Mesozoic and Tertiary Palaeobotany of Great Britain

C.J. Cleal

Department of Biodiversity and Systematic Biology,
National Museums and Galleries of Wales,
Cardiff, UK

B.A. Thomas

Welsh Institute of Rural Studies,
University of Wales Aberystwyth,
Aberystwyth, UK

D.J. Batten

Institute of Geography and Earth Sciences
University of Wales Aberystwyth,
Aberystwyth, UK

and

M.E. Collinson

Geology Department,
Royal Holloway University of London,
Egham, UK

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Chapter 3

The Jurassic palaeobotany of Yorkshire

B.A. Thomas and D.J. Batten

History of research

INTRODUCTION

The Cleveland Basin in northern England (see Figures 3.2 and 3.12) is one of the classic areas in the world for Mesozoic palaeobotany. This is partly because it is located in Europe where much of the early research in palaeobotany was centred. However, it also reflects the diversity and fine preservation of the floras, which are among the best in the European Palaeoarea (*sensu* Vakhrameev *et al.*, 1978) that extended over most of the northern mid-latitudes in Early and Middle Jurassic times, including much of Europe and North America. Over 300 species have been identified from Yorkshire, including spore-producing clubmosses, horsetails and ferns, and several groups of seed plants such as cycads, bennettites, caytonias, ginkgos and conifers. Many of these species have their type locality in Yorkshire.

Incorporation of plant material into the accumulating delta sediments led to the fossiliferous plant beds that have been found at over 500 sites throughout Yorkshire. Inevitably some deposits are richer in species than others and it is these that have yielded the most information through recognition and association of separated parts from the plants of one species. The preservation is often very good, permitting the preparation of cuticles and the recovery of spores and pollen from fructifications. A complete list of the described species from the GCR sites is given in Table 3.1 (pp. 32–6).

HISTORY OF RESEARCH

Fossil plants from the Yorkshire coast were first described and rather crudely figured in 1822 by Young (a Nonconformist minister) and Bird (an artist who for a time was also curator at the Whitby Museum). Although this work had little scientific merit it did, however, encourage others to search for fossils in the area. Further collecting and the interest it generated led to the establishment of both the Whitby and Scarborough museums.

William Bean and his nephew John Williamson were the two most active collectors of Yorkshire Jurassic plants in the early 19th century. Bean was an incredibly enthusiastic collector. He exchanged and sold specimens to such an extent that they can be found in many other British and foreign museums. Williamson, through his enthusiasm, became the curator of the Scarborough Museum. He knew William Smith, who has been described as 'the Father of English Geology', Smith's nephew John Phillips and Sir Roderick Murchison. Smith was originally a surveyor and the author of the famous *Map of the Strata of England and Wales* published in 1815. In 1813 he visited north-east Yorkshire to examine some of the coal pits that were scattered through the central moorlands in order to report on their economic importance. Coal had been mined spasmodically in the area from 1648, but, by the mid-18th and early 19th centuries was concentrated in the Coxwold–Gilling Trough. The largest mine was the Birdforth Colliery (*c.* SE 481 772), which was sunk to a depth of 46 metres in 1760 and employed more than 30 men until it closed in 1798. Most mines were, however, much smaller adits that were worked for fuel to burn lime, which was very much in demand as a soil fertilizer. In the summer of 1821, Smith published his geological map of Yorkshire in four sheets. In 1824 he moved, with his nephew, to live in Scarborough. Then, in 1829, Phillips published his *Illustrations of the Geology of Yorkshire*, which for the first time placed the geology of east Yorkshire on a sound scientific basis. He included descriptions and drawings of fossil plants, but the latter were far from accurate.

At the same time, the renowned French palaeobotanist Adolphe Brongniart was working on his great publication *Histoire des Végétaux Fossile*, which was published in Paris (Brongniart, 1828b–1838). He described and figured 22 species of Jurassic plants from the Yorkshire coast in the second of these works.

The important *Fossil Flora of Great Britain* by Professor John Lindley and William Hutton was published in parts between 1831 and 1837. It contained drawings and descriptions of several Yorkshire Jurassic plants supplied by Bean, Phillips and Dr Murray Dunn (secretary of the Literary and Philosophical Society of Scarborough) but most importantly by John Williamson's son, William Crawford Williamson (1816–1895), who was later to make his name in Carboniferous palaeobotany after becoming Professor of Botany and Geology at the University College in Manchester. He is now known as the founder of modern palaeobotany in Britain.

Williamson drew the Yorkshire Jurassic specimens for the *Fossil Flora of Great Britain*, which came as a surprise to Lindley when Williamson

Table 3.1 Records of plant fossils from the Yorkshire Jurassic GCR sites. These records have been gleaned from published accounts, largely by Harris (1961a, 1964, 1969, 1979a,b; Harris *et al.*, 1974), Hill *et al.* (1985), Hill and van Konijnenburg-van Cittert (1973), Spicer and Hill (1979), van Konijnenburg-van Cittert (1971, 1975a,b, 1978, 1981, 1987, 1989), and van Konijnenburg-van Cittert and Morgans (1999), from archived field notes in the Natural History Museum (London), and from examining collections in that museum and the National Museum and Gallery, Cardiff. Records known to fall outside the boundaries of the sites have been omitted, but those over which there is some doubt have been included.

1. Whitby-Saltwick
2. Runswick Bay
3. Roseberry Topping
4. Broughton Bank (Hasty Bank)
5. Hillhouse Nab
6. Hayburn Wyke
7. Botton Head
8. Beast Cliff (Robin Hood's Bay)
9. Maw Wyke
10. Red Cliff (Gristhorpe Bay/Cayton Bay)
11. Cloughton Wyke
12. Scalby Ness.

Key to symbols:

+ record for the site;
‡ the only record for Yorkshire;
× type locality for the species;
Ø the only record for the species;
s in the Solonites Bed.

	1	2	3	4	5	6	7	8	9	10	11	12
BRYOPHYTA												
Hepaticites arcutus (L. and H.) Harris										×	+s	
H. haiburnensis Harris						Ø						
H. hymenoptera Harris										×		
H. wonnacottii Harris										×		
EQUISETALES												
Annulariopsis simpsonii (Phillips) Harris	×							+?				
Equisetum beanii (Bunbury) Harris		+	+					+			+	
E. columnare Brongniart	+	+	+	+	+	+	+	+		+	+	
E. filium Harris					×							
E. laterale Phillips	+	+		+		+	+			+	+	
Neocalamites hoerensis (Schimper) Halle		+	+			+					+	
N. nathorstii Erdtman	×							+				
Schizoneura stenophylla Harris								Ø				
LYCOPODIALES												
Lycopodites falcatus L. and H.		+								+	+s	
FILICOPSIDA												
Angiopteris blackii van Cittert		+	+	+								
A. neglecta van Cittert				+								
Aspidistes thomasii Harris								+		×		
Cladophlebis aktashensis Turutanova-Ketova			+	+		+					+	
C. denticulata (Brongiart) Fontaine*		+	+	+			+			+	+	
C. haiburnensis (L. and H.) Brongniart	+						×	+		+		
C. harrisii van Cittert†				+			+					
Clathropteris obovata Oishi	+		+	+	+	+	+	+	+			
Coniopteris bella Harris	+				+	+				+		+
C. burejensis (Zalessky) Seward								+				
C. concinna (Heer) Chen, Li and Ren								+				
C. hymenophylloides (Brongniart) Seward	+	+		+		+		+	+	+	+	+
C. margaretae Harris											Ø	
C. murrayana (Brongniart) Brongniart	+	+		+		+		+	+	+	+s	
C. simplex (L. and H.) Harris	+	+				+	+	+	+		+	

* *Cladophlebis denticulata* probably consists of two natural taxa, the large pinnules being the sterile foliage of *Todites denticulata* and the smaller that of *Osmundopsis sturii*.

† *Cladophlebis harrisii* is probably the fertile foliage of *Osmundopsis hillii*.

Table 3.1 – *contd.*

	1	2	3	4	5	6	7	8	9	10	11	12
FILICOPSIDA – *contd.*												
Dicksonia kendalliae Harris			×	+								
D. mariopteris Wilson and Yates								+		+		
Dictyophyllum rugosum L. and H.	+		+	+	+	+	+	+		+	+s	
Eboracia lobifolia (Phillips) Thomas			+	+	+	+	+	+	+	+	+	
Hausmannia dichotoma Dunker			+		+		+					
Klukia exilis (Phillips) Raciborski						+	+	+		+	+s	
Kylikipteris arguta (L. and H.) Harris								+		+	+	
Marattia anglica (Thomas) Harris			+	+				+				
Matonia braunii (Goeppert) Harris	+		+		+	+	+		+	+		
Matonidium goeppertii (Ettingshausen) Schenk	+					+				+	+	
Osmundopsis hillii van K.-van C.				×								
O. cf. *plectophora* Harris				+								
O. sturii (Raciborski) Harris										+	+	
Phlebopteris braunii (Goeppert) Harris	+				+					+		
P. dunkeri (Schenk) Schenk	+	+						+				
P. polypodioides Brongniart								+		+	+	
P. woodwardii Leckenby	+		+	+		+	+	+	+	+	+	+
Selenocarpus muensterianus (Presl) Schenk			+	+								
Sphenopteris metzgerioides Harris											+	
Stachypteris spicans Pommel	+			+								
Todites denticulatus (Brongniart) Krasser	+								+	+	+	
T. princeps (Presl) Gothan	+					+		+		+	+	
T. thomasii Harris										×		
T. williamsonii (Brongniart) Seward	+		+				+	+		+	+	
GYMNOSPERMOPHYTA												
CAYTONIAS												
Amphorispermum pullum Harris										×		
Caytonanthus arberi (Thomas) Harris										×		
C. onocodes Harris										×		
C. sp.			+				+					
Caytonia kendallii Harris			+	+								+
C. nathorstii (Thomas)										×		+
C. sewardii Thomas										×		
Sagenopteris colpodes Harris	+		+	+	+		+			×	+	
S. phillipsii (Brongniart) Harris			+		+		+			×		
PTERIDOSPERMS												
Ctenis exilis Harris								×		+		
C. kanebarai Yokoyama			+	+	+							
C. reedii Harris										×		
C. cf. *Stemantiana* Harris												
C. sulcicaulis (Phillips) Ward										×	+s	
Ctenozamites cycadea (Bergen) Schenk			+	+			+					
C. leckenbyi (Leckenby) Nathorst			+	+				+		×		
C. megalostoma Harris							+					
C. ranebarai Yokoyama							+					
C. sp. A of Harris										+		
Pachypteris lanceolata Brongniart			+	+	+	+	+			+	+	
P. papillosa (Thomas and Bose) Harris			×	+	+	+	+					
Pteroma thomasii Harris			+	×			+					
pollen	+		+	+				+			+	
CYCADALES												
Allicospermum spp.				+			+					
Androstrobus balmei Hill		Ø										
A. major van K.-van C.		+	+	+			+					
A. manis Harris										Ø		

Table 3.1 – ***contd.***

	1	2	3	4	5	6	7	8	9	10	11	12
CYCADALES – ***contd.***												
A. prisma Thomas and Harris			+	×			+					
A. szei Harris										×		
A. wonnacottii Harris	+			+			+			×	+s	
A. sp. A of Harris			+	+								
Beania gracilis Carruthers				+			+			+	+	
B. mamayi Thomas and Harris											+	
B. sp.		+		+		+						
Deltolepis calyptra Harris	+			+				×			+	
D. crepidota Harris										×		
D. mitra Harris				Ø								
Hastystrobus muirii van K.-van C.				×								
Nilssonia compta (Phillips) Bronn			+	+	+	+	+	+		+		+
N. kendallii Harris	+		×	+	+		+					
N. cf. *leckenbyi*			+	+								
N. revoluta Harris												
N. syllis Harris			+	+		+	+	×				
N. tenuicaulis (Phillips) Fox-Strangways	+			+						×		+
N. tenuinervis Seward	+	+	+	+	+		+	+	+	+	+s	+
N. thomasii Harris	×		+	+	+	+		+				
N. sp. A of Harris	+		×			+		+		+		
N. sp. B of Harris								×		+		
Paracycas cteis Harris				×			+	+				
Pseudoctenis herriesii Harris	×		+	+				+				
P. lanei Thomas	+	+	+	+	+	+	+	+		+		
P. locusta Harris										×		
P. oleosa Harris	+		+	+	+	+	+	+				
Stenopteris nana Harris	×								+			
S. nitida Harris										×		
S. williamsonis (Brongniart) Harris			+			‡		+		+	+	
BENNETTITALES												
Anomozamites nilssonii (Phillips) Seward			+	+				+		×	+	
A. thomasii Harris			Ø									
Bennetticarpus diodon Harris								Ø				
B. litchii Harris								Ø				
Bucklandia gigas Seward		+				×						
B. pustulosa Harris				+	+			+		+	×s	
B. sp. B of Harris										Ø		
Cycadolepis eriphous Harris											Ø	
C. hallei Harris											×s	
C. hypene Harris	×		+	+	+		+	+				
C. nitens Harris										×	+s	
C. spheniscus Harris	+			+		+	+	×			+	
C. stenopus Harris										×	+s	
C. thysanota Harris	×		+								+	
C. sp. nov. of Hill *et al.*		×										
Nilssoniopteris major (L. and H.) Florin	+			+			+			+		+
N. pristis Harris										+	×s	
N. vittata (Brongniart) Florin			+	+				+		+	+s	
Otozamites anglica (Seward) Harris	×											
O. beanii (L. and H.) Brongniart						+		+		×	+s	
O. falsus Harris	+				+		+					
O. gramineus (Phillips) Phillips	×		+	+		+		+	+	+		
O. graphicus (Leckenby) Saporta	+		+	+	+	+		+		+	+	+
O. leckenbyi Harris				+		×						
O. marginatus Saporta										+		
O. mimetes Harris						×					+	

Table 3.1 – *contd.*

	1	2	3	4	5	6	7	8	9	10	11	12
BENNETTITALES – *contd*												
O. parallelus Phillips	+					×						
O. penna Harris	+		+	+		+				+	+	
O. simpsonii Harris	×	+	+						+			
O. tenuatus (Leckenby) Phillips						×		+	+			
O. thomasii Harris			+							Ø		
Pterophyllum cycadites Harris and Rest										+		
P. fossum Harris	+						+			+		
P. thomasii Harris				+		+	+	+	+	+	×s	
Ptilophyllum hirsutum Thomas and Bancroft	+	+	+			+	+	+				+
P. pecten (Phillips) Harris			+							+	×s	
P. pectinoides (Phillips) Morris	+	+	+	+	+	+	+	+		+	+	+
Large coprolites of *P. pectinoides*			+									
Weltrichia pecten (Leckenby) Halle										+?	×s	
W. setosa (Nathorst) Harris	Ø										+	
W. sol Harris	×	+				+						
W. spectabilis (Nathorst) Harris	×			+								
W. whitbiensis (Nathorst) Harris	×		+	+				+				
W. sp. nov. of Hill *et al.*		×										
Williamsonia gigas Carruthers	+	+				+			+			
W. hildae Harris	+		+	+								
W. hildae Harris: buds	+			+	+			+				
W. leckenbyi Nathorst								+		+	+s	
Williamsoniella coronata Thomas		+	+				+			×	+	
W. lignieri (Nathorst) Harris	+											
W. papillosa Cridland	×						+	+		+		
Zamites gigas (L. and H.) Morris	+	+	+	+		+	+	+	+	+	+	+
Z. quiniae Harris	+		+						+			
Z. sp. nov. of Harris							+					
GINKGOALES												
Baiera furcata (L. and H.) Braun	+	+	+			×						
Seeds of *Baiera furcata* (L. and H.) Braun												+
Eremetophyllum pubescens Thomas										×	+	+
E. whitbiense Thomas	×	+	+	+			+	+				
Ginkgo digitata (Brongniart) Heer	+		+			+				+	+	+
G. huttoni (Sternberg) Heer				+		+				+	+	×
G. huttoni (Sternberg) Heer male cones												×
G. huttoni (Sternberg) Heer seeds												×
G. longifolius (Phillips) Harris						×		+		+	+	
G. sp. cf. *sibirica* Heer			+	+				+		+		
G. whitbiensis Harris	×		+	+								
Pseudotorellia tibia Harris and Millington					×							+
P. sp. nov. of Harris and Millington							+					
Sphenobaiera gyron Harris and Miller				×			+					
S. longifolia (Pomel) Florin	+		+	+								
S. ophioglossum Harris and Miller	+								+			
S. pecten Harris		+				+		+	+			
CZEKANOWSKIALES												
Czekanowskia blackii Harris and Miller				+								×
C. furcula Harris and Miller	×	+	+			+	+					
C. microphylla (Phillips) Seward							+			×		
C. thomasii Harris and Miller										×		
C. sp. A of Harris and Miller												Ø
C. sp. B of Harris and Miller						+	+					
C. sp. C of Harris and Miller											+	
C. sp. D of Harris and Miller									+			
Desmiophyllum gramineum Harris and Miller	+											

Table 3.1 – *contd.*

	1	2	3	4	5	6	7	8	9	10	11	12
CZEKANOWSKIALES – ***contd.***												
Inoxostrobus whitbiensis Harris and Miller	Ø											
Leptostrobus cancer Harris						+		+		+	+s	
Solonites vimineus (Phillips) Harris		+	+	+	+	+			+	×	+s	
Sphenarion muiriae Harris and Miller												Ø
PINALES												
Araucarites phillips Caruthers	+	+		+	+		+			+		+
Brachyphyllum crucis Kendal				+	+	+	+	+		+		
B. crucis with attached male cone				+								
B. mamillare L. and H.	+	+		+	+	+	+	+		+	+	+
B. mamillare with attached male cones	+											
Bilsdalea dura Harris				+			+			+	+	
Carpolithes cepa Harris	+											
Classostrobus cloughtonensis van K.-van C.											Ø	
Cyparissidium blackii Harris			+							+		+
C. rudlandicum Harris					+							
Elatides thomasii Harris		+		+	+		+	+			+?	
E. williamsonii (L. and H.) Nathorst	+			+?						+	+s	+
E. williamsonii with male and female cones										+		
Elatocladus laxus (Phillips) Harris	+		+	+			+			+		
E. ramosus (Florin) Harris	+		+	+				+				
E. setosus (Phillips) Harris	+					×	+	+				
E. sideriticus (Bose) Harris				+		×						
E. zamioides (Leckenby) Seward										Ø		
Geinitzia divaricum (Bunbury) Harris				+						×		
G. rigida (Phillips) Harris					+	+	+		+	×	+	
Hirmeriella estoniensis (Kendall) Harris			+			+			+		+	
H. kendalliae Harris	+										×	
H. sp. of Spicer and Hill				+								
Lindleycladus lanceolatus (L. and H.) Harris	+		+			+	+					
Masculostrobus harrisii van K.-van C.											×	
Marskea jurassica (Florin) Harris	+			+		+	+	×				
Pagiophyllum araucarina (Pomel) Saporta		+										
P. fragilis (Bose) Harris												
P. insigne Kendall										×		
P. kurii (Schimper) Salfeld	+											
P. maculosum Kendall	+									+	+	
P. ordinatum Kendall					+			+			×	
P. cf. *pegrinium* Black												
Palissya harrisii Hill				×								
Pityanthus scalbiensis van K.-van C.	+?									+		×
Pityocladus scarburgensis Harris	+											
Poteridion hallei Harris	+											
Scarburgia hillii Harris	+?		+									×
Schizolepis liasokeuperianus Braun										‡		
Torreya gracilis Florin	+										+	
T. valida Florin												
Trulla nitens Harris											×s	
WOODS												
Cupressinoxylon spp. of Morgans						+				+	+	+
Taxodioxylon spp. of Morgans						+						
Xenoxylon phyllocladoides Gothan						+				+		
Cedroxylon spp. of Morgans						+						+

enrolled as a student of his in London (Williamson, 1896). One species figured by Lindley and Hutton illustrates especially well how they relied on the Scarborough collectors. Bean was mentioned several times in their book as supplying the fossils and they named one, *Cyclopteris beanii*, after him. Interestingly they pointed out that it was in fact John Williamson who had collected it, William Williamson who had described and drawn it, and Mr Dunn who had given an account of its usual appearance, while William Bean had merely sent it to Hutton. Brongniart (1849) later transferred this species to the genus *Otozamites*.

A significant discovery made by Lindley and Hutton was that cuticles could be prepared from these fossils. This should have enabled the study of the flora to be developed in a significant way, using anatomical data of a type that was then rarely used in palaeobotany. However, for reasons that are difficult to explain, their discovery seems to have been effectively ignored and it was not until nearly a century later that H. Hamshaw Thomas started properly to develop cuticle studies on these fossils (see below).

Leckenby (1864) described and figured some new specimens, most of which are now in the Sedgwick Museum in Cambridge. Other scattered publications make reference to fossil plants from the Yorkshire coast, but the next major piece of work was by the Swedish palaeobotanist Alfred Nathorst. This was an unillustrated account, in Swedish, of his visit to English museums and the coast in 1880. Fox-Strangways and Barrow (1892) published a long list of plant fossils in the second edition of the Geological Survey Memoir on the region. Interestingly an acknowledgement is given in this work to the help given by the palaeobotanist Clement Reid who is better known for work on Tertiary plant fossils.

Albert C. Seward (1863–1941) was probably the most important British palaeobotanist living around the turn of the 20th century (for bibliographical details see Harris, 1941c). He had, in fact, studied with William Williamson in Manchester in 1886, although he subsequently concentrated on Mesozoic plants for most of his career. In 1900, Seward catalogued the fossil plants in the British Museum (Natural History) (now the Natural History Museum, London) that had been collected from the Yorkshire coast, although in so doing he included details of specimens that he had examined in other British and continental museums (Seward, 1900a). Seward was a prolific writer and included details of Yorkshire Jurassic plants in his seminal four-volume work, *Fossil Plants* (1898–1919). Unfortunately his catalogue showed no fundamental difference in technique from that of Brongniart. The fossils to both of them were 'impressions with carbon' and, although Seward knew how to prepare cuticles and must have been aware that Lindley and Hutton had already prepared them from Yorkshire fossils, he did not believe that they could be of any value (Harris, 1961a).

This idea that fossils were merely 'pictures on the rock' changed with the work of the Swedish palaeobotanist Nathorst and his colleague Thore Halle. They prepared cuticles from specimens that they had collected themselves and showed that cuticle characters were of supreme importance, especially when studying reproductive organs. As Harris (1961a) has pointed out, the large slabs of foliage that previously had always been sought after were suddenly no longer as important. Collecting had passed into the hands of the researcher, and Nathorst and Halle, and then Rudolf Florin, all came from Stockholm to Yorkshire for the purposes of collecting material for research.

Hamshaw Thomas (1885–1962) was, like Seward, at Cambridge for most of his career, but, unlike Seward, Thomas believed passionately in fieldwork and collecting for himself (for bibliographical details, see Harris, 1963). He had worked for a while with the Scottish palaeobotanist Robert Kidston and then with Nathorst in Sweden where he appreciated fully the value of cuticle studies. In fact, Thomas came back with the extreme view that the fossil was not merely a black mark on the rock but a whole organ. If he could not see every cell of such a compressed organ then it was a failure of technique or observation. Thomas went to Yorkshire to collect for himself, although the localities were forgotten and he was told that they were worked out. Collecting cannot have been easy at first and he only rediscovered the famous Gristhorpe Bed when he had given up looking for plant fossils and was collecting a seaweed. The seaweed was firmly attached to a piece of rock that broke off with it revealing a plant fossil. This was an incredible piece of luck considering the wealth of material that has subsequently come from this bed. Another important discovery of his was a layer of thick leathery brown leaves (*Pachypteris lanceolata*) found in a landslide at Roseberry Topping. He even stuck them onto Christmas cards for his friends. Thomas collected a great number of specimens between 1910 and 1914, often with the help of an amateur, the Reverend George Lane of the Cleveland Naturalists. The Great War interrupted Thomas' research but he returned repeatedly to Yorkshire for several years afterwards.

Thomas published a number of papers on Yorkshire Jurassic plants. In 1913, with Bancroft, he studied cycadophyte leaves and divided them into two groups on epidermal characters they saw in cuticle preparations. This division into the cycads and what has become known as the cycadeoids is still good today. Perhaps his best-known work, however, was on the Caytoniaceae when he showed that the seed-bearing *Caytonia*, the pollen organ *Antholithus* and the leaves *Sagenopteris* all belong to the same plant (Thomas, 1925). This was based on frequent association in some strata, their complete absence from others, and the close similarity of epidermal structure in all their petiole-like bases. His work on interpreting *Caytonia* itself involved collecting hundreds of specimens, dissecting some, sectioning others and preparing cuticles from yet more. This was his greatest work. Unfortunately, Thomas was too much of a perfectionist, like Kidston who influenced him. He believed that he should collect for himself, study, and then go back for more until he had sufficient material to confirm all the points on which he would publish. As a result, only a fraction of his work on the plant fossils he discovered appeared in print. He stopped collecting around 1925, although from about that date staff at the British Museum (Natural History), notably Maurice Wonnacott, started collecting, eventually amassing a great amount of material.

Next on the scene was Tom Harris (1903–1983), who went to Cambridge and ended up working with Seward. After studying the Greenland Rhaeto–Liassic flora and visiting Stockholm to learn cuticle preparation from Halle, he eventually made the Yorkshire Jurassic succession his own (for bibliographical details, see Chaloner, 1985). Harris moved to Reading in 1935 where he became Professor of Botany and stayed for the rest of his career. He started working on the Yorkshire Jurassic material during the early years of World War II, having realized that Hamshaw Thomas had not published on the flora since 1925. After the war he visited Yorkshire many times, collecting from all the localities that he could find, often with research students or on holiday with his family, and travelling around on his bicycle. His aim was to look for plant fossils in every exposure, and he spent a great deal of time walking the length and breadth of northern Yorkshire. In so doing he found over 500 localities, although very few of them yielded assemblages worthy of study. Fortunately, Harris' approach, although rigorous, was not perfectionist. In 1947 he expressed the view that knowledge of the Yorkshire Jurassic flora should be brought up to date (Harris, 1947), so he went ahead and did just that. He published his work in a long series of papers mainly in the *Annals and Magazine of Natural History* (Harris, 1941a, 1942a,b, 1943a,b, 1944a,b, 1945a–c, 1946a–c, 1948, 1949a,b, 1950, 1951, 1952a,b, 1953). Later, he compiled all the species accounts, together with new work, in the five-volume *Yorkshire Jurassic Flora* (1961a, 1964, 1969, 1979a; Harris *et al.*, 1974). Among his papers Harris cleared up a problem that Thomas had conveniently side-stepped; he recognized two species of *Caytonia*. Harris not only showed that there were two species of *Sagenopteris* and then that there were two species of the male pollen-producing organs, but also that there were good associations between the two respective sets. He also cleared away the possibility that *Caytonia* was angiosperm-like when he found gymnospermous bisaccate pollen inside it. Thomas had found pollen attached to the lip, which he thought to be the stigma of a fruit. However, Harris' work demonstrated quite clearly that the pollen that had landed on Thomas' 'stigma' were the failures, not the successes. The successful gymnospermous pollen grains were inside what Harris was now calling a cupule.

Although Harris published a great deal and appears to have found out so much, he always maintained that his work was certainly nowhere near finished and that further collecting would turn up new discoveries. He believed that the collector was more likely to become exhausted than the locality.

A number of papers were published by Harris' research student Mabel Kendall (1947, 1948, 1952), and by some of his undergraduates in projects that partially fulfilled the requirements of their BSc degrees. Others workers have continued Harris' approach to the Yorkshire Jurassic succession. Christopher Hill, then at the Natural

History Museum, London, was fortunate in having material from a 'new' site north of Whitby (Runswick) brought to his notice by Ron Williams (an amateur collector). Han van Konijnenburg-van Cittert (Utrecht University) has also been very active in palaeobotanical research on the Yorkshire Jurassic flora, and more recently Helen Morgans (Leicester University) has studied the conifer woods from the succession (Morgans, 1999). Together, these two have written a field guide to the Yorkshire Jurassic flora of four coastal sites (van Konijnenburg-van Cittert and Morgans, 1999).

It is perhaps interesting at this point to contemplate one of Harris' own reflections on his work. In 1974, he suggested that he should have attempted to continue with his earlier Greenland studies rather than turning to the Yorkshire Jurassic succession, on which the most obvious work had already been done. He even went so far as to suggest that he should have concentrated his efforts on the 10 good localities rather than spending about 30 two-week trips walking many thousands of miles searching the hills for indifferent localities. This reflection on his choice of study area was probably meant to be thought-provoking rather than a damning assessment of his major work. His comments about the comparative value of the sites is, however, very pertinent to GCR work, for only those localities yielding a selection of floras have been judged to be worthy of GCR status and described in the present volume.

PALAEOGEOGRAPHICAL SETTING

During Early and Middle Jurassic times, most of the world's land remained connected together in the Pangea Supercontinent (Figure 3.1). It was a time of 'greenhouse' conditions, with relatively high atmospheric CO_2 levels and high global temperatures, although towards the end of the Middle Jurassic Epoch there is evidence of a lowering of temperatures (Frakes *et al.*, 1992). There was also a relatively low temperature gradient between low and high latitudes, with little ice being present at the poles.

There was some latitudinal variation in land vegetation, but nothing like that seen today; there were, for instance, no equivalents of today's tropical rain forests or tundra vegetation (Ziegler *et al.*, 1994). Consequently, it is not normal to recognize different palaeokingdoms in the floras of this time. Three palaeoareas were, however, delineated by Meyen (1987): the Siberian, in north-eastern Europe, Siberia, Kazakhstan and northern China; the European,

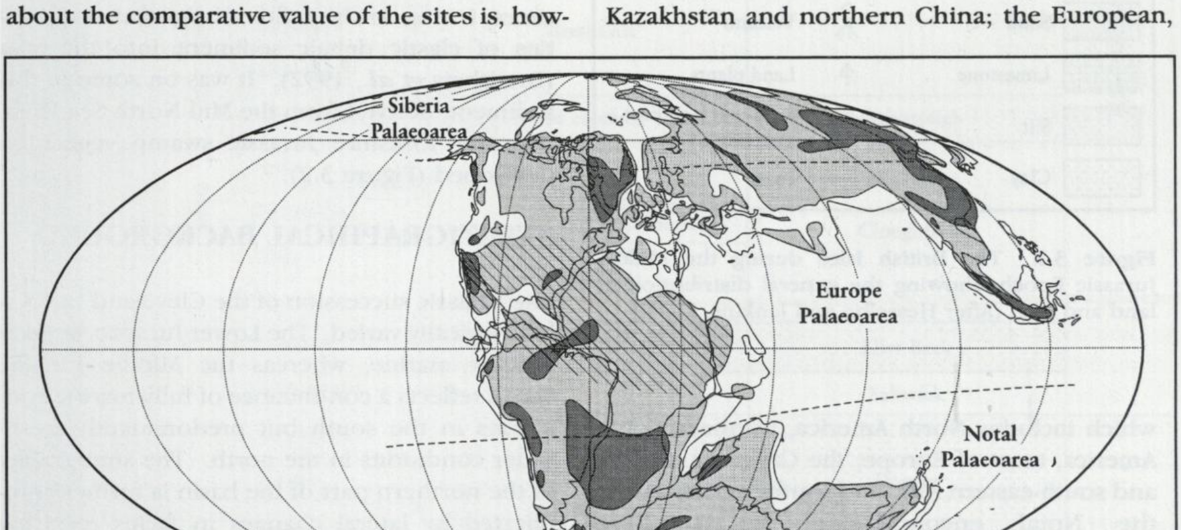


Figure 3.1 Palaeogeography of the Middle Jurassic world, showing main areas of land and mountains. Based on Smith *et al.* (1994). Also shown are the main palaeofloristic areas, based on Meyen (1987) and Vakhrameev (1991).

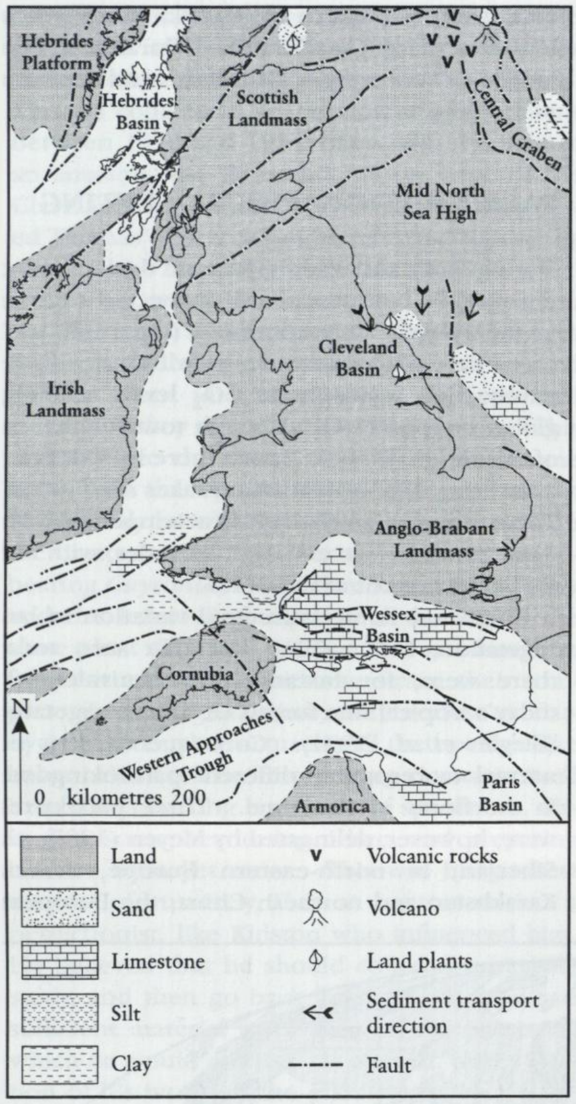


Figure 3.2 The British Isles during the Middle Jurassic Epoch, showing the general distribution of land and sea. (After Hesselbo and Jenkins, 1995.)

which includes North America, northern South America, most of Europe, the Caucasus, Middle and south-eastern Asia, and southern China; and the Notal encompassing the southern Gondwana continents. In addition, a large part of the tropical land area was a desert. In this palaeofloristic scheme, Yorkshire lies within the Europe Palaeoarea.

Alexander (1992) suggested that the British climate during the Middle Jurassic Epoch was warm, wet and subtropical because of the wide range of sand-body shapes that were generated as a result of variations in fluvial channel form, migration, and aggregation patterns. The common occurrence of fine sediment fractions in the channel deposits is also characteristic of humid, and subtropical, marine-influenced accumulations, because flocculation of fine sediments occurs at lower salinity in warmer climates. This interpretation of the climate is supported by Morgans' (1999) observation that Jurassic conifer woods from Yorkshire show distinct growth rings with narrow late wood and low to moderate annual sensitivity, all characters of little seasonal change and no shortage of water. Using multivariate analyses of spore and pollen assemblages, Hubbard and Boulter (1997) concluded that the Middle Jurassic climate was subject to regular, but not extreme, oscillations with perhaps increasing humidity. Temperatures dropped slightly near the Aalenian–Bajocian transition and then increased gradually until the Callovian. The Callovian climate was probably warmer and more humid than that of the Bathonian Age.

The high global temperatures and absence of significant polar ice meant that sea levels were relatively high. Consequently, much of Britain was below sea level during the Early Jurassic Epoch. However, a significant regression of the sea occurred in Britain during late Aalenian times, owing to the influx of significant quantities of clastic deltaic sediment into the area (Bradshaw *et al.*, 1992). It was on some of this sediment, derived from the Mid North Sea High, that the Yorkshire Jurassic swamp vegetation developed (Figure 3.2).

STRATIGRAPHICAL BACKGROUND

The Jurassic succession of the Cleveland Basin is lithologically varied. The Lower Jurassic Series is entirely marine, whereas the Middle Jurassic Series reflects a continuance of fully marine conditions in the south but predominantly freshwater conditions in the north. The stratigraphy of the northern part of the basin is further complicated by lateral changes in facies resulting from extensive input of deltaic sediment from the Mid North Sea High. The general stratigraphical scheme used in this chapter is summarized in Figure 3.3.

The first geological survey of the area by Fox-Strangways and Barrow (1892) provided what was to become, for many years, the standard comprehensive stratigraphical account of the region. His divisions are still in use although

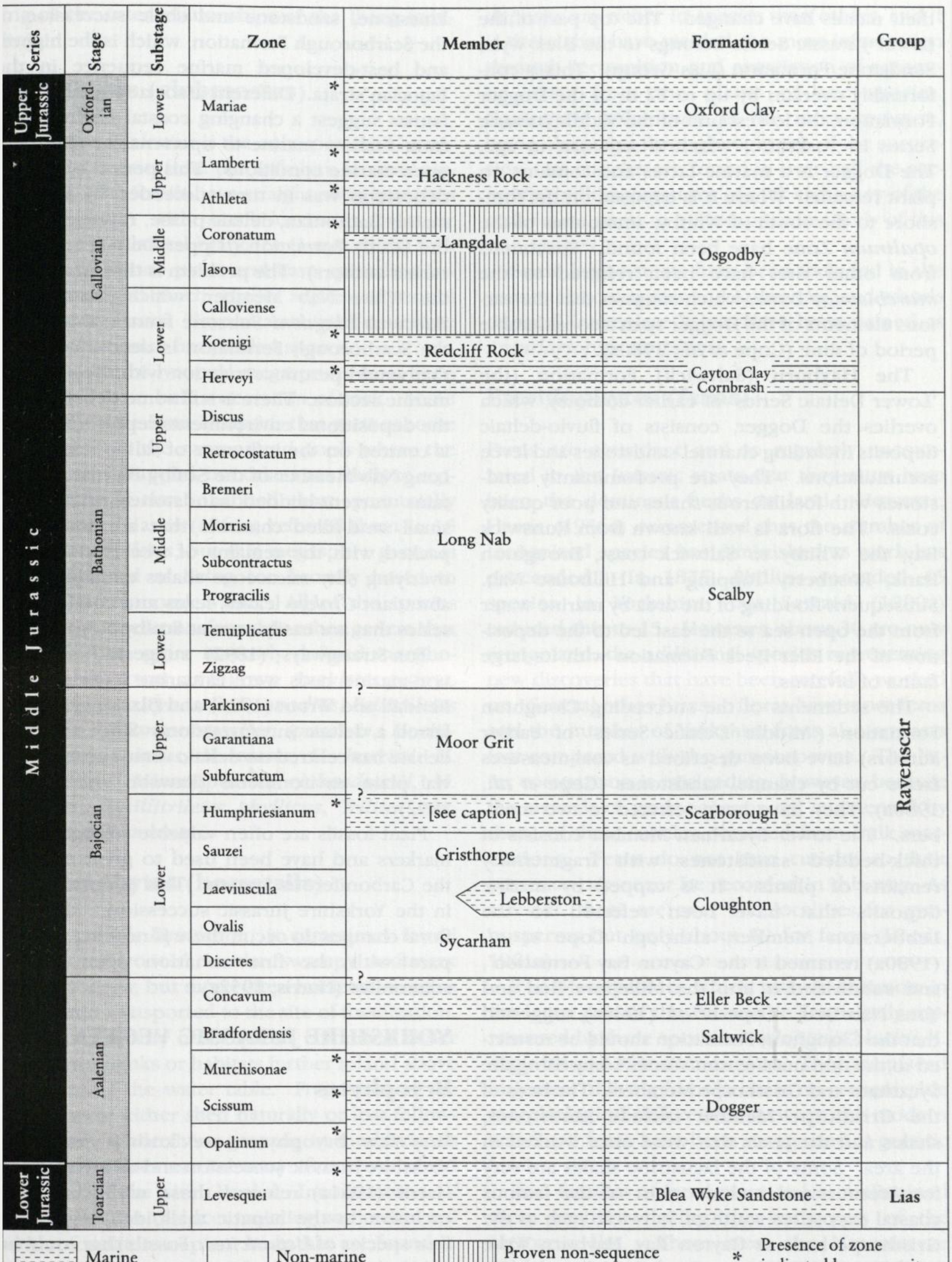


Figure 3.3 Summary of the Middle Jurassic stratigraphy of the Cleveland Basin, (based on Cox and Sumbler, in press, a companion GCR volume on British Middle Jurassic Stratigraphy). The Yorkshire Jurassic flora occurs in the three non-marine units, the Saltwick, Cloughton and Scalby Formations (the Lower, Middle and Upper Deltaic 'Series' of former authors). At its type locality, the Scarborough Formation has been divided into seven members (from below these are the Helwath Beck, Hundale Shale, Hundale Sandstone, Spindel Thorn Limestone, Ravenscar Shale, White Nab Ironstone and Bogmire Gill members.

their names have changed. The top part of the Lower Jurassic Series belongs to the Blea Wyke Sandstone Formation (Lias Group). This is conformably overlain by up to 12 m of the Dogger Formation, the lowest unit of the Middle Jurassic Series in Yorkshire, which is Aalenian in age. The Dogger is a marine facies and contains no plant remains. Where it is exposed on the foreshore to the south of Whitby, ammonites of the *opalinum* Zone have been found. Specimens from other sites have been referred to the *murchisonae* Zone, which suggests that the various elements of the Dogger span a considerable period of time (Cope *et al.*, 1980a).

The Hayburn (Saltwick) Formation (the 'Lower Deltaic Series' of earlier authors), which overlies the Dogger, consists of fluvio-deltaic deposits including channel sandstones and levée accumulations. They are predominantly sandstones with fossiliferous shales and poor quality coals. The flora is well known from Runswick Bay, the Whitby to Saltwick coast, Broughton Bank, Roseberry Topping and Hillhouse Nab. Subsequent flooding of the area by marine water from the open sea to the east led to the deposition of the Eller Beck Formation with its large fauna of bivalves.

The sediments of the succeeding Cloughton Formation ('Middle Deltaic Series' of earlier authors) have been described as coal-measures facies cut by channel sandstones (Cope *et al.*, 1980a). They have been referred to two members. The lower Sycarham Member consists of thick-bedded sandstones with fragmentary remains of plants. It is capped by marine deposits that have been referred to the Lebberston Member, although Cope *et al.* (1980a) renamed it the 'Cayton Bay Formation', and subdivided it into the Millepore Bed and Yons Nab Bed. Cope *et al.* (1980a) suggested that the Cloughton Formation should be restricted to the non-marine sandstones comprising the Sycarham and Gristhorpe Members. The beds of the Gristhorpe Member include sandstones, shales and the coals that were once worked in the area. Some of the lacustrine shales are very fossiliferous and include most of the famous coastal exposures south of Saltwick, such as the Gristhorpe beds at Cayton Bay, Hayburn Wyke and Cloughton Wyke. Extensive sheet sands/sandstones of crevasse-splay origin overlie the shales and are themselves channelled with sandstone infill.

The fourth marine transgression led to the limestone, sandstone and shale succession of the Scarborough Formation, which is the highest and best-developed marine sequence in the Bajocian strata. Different associations of marine faunas suggest a changing coastal environment from shallow marine to open-marine shelf and open marine conditions. This period of marine deposition was in turn succeeded by the last, mainly Bathonian, deltaic phase, represented by the Scalby Formation ('Upper Deltaic Series' of earlier authors). The problem is that, apart from the White Nab Member, which has yielded *Teloceras blagdeni* Subzone faunas, the rest of the Scarborough Formation is devoid of fossils that would permit correlation with the standard marine section. There is still some debate about the depositional environments represented; this is centred on the influence of saline tides. The Long Nab Member of the Scalby Formation contains current-bedded sandstones with many small sand-filled channels that are sometimes packed with the remains of tree trunks. The overlying silty micaceous shales contain locally abundant *Ginkgo* leaves, ferns and conifer cone scales that are easily seen at Scalby Ness.

Fox-Strangways (1892) suggested that the non-marine beds were estuarine in origin, but Kendall and Wroot (1924) and Black (1929) preferred a deltaic interpretation. Since then the debate has centred on deltaic versus coastal alluvial plain environments (Rawson and Wright, 1992).

Plant fossils are often valuable stratigraphical markers and have been used to great effect in the Carboniferous System. This is not the case in the Yorkshire Jurassic succession. Although floral changes do occur, there is nothing to compare with the fine zonation seen in the ammonites (Harris, 1952c).

YORKSHIRE JURASSIC VEGETATION

Bryophytes

Very few bryophytes are known from the Yorkshire Jurassic succession and all are thalloid. Harris (1961a) referred those with characters exclusive to the hepatic thalloid liverworts to four species of *Hepaticites*. Fossils that could be either algae or thalloid liverworts were placed in *Thallites*. No moss-like remains have ever been found. Harris concluded that the bryophytes are unsatisfying fossils because they fail to provide evidence that could lead to a better understanding of the inter-relationships of the living families.

Lycophytes (clubmosses)

Lycopodites falcatus is the only species of lycopsid shoot known from the Yorkshire Jurassic succession. The fossils have straight main branches (2-mm thick) with small leaves in pairs or whorls. The lateral branches (1-mm thick) fork unequally in one plane and have spreading lateral leaves and much smaller adpressed ventral and dorsal leaves. Several associated cones are known, but none has yielded spores.

A number of lycopsid megaspores have been described from bulk maceration of rock. Some probably came from lycopsids that grew at some distance from the swamps and pools where the spores were trapped, but others are likely to represent plants that inhabited these perennially wet places. Harris (1961a) referred them to 15 species of *Triletes*, but this megaspore genus is now regarded as being too broadly based to have any taxonomic value. All of the species have since been transferred to other genera that are based on more narrowly defined morphological characters, as follows: *Aneuletes patera*, *Bacutriletes corynactis*, *B. onodios*, *Echitriletes hispidus*, *Erlansonisporites sparassis*, *Horstisporites areolatus*, *H. casses*, *H. harrisii*, *H. kendalliae*, *Minerisporites richardsonii*, *M. volucris*, *Paxillitriletes phyllicus*, *Trilites candoris* and *T. murrayi*.

Sphenophytes (horsetails)

The horsetail, *Equisetum*, is sometimes found upright or rooted in the swampy sediment where it grew, but more often horsetail remains have been transported to the site of fossilization. The vast majority of the plants colonized either drier river banks or habitats further inland above the level of the water table. Fragments of the plants were either shed naturally or lost following death, while those growing in the lowlands were sometimes carried away after erosion and collapse of the river banks. Incorporation of horsetails into the accumulating sediments led to the fossiliferous plant beds that are found in over 500 localities throughout Yorkshire. Harris (1961a) recognized nine species that he deliberately referred to the living genus because he did not detect any recognizable morphological differences between them. Inevitably some deposits are richer in species than others, and it is these that have yielded the most information through recognition and association of separated parts from the plants of one species. *Equisetum columnare* is the most common, being abundant throughout much of the succession. Its cuticles are found in over half the successful bulk macerations of rock and many of the coal seams seem to be composed entirely of this one species.

Some larger stems have been included in the genera *Neocalamites* and *Calamites*, and whorls of small lanceolate leaves have been named as *Annulariopsis simpsonii*.

Pteridophytes (ferns)

Ferns are abundant and so regularly encountered in the Jurassic strata that they must have been the dominant herbs on land. However, Harris (1956a) commented that the number of recognized species has diminished as work has proceeded. In 1875, Phillips recorded 45 species in Yorkshire, but Seward (1900a) reduced this to 15. However, about 30 are now recognized, the additional species representing new discoveries that have been carefully worked on. Several other Jurassic floras have more ferns and the number of Yorkshire ferns also appears low compared with the gymnosperms. The latter comparison is misleading, however, because the records of gymnosperms are augmented by those of their cuticles obtained from bulk macerations. Ferns do not have cuticles so their presence can never be recorded in this way. As a result, there are over 500 localities for gymnosperms but only about 50 for ferns (Harris, 1961a).

The Marattiaceae, which was so common in the latter part of the Palaeozoic Era, is only represented by three species: *Angiopteris blackii*, *A. neglecta* and *Marattia anglica*. They are placed in genera of living ferns because no recognizable morphological differences between the modern and fossil ferns have been recognized at generic level.

Two families of ferns more or less maintained their position during the early part of the Mesozoic Era. These were the Matoniaceae (*Phlebopteris*, *Selenocarpus* and *Matonidium*) and Osmundaceae (*Todites* for fertile, and *Cladophlebis* for similar, sterile fragments; *Osmundopsis* for fertile pinnae with reduced pinnules). A reconstruction of a typical Jurassic

Figure 3.4 Reconstruction of a typical Jurassic fern of the family Osmundaceae with fronds of the *Todites*-type. The main plant has a trunk about 50 cm tall, giving off basal runners that form accessory plants. (Based on work on the Jurassic floras of Iran by Schweitzer and redrawn from Thomas and Spicer, 1987.)

osmundacean fern is shown in Figure 3.4.

One section of the Dipteridaceae (the Camptopteridae with *Dictyophyllum* and *Clathropteris*) rapidly declined almost to extinction, but the other section (Dipterideae with *Hausmannia*) was always present in small numbers. The Schizaeaceae had also declined, with only one species, *Klukia exilis*, represented. In great contrast, the Dicksoniaceae was described by Harris as 'surging in like an invader' by appearing during the Middle Jurassic Epoch in many parts of the world. The Dicksoniaceae is the largest family of Yorkshire Jurassic ferns and, of these, *Coniopteris hymenophylloides* is by far the most common. Both sections of the family (subfamilies Dicksonioideae and Thyrso-

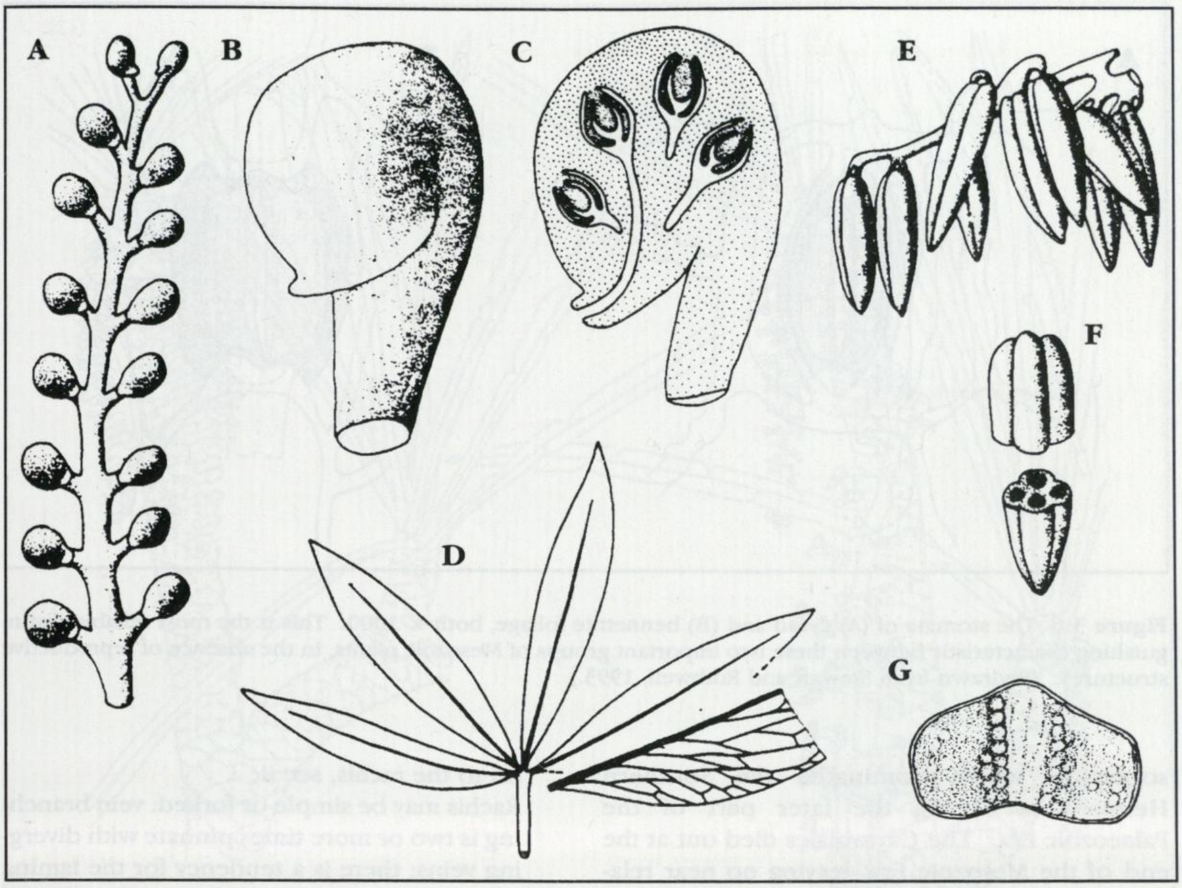


Figure 3.5 Parts of the plant that make up our concept of *Caytonia*. (A) A 5 mm axis with laterally attached fruits; (B) a close-up of one of the individual fruits; (C) section through a fruit showing ovules; (D) leaf with three to seven leaflets each up to 7 cm long; (E) male reproductive branch; (F) a single pollen-organ (*c.* 1 cm long) consisting of four fused pollen-sacs; (G) a pollen grain, × 1000. This illustration is largely based on the work of T.M. Harris on the Yorkshire Jurassic flora. (Redrawn from Thomas and Spicer, 1987.)

pteridoideae) are known from the Jurassic System onwards although their proportions become reversed. There are about 40 living species in the Dicksonioideae and only one in the Thyrsopterioideae but in the Yorkshire flora the numbers are two (in *Dicksonia*) and nine (in *Coniopteris*, *Kylikipteris* and *Eboracia*) respectively.

Aspidistes thomasii was included in the Aspideae by Harris (1961a) because a protective flap (indusium) covers its sporangial masses (sori) as in many modern ferns.

Caytoniaceae

This isolated family consists of no more than one type of plant that is represented in the fossil record by isolated organs (Figure 3.5). The leaves, called *Sagenopteris*, bear two pairs of leaflets on petioles. The fruits, called *Caytonia*, were borne in nearly opposite pairs on short axes. They were fleshy and edible, and their remains have been found in coprolites. Thomas (1925, 1934) thought they were allied to the angiosperms but Harris (1940, 1960) later showed them to be gymnospermous fruits containing several seeds. The pollen organs, called *Caytonanthus*, had pollen sacs terminally attached to forked branchlets on a main rachis.

Dispersed pollen similar to that in *Caytonanthus* has been found inside *Caytonia* fruits. This intimate association of pollen (known as *Vitreisporites*) and fruit is supported by further regular occurrences of fruits and leaves, which led Harris (1964) to recognize three groupings representing the remains of three different plant species. There is, however, no reliable reconstruction of the whole plants although they were most probably shrubs.

Caytonia probably evolved from the glos-

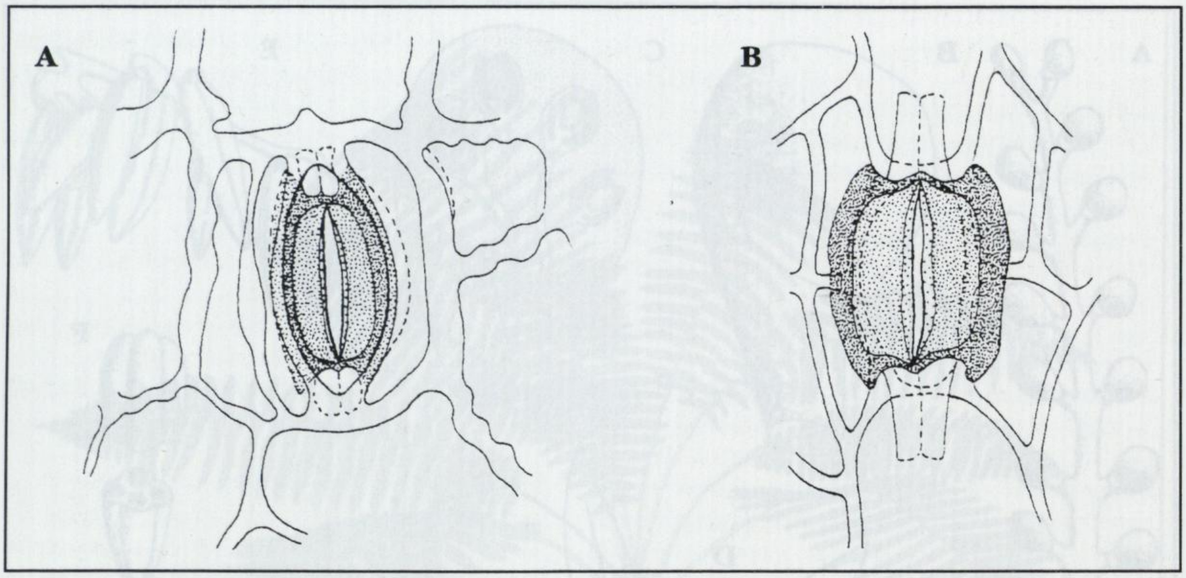


Figure 3.6 The stomata of (A) cycad and (B) bennettite foliage, both × 1000. This is the most reliable distinguishing characteristic between these two important groups of Mesozoic plants, in the absence of reproductive structures. (Redrawn from Stewart and Rothwell, 1993.)

sopterids, which dominated the Southern Hemisphere during the later part of the Palaeozoic Era. The Caytoniales died out at the end of the Mesozoic Era, leaving no near relatives.

Cycadales

Many isolated leaves and fragments of leaves found throughout the deposits of the Mesozoic Era were at one time thought to be the remains of cycads. Today this is a relatively rare group of mainly tropical plants; it includes *Cycas*, *Zamia*, *Macrozamia*, *Encephalartos* and a few other, less common genera. They have a succulent, usually unbranched, trunk which gives the plants the appearance of a small palm tree. Some species are rather different in appearance, having a small tuberiferous underground stem.

We now know that there are in fact three groups of Jurassic plants with leaves of this type: cycads, bennettites and a heterogeneous group informally known as pteridosperms. They can be separated using the following key, although it must be stressed that this is merely a guide because there are doubtless exceptions.

i. Rachis never forked; vein branching is simply pinnate and the veins are nearly parallel; lamina of pinnae never strongly decurrent on to the rachis, see ii;
Rachis may be simple or forked: vein branching is two or more times pinnate with diverging veins; there is a tendency for the lamina of a pinna to be strongly decurrent on to the rachis = **pteridosperms**;

ii. Stomata haplocheilic (Figure 3.6A) = **cycads**;.
Stomata syndetocheilic (Figure 3.6B) = **bennettites.**

Of the genera of cycad-like leaves known from the Yorkshire Jurassic succession, *Nilssonia*, *Ctenis* and *Paracycas* are really cycads. A good many genera of other isolated organs can, however, be classified on more or less good evidence as cycads. A number of associations of separate organs permit some of them to be linked together. Male and female organs are known for *Nilssonia* and male organs for *Pseudoctenis*. However, perhaps the best example of a reconstructed cycad is the plant usually referred to as *Beania* (Figure 3.7). Unlike living cycads, it had branched stems, with each branch terminating in a cluster of elongated, very irregularly divided leaves called *Nilssonia tenuinervis*. Both male and female cones in living cycads tend to be stiff structures that stand proud of the crown of leaves, but in *Beania* they hung from the crowns rather like catkins (Harris, 1961b). The male

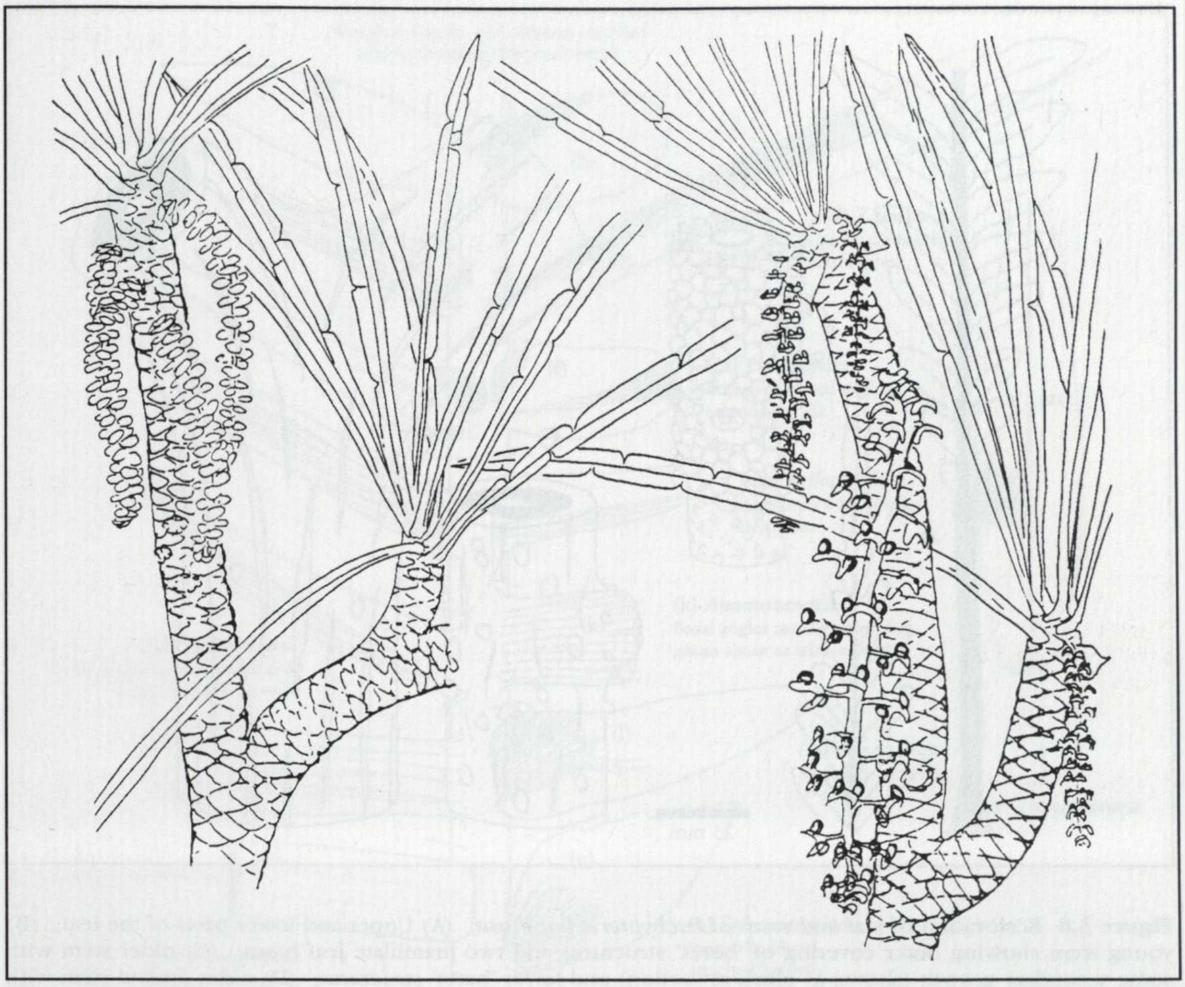


Figure 3.7 Classic reconstruction of a Jurassic cycad, the *Beania* tree. The branch on the left bears male cones and the branch on the right bears female cones (about 10 cm long). (Redrawn from Harris, 1961.)

organs are called *Androstrobus wonnacottii* and the female organs *Beania mamayi* from which the whole plant gets its name. Harris (1961b) suggested, on the basis of the local abundance of *Nilssonia* leaves, that *Beania* must have been a dominant tree of the swamps or river banks.

Pseudoctenis lanei is associated with the massive male cone *Androstrobus prisma* in three localities in Yorkshire, strongly suggesting to Harris (1961b) that they belonged to the same parent plant. Later he referred to the possibility of *Androstrobus szei* having been borne by a plant with *Ctenis sulcicaulis* leaves (Harris, 1964). This was supported by Hill (1990) who, as a result of further collecting from the Gristhorpe Bed, found both of these species in intimate association. However, the regular anastomosing venation of *Ctenis* separates it from the other cycad leaves. *Androstrobus szei* is also unusual in having fibrous microsporophylls and *Ginkgo*-like sculpture on its pollen, which led Hill (1990) to suggest that a new family is needed for *Ctenis sulcicaulis* and *Androstrobus szei*.

Pteridosperms

The informal group known as the Pteridosperms includes the foliage genera *Ctenozamites*, *Stenopteris* and *Pachypteris* (e.g. Figure 3.8). A little is known about the reproductive methods of the pteridosperms. For example, the two species of *Pachypteris* have leathery fern-like leaves and their pollen-producing organ is thought to be *Pteroma*, which has simple pinnate structures about 3 cm long, its short pinna terminating in fertile heads. Because of this,

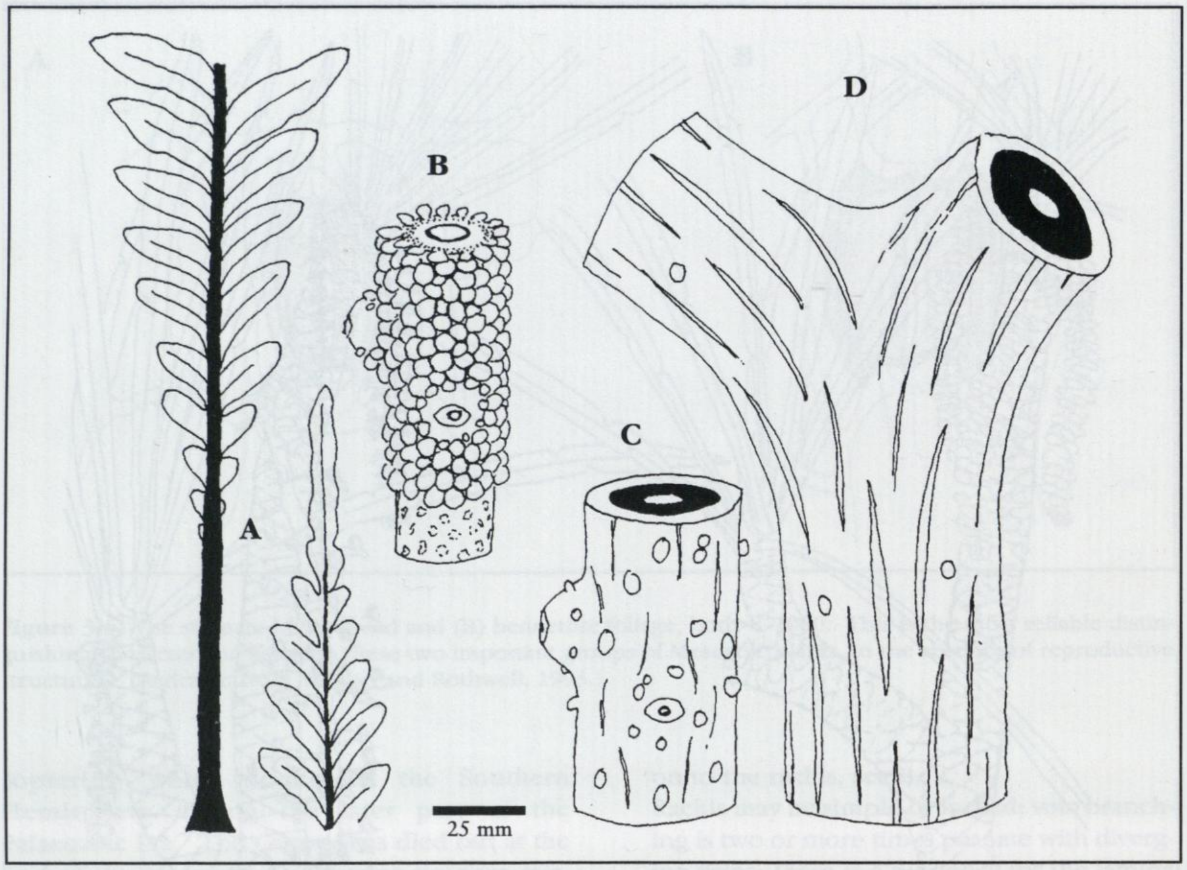


Figure 3.8 Restoration of leaf and stem of *Pachypteris papillosa*. (A) Upper and lower parts of the leaf; (B) young stem showing outer covering of 'beret' structures and two mamillate leaf bases; (C) older stem with some secondary growth (shown as black in section) and fewer 'beret' structures; (D) older, forked stem with most 'beret' structures now missing. (Redrawn from Harris, 1983.)

Pachypteris is now placed in the Corystospermaceae, a family better known from the lower Mesozoic deposits of southern high latitudes, such as South Africa and Australia.

Bennettitales

Many cycad-like leaves found in the Yorkshire Jurassic succession, including *Anomozamites*, *Dictyozamites*, *Nilssoniopteris*, *Pterophyllum*, *Ptilophyllum*, *Otozamites* and *Zamites*, in fact belong to the bennettites (Figure 3.9). Within these genera, division into species often relies on epidermal studies. However, although the combination of visual and microscopic characters permits satisfactory species determinations to be made, the differences are small and they form a nearly continuous sequence. The few remains of stems believed to be bennettitalean are included in the genus *Conites*.

Bennettitalean reproductive organs are often called flowers because of their superficial resemblance to angiosperm inflorescences. They cause great problems because hardly any two of them are known equally well and in comparable ways (Harris, 1969). *Williamsonia* Carruthers is a genus of female 'flowers'; bisexual 'flowers' are referred to *Williamsoniella* Thomas and male 'flowers' to *Weltrichia* Braun (Figure 3.10). All simple scale leaves with bennettitalean stomata are included in *Cycadolepis* (Harris, 1969). All female organs that are not fully known, and cannot be included with certainty in *Williamsonia* or *Williamsoniella*, are referred to *Bennetticarpus*.

The plants themselves varied considerably in form and we believe that there is sufficient evidence to recognize two families within the group. The Williamsoniaceae consisted of shrubs with slender, profusely branched stems

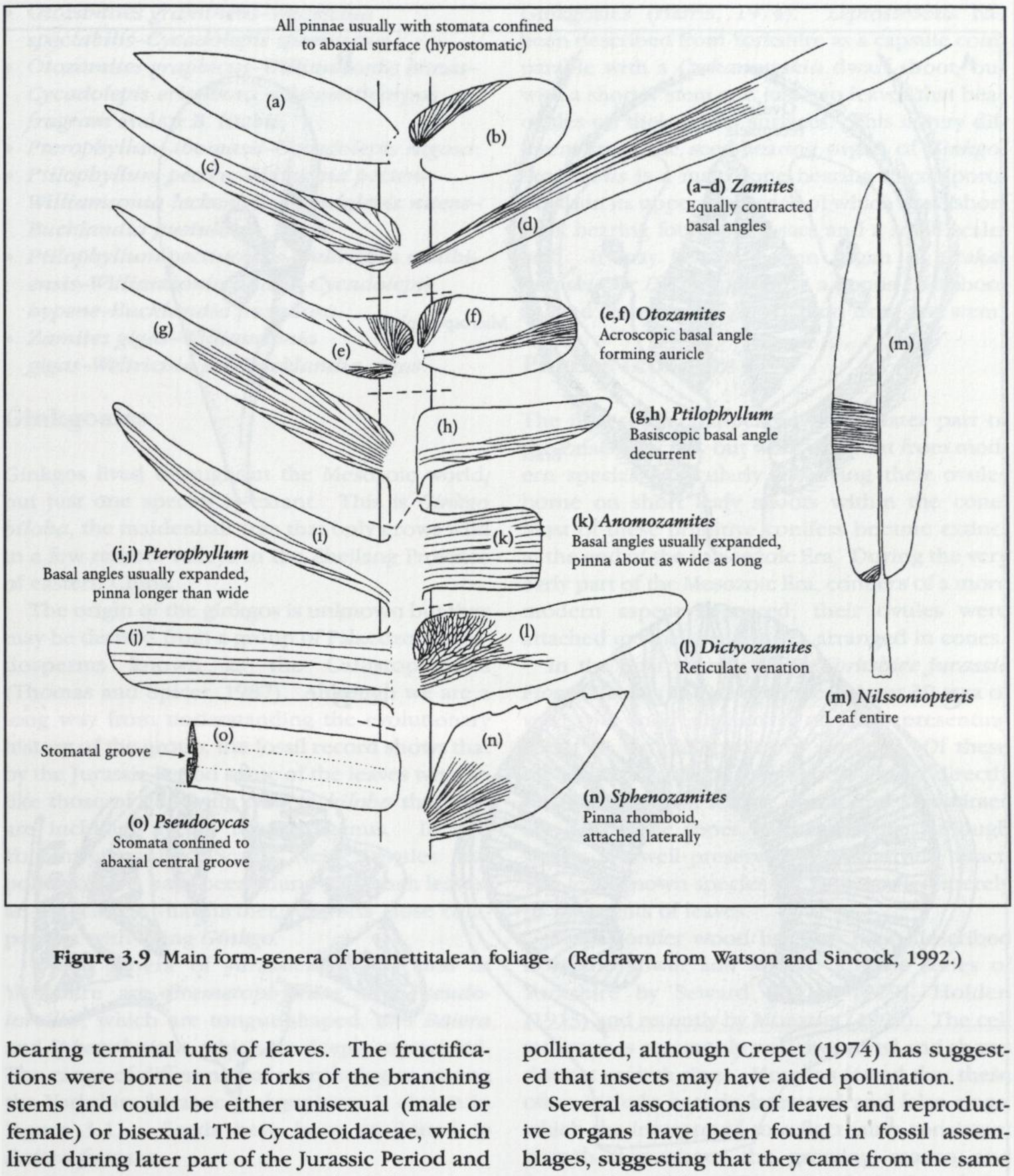


Figure 3.9 Main form-genera of bennettitalean foliage. (Redrawn from Watson and Sincock, 1992.)

bearing terminal tufts of leaves. The fructifications were borne in the forks of the branching stems and could be either unisexual (male or female) or bisexual. The Cycadeoidaceae, which lived during later part of the Jurassic Period and the Cretaceous Period, consisted of plants having robust, unbranched trunks covered in the scaly bases of lost leaves, and a terminal crown of leaves. Some had tall trunks, others were short and stockier and must have resembled large pineapple fruit. The reproductive organs are usually referred to as 'cones', although they are sometimes called 'flowers'. They grew in the axils of the leaves and, initially at least, were sunk deep within the leaf bases and scales. The generally accepted idea is that they were self-pollinated, although Crepet (1974) has suggested that insects may have aided pollination.

Several associations of leaves and reproductive organs have been found in fossil assemblages, suggesting that they came from the same parent plant. These are as follows:

- *Anomozamites nilssonii–Bennetticarpus diodon–Cycadolepis stenopus*;
- *Nilssoniopteris major–Williamsoniella papillosa*;
- *Nilssoniopteris vittata–Williamsoniella coronata*;
- *Otozamites beanii–Williamsonia himas–Weltrichia setosa–Cycadolepis eriophous*;
- *Otozamites falsus–Cycadolepis pelecus*;

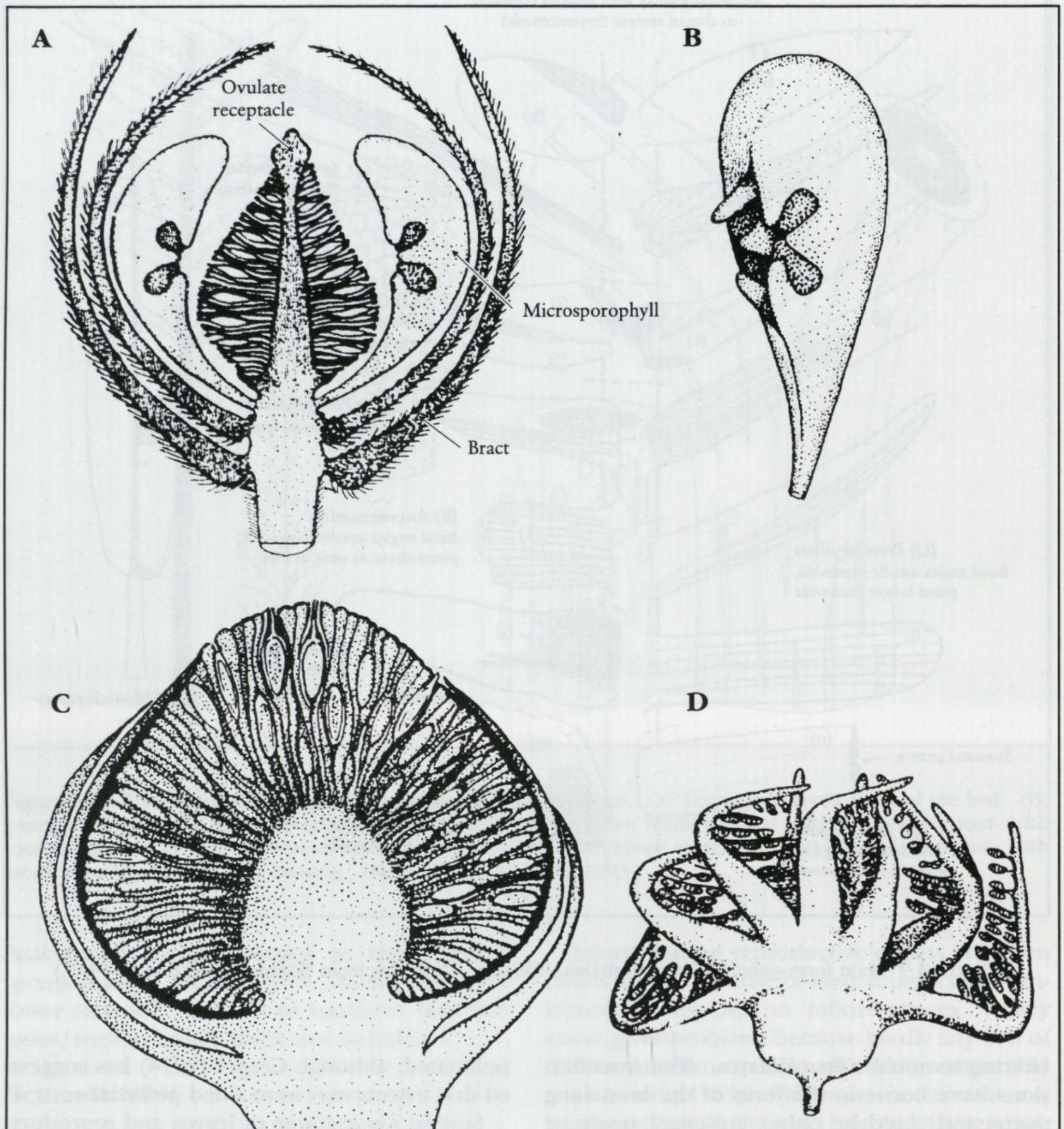


Figure 3.10 Reproductive structures of the bennettites. (A) Section through the bisexual flower *Williamsoniella coronata*, showing ovulate receptacle in the centre, surrounded by pollen-bearing organs, which in turn are surrounded by bracts; × 3. (B) Enlarged pollen-bearing organ from the same flower; × 5. (C) A section through the female flower *Williamsonia harrisiana*, showing a central ovulate receptacle surrounded by bracts; × 3. (D) Male flower, *Weltrichia spectabilis*, about natural size, showing cup-shaped arrangement of pollen-bearing structures. The *Williamsoniella* and *Weltrichia* are based on fossils from the Yorkshire Jurassic succession, the *Williamsonia* on fossils from the Rajmahal Hills in India. (Redrawn from Stewart and Rothwell, 1993.)

- *Otozamites gramineus–Weltrichia spectabilis–Cycadolepis spheniscus*;
- *Otozamites graphicus–Williamsonia himas–Cycadolepis eriophous – Bennetticarpus fragram* and/or *B. litchii*;
- *Pterophyllum thomasii–Cycadolepis rugosa*;
- *Ptilophyllum pecten–Weltrichia pecten–Williamsonia leckenbyi–Cycadolepis nitens–Bucklandia pustulosa*;
- *Ptilophyllum pectinoides–Weltrichia whitbiensis–Williamsonia hildae–Cycadolepis hypene–Bucklandia pustulosa*.
- *Zamites gigas–Williamsonia gigas–Weltrichia sol–Bucklandia gigas*.

Ginkgoales

Ginkgos lived throughout the Mesozoic world, but just one species is extant. This is *Ginkgo biloba*, the maidenhair tree that only grows wild in a few remote valleys in the Zhejiang Province of eastern China.

The origin of the ginkgos is unknown but they may be derived from a group of Palaeozoic pteridosperms known as the Callistophytales (Thomas and Spicer, 1987). Although we are a long way from understanding the evolutionary history of the group, the fossil record shows that by the Jurassic Period some of the leaves were so like those of the living *Ginkgo biloba* that they are included in the modern genus. In one Yorkshire locality (Scalby Ness), ovules and pollen organs have been found with such leaves, an association that further supports close comparison with living *Ginkgo*.

Other genera of Jurassic leaves found in Yorkshire are *Eremetophyllum* and *Pseudotorellia*, which are tongue-shaped, and *Baiera* and *Sphenobaiera*, which are deeply segmented. The range of different leaf morphologies among the Yorkshire Jurassic ginkgophytes is shown in Figure 3.11. Seeds have been attributed to *Baiera furcata*.

Czekanowskiales

The species included in this order have leaves that were borne in limited numbers on short shoots surrounded by scale leaves. The foliage leaves are either simple or linear (*Solonites*) or consist of a fan-shaped system of slender, forking segments (*Czekanowskia* and *Sphenarion*).

Until reproductive organs were found, *Czekanowskia* was confidently placed in the Ginkgoales (Harris, 1974). *Leptostrobus* has been described from Yorkshire as a capsule comparable with a *Czekanowskia* dwarf shoot, but with a shorter stem and just two leaves that bear ovules on their upper surfaces. This is very different from the seed-bearing organ of *Ginkgo*. *Ixostrobus* is a male cone bearing microsporophylls in its upper part, each of which has a short stalk bearing four pollen sacs and a small scale-leaf. It may be the pollen organ of *Czekanowskia* or *Desmiophyllum*, a genus of ribbon-shaped leaves found in isolation from any stem.

Pinales (conifers)

The first conifers appeared in the later part of the Palaeozoic Era, but were different from modern species particularly in having their ovules borne on short leafy shoots within the cone. Most of these primitive conifers became extinct at the end of the Palaeozoic Era. During the very early part of the Mesozoic Era, conifers of a more modern aspect appeared; their ovules were attached to small seed-scales arranged in cones.

In the final volume of his *Yorkshire Jurassic Flora*, Harris (1979a) described about 30 taxa of vegetative and reproductive organs representing about 23 natural species of conifers. Of these the best known have leafy shoots linked directly or indirectly with female cones and sometimes also with male cones. Other shoots, although sterile, are well preserved and relatively intact. The least-known species are represented merely by fragments of leaves.

Fossil conifer wood has also been described from the Lower and Middle Jurassic series of Yorkshire by Seward (1904, 1919), Holden (1913) and recently by Morgans (1999). The cell structure is commonly well preserved and shows distinct growth rings. Morgans found that these often include narrow latewood and false rings, which she interpreted to reflect fairly consistent growth throughout the growing season and from year to year. Water supply is thought to have been the main limiting factor affecting growth. It was probably more restricted during Bathonian times than earlier in the Jurassic Period because wood collected from the Scalby Formation shows a transition towards narrower rings of more variable width, proportionally wider latewood and more false rings.

Harris referred the conifer remains in the Yorkshire Jurassic flora to eight families, basing his definite attributions on evidence of

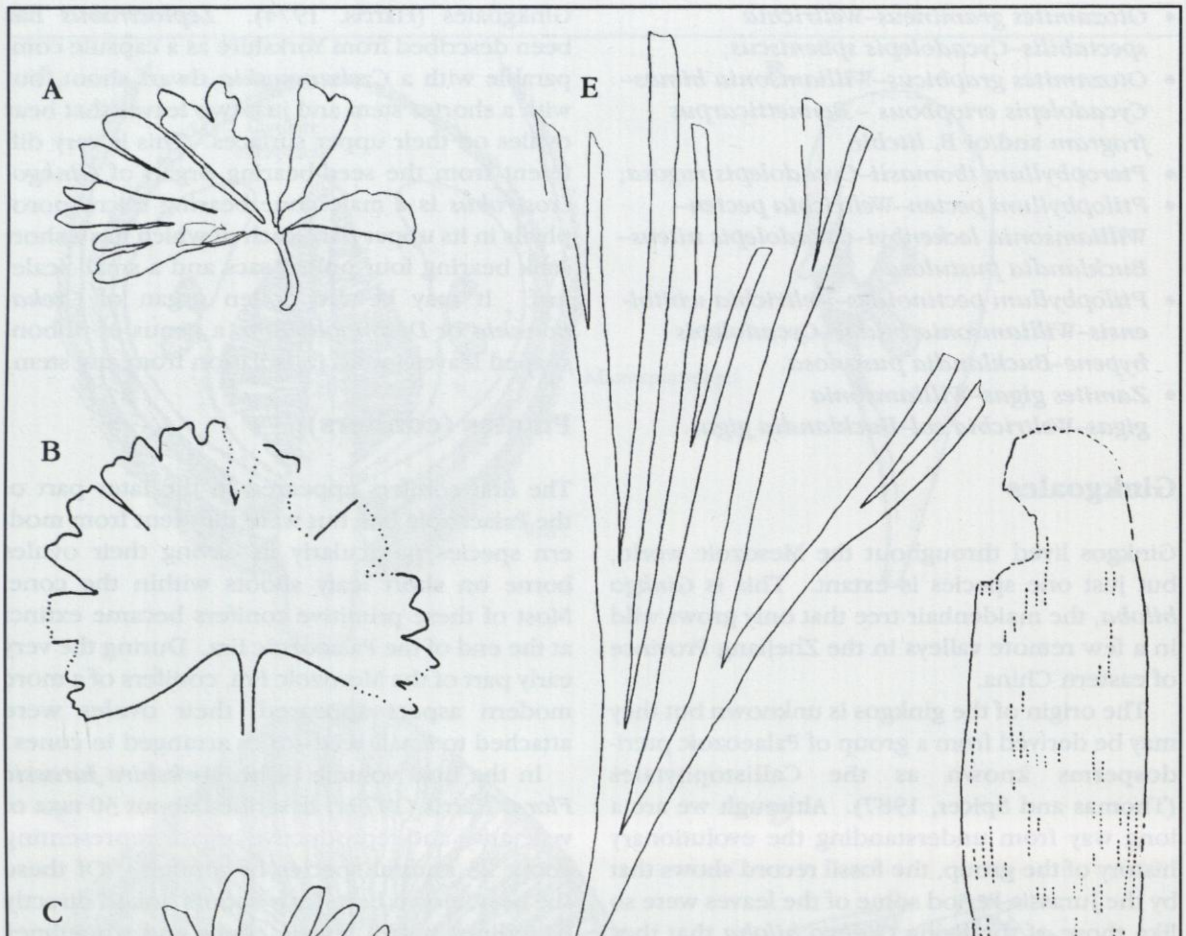


Figure 3.11 Range of different ginkgophyte leaves found in the Yorkshire Jurassic floras, all about natural size. (A) *Ginkgo huttonii*; (B) *G. digitata*; (C) *G.* cf. *sibirica*; (D) *Baiera furcata*; (E) *Sphenobiaera longifolia*; (F) *Eretmophyllum whitbiensis*. (Redrawn from Harris *et al.*, 1974.)

reproductive organs and his tentative ones on cuticle characters. He also recorded specimens of *Bilsdalea dura*, whose family affinities could not be determined. Morgans (1999) identified a ninth family based on wood remains.

Araucariaceae

Today this family is restricted to the Southern Hemisphere. It includes the monkey puzzle and the Norfolk Island Pine. In the Mesozoic Era, however, it had a worldwide distribution. In the Yorkshire Jurassic flora, it is represented by *Brachyphyllum mamillare* with its female cone *Araucaria phillipsii*. Morgans (1999) also reported the araucariacean wood *Araucarioxylon lindlei*.

Cephalotaxaceae

This family has a very limited fossil record, and today all six living species of *Cephalotaxus* are restricted to eastern Asia. The cones are very unusual in that only one ovule develops, forming a large olive-like seed with a stony layer surrounded by an outer fleshy one. There is just one species in the Yorkshire Jurassic succession, *Elatocladus zamioides*.

Cheirolepidiaceae

Harris (1979a) referred to this family as the Hirmeriellaceae but this has now been superseded by Cheirolepidiaceae. It was perhaps the most successful conifer family in the Mesozoic Era although it became extinct at the end of the Cretaceous Period. In Yorkshