not now generally accepted, following a reinterpretation of the form of the pollen grain, and its discovery both in the micropyles of gymnospermous seeds and in the apparently gymnospermous male cone *Hastystrobus*.

Species List

All identifications have been supported where possible by preparations of cuticles and spores or pollen. The current name and literature reference are followed by location of vouching specimens in museum collections, with catalogue numbers of type specimens from Hasty Bank.

U: University of Utrecht
BM: British Museum (Natural History), Department of Palaeontology
LDS: University of Leeds (Palaeobotanical collections)

Work in progress is designated "MS", and estimates of abundance are given according to the following scale.

(1) Less than 5 specimens known at time of press
(2) 5–100 specimens known (or seen during fieldwork)
(3) 100–500 specimens
(4) 500 or more specimens
(5) Many thousands of specimens seen

Most of the species are unevenly distributed through the bed, so that even those known from many thousands of specimens may be dominant and abundant locally but rare or absent elsewhere. Only one species (*Phlebopteris woodwardi*) is more or less evenly distributed throughout.

Finally, we hope that this list (which has doubled known species records in the last five years) will soon be longer. The Hasty Bank plant bed is far from exhausted.

Acknowledgments

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PTERIDOPHYTA

Equisetales

Equisetum columnare Brongniart (Harris, 1961, 15–20), U, BM, LDS, (5).

Marattiales

Angiopteris neglecta van Cittert (van Cittert, 1966; Hill, MS—to be given a new generic name), U 1371 (type specimen), LDS, (3).

Marattia anglica (Thomas) Harris (Harris, 1961, 72–75; van Cittert, 1966), U, BM, LDS, (4).

Osmundales

Osmundopsis sp. (cf. Harris, 1961, 99–100), LDS, (1).

FILICALES

Matoniaceae

Phlebopteris woodwardi Leckenby (Harris, 1961, 106–109), LDS, (2).

Dipteridaceae

Dictyophyllum rugosum Lindley & Hutton (Harris, 1961, 117–123), U, LDS, (3).

Clathropteris obovata Oishi (Harris, 1961, 123–126), U, BM, LDS, (3).

Schizaeaceae

Stachypteris spicans Pomel (isolated fertile pinnae) (Harris, 1961, 135–140), LDS, (1).

Dicksoniaceae

Coniopteris murrayana (Brongn.) Brongniart (Harris, 1961, 158–164), BM, LDS, (3).

Dicksonia kendalli Harris (Harris, 1961, 179–181), U, LDS, (1).

Unclassified Ferns (sterile foliage)

Cladophlebis denticulata (Brongn.) Fontaine (form with rather small teeth) (Harris, 1961, 78–87), LDS, (1).

C. aktashensis Turutanova—Ketova (Harris, 1961, 190–192), LDS, (1).

C. harrisii van Cittert (van Cittert, 1966) (= *Selenocarpus muensterianus* (Presl) Schenk of Harris, 1961), U, BM: V.52136 (type specimen), LDS, (4).

Sterile foliage similar in form to that of *Dicksonia kendalli* is also known, but it is indistinguishable from certain other species (see Harris, 1961, p. 176). (3).

GYMNOSPERMS

CAYTONIALES

Sagenopteris colpodes Harris ("large form" of leaf) (Harris, 1964, 4–8), U, BM, LDS, (4).

Caytonia kendalli Harris ("fruit") (Harris, 1964, 24–27), U, BM, LDS, (4).

CYCADALES AND PTERIDOSPERMS (foliage)

Nilssonia tenuinervis Seward (Harris, 1964, 33–37), U, BM, LDS, (5).

N. thomasi Harris (Harris, 1964, 37–39), BM, (1).

N. syllis Harris (Harris, 1964, 42–46; 176), U, BM, LDS, (3).

N. tenuicaulis (Phillips) Fox-Strangways (Harris, 1964, 46–49), U, (1).

N. compta (Phillips) Bronn. (Harris, 1964, 50–54), U, LDS, (1).

N. kendalli Harris (Harris, 1964, 55–58), U, BM, LDS, (5).

Paracycas cteis (Harris) Harris (Harris, 1964, 67–70), U, BM, LDS, (2).

Pseudoctenis oleosa Harris (Harris, 1964, 78–82), BM, LDS, (3).

P. lanei Thomas (Harris, 1964, 82–86), U, BM, LDS, (4).

Ctenozamites cycadea (Berger) Schenk (Harris, 1964, 95–99), U, BM, LDS, (4).

Ctenis kaneharai Yokoyama (Harris, 1964, 112–117), U, BM, LDS, (3).

Pachypteris papillosa (Thomas & Bose) Harris (Harris, 1964, 125–136), U, BM, LDS, (5).

P. lanceolata Brongniart (Harris, 1964, 137–147; 176), LDS, (1).

CYCAD-LIKE REPRODUCTIVE ORGANS

Androstrobus wonnacotti Harris (male cone) (Harris, 1964, 159–160), BM, LDS, (2).

A. prisma Thomas & Harris (male cone) (Harris, 1964, 160–161), U, BM, LDS, (3).

A. sp. A Harris (male cone scale) (Harris, 1964, 163), BM, LDS, (2).

A. major van Konijnenburg (male cone scales) (van Konijnenburg, 1968) U 2964 (type specimen), LDS (including sterile scales), (2).

Hastystrobus muirii van Konijnenburg (male cone) (van Konijnenburg, 1971, 30–33; 1972), U 1496 (type specimen), (1).

Beania spp. (female cones) (Harris, 1964, 169–170), U, BM, LDS, (3 or less).

Palaeocycas sp. nov. (megasporophyll) (Hill, MS; cf. Florin, 1933), LDS, (2).

Allicospermum spp. (isolated seeds) (Harris, 1964, 164), BM, LDS, (3).

PTERIDOSPERM-LIKE REPRODUCTIVE ORGAN

Pteroma thomasi Harris (male) (Harris, 1964, 170–175), U, BM: V.45493 (type specimen) LDS, (3)

BENNETTITALES (foliage)

Zamites gigas (Lindley & Hutton) Morris (F. M. Quin, in Harris, 1969, 4–8), U, (1).

Zamites sp. (Hill, MS), LDS, (1).

Otozamites graphicus (Leckenby) Schimper (Harris, 1969, 16–21), LDS, (2).

O. leckenbyi Harris (Harris, 1969, 23–26), BM, (1).

O. gramineus (Phillips) Phillips (Harris, 1969, 29–33), U, (1).

Ptilophyllum pectinoides (Phillips) Phillips (Harris, 1969, 56–61), U, BM, LDS, (5).

Nilssoniopteris vittata (Brongn.) Florin (Harris, 1969, 68–72), U, BM, LDS, (4).

Anomozamites nilssoni (Phillips) Seward (Harris, 1969, 79–84), U, (1).

Pterophyllum thomasi Harris (Harris, 1969, 93–97), U, (1).
P. sp. nov. (Hill, MS), LDS, (1).

BENNETTITALEAN REPRODUCTIVE ORGANS

Cycadolepis hypene Harris (female flower perianth scales) (Harris, 1969, 114–117), U, BM, LDS, (4).
C. sp. (hairy) (Hill, MS; Harris, 1969, 103), LDS, (1).
Williamsonia hildae Harris (female flower) (Harris, 1969, 135–139), U, BM, LDS, (3).
Weltrichia spectabilis (Nathorst) Harris (male flower) (Harris, 1969, 166–168), U, (1).
W. whitbiensis (Nathorst) Harris (male flower) (Harris, 1969, 171–172), U, BM, LDS, (3).

GINKGOALES (leaves)

Ginkgo huttoni (Sternberg) Heer (Harris, 1948; 1973, *in press*), U, BM, (1).
Eretmophyllum whitbiense Thomas (Thomas, 1913; Harris, 1973 *in press*), BM, LDS, (3).
Solenites vimineus (Phillips) Harris (Harris, 1951; 1973 *in press*), U, BM, LDS, (2).
Sphenobaiera gyron van Konijnenburg—*nomen nudum*, in van Konijnenburg, 1968. (Harris, 1973, *in press*), U, BM, LDS, (5).

TAXADS AND CONIFERS

TAXADS

Marskea thomasiana Florin (shoots and leaves) (Florin, 1958, 301–303), BM, (2).

CONIFERS

HIRMERELLA (*Cheirolepis*) GROUP

van Konijnenburg, 1971, 59–65, gives a useful summary of recent research on this extinct group of early conifers.
Brachyphyllum crucis Kendall (shoots) (Kendall, 1952), U, BM, LDS, (5).
(this species was recorded in error as *Brachyphyllum expansum* by Harris, 1964, 176.)
B. crucis (male cone) (van Konijnenburg, 1971, 1972), U 2984, (1).
Hirmerella sp. nov. (female cone of *Brachyphyllum crucis*, with cone scales of *Cheirolepis* form) (Hill, MS), U, LDS, (2).

Araucariaceae

Brachyphyllum mamillare Brongn. (shoots) (Kendall, 1947, 1952), U, BM, LDS, (3).
B. mamillare (male cone) (van Konijnenburg, 1971, 51–57), U, LDS, (2).
Araucarites phillipsi Carruthers (female cone scale of *Brachyphyllum mamillare*) (Kendall, 1947), LDS, (2).

Palissyaceae sensu Florin

Palissya sp. nov. (female cone) (Hill, MS; Florin, 1958, 267–276), LDS, (2).

Taxodiaceae

Elatides sp. nov. (shoots, with male and female cones often in attachment) (Harris, MS; cf. *E. williamsonii*, Harris, 1943), U, BM, LDS, (5).
Haiburnia setosa (Phillips) Harris (Harris, 1952), T. M. Harris collection, University of Reading. (1).

UNCLASSIFIED CONIFERS (shoots and leaves)

Bilsdalea dura Harris (Harris, 1952; Florin, 1958, 314–317), LDS, (2).
Sewardiodendron laxum (Phillips) Florin (Florin, 1958, 303–307; Hill, MS—foliage attributed to *Palissya sp. nov.*), BM, LDS, (2).

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THE PROBLEM OF COLOUR PATTERNS AND THEIR VARIATION IN THE GENUS *VESPA*

T. R. Birkhead

Several authors have produced keys for the social wasps, Vespinae (Laidlaw 1934 Smith 1963). However, these do not appear to be totally reliable since the British species (excluding the Hornet *Vespa crabro*), *V. vulgaris*, *V. germanica*, *V. rufa*, *V. sylvestris*, *V. norvegica* and *V. austriaca* are very similar and because the markings of each species are not consistent. Variations of colour patterns of *Vespa* spp. have been recorded by a number of workers (Laidlaw 1934, Robson & Richards 1936: 173, Wynne-Edwards 1963), but no explanation for this variation has been offered. The present paper presents suggestions for how and why such variation should occur.

Although very little is known about the evolution of the genus *Vespa* it seems likely that any common ancestor would have already possessed the striking black and yellow aposematic (i.e. warning) colouration in conjunction with a powerful sting. As the different species evolved it remained advantageous to maintain this colouration. It would be of further benefit if, as the number of species increased they remained similar; thus enhancing the advantages conferred by Mullerian mimicry (see Ford 1964), since predators would only have to encounter a few individuals of *any* species in order to learn to avoid them *all*.

Variations in the colour patterns of the *Vespa* spp. prevents humans from rapidly and effectively separating the different species, and potential predators with similar visual systems are likely to experience similar difficulty, particularly when the insects are in flight. Selection will therefore tend to favour variability as long as it results in a confusing similarity between species. This is unlikely to be disadvantageous to the wasps themselves since species recognition is probably by other means, such as olfactory or auditory.

Laidlaw (1934) has discussed variation in the male caste. Males are produced from the unfertilized eggs laid by workers (Spradberry 1965) and are therefore haploid. The fact that variation is extensive in males, suggests that the variability of workers' colour patterns may directly effect the colour patterns of the males they produce. Figure 1. shows the possible genetic relationships between the different castes. Thus if males always mate with queens from their own colony, this may tend to restrict variation by increasing homozygosity. Whereas males mating with queens of other colonies would probably favour variation by increasing genetic diversity. However, a rigorous control mechanism must operate in order to maintain a balance, since variation must only be such as to confuse potential predators, too much or too little would result in the loss of this ability. Unfortunately, at present, reproductive strategy and the extent of in-breeding and out-breeding in *Vespa* spp. is poorly known.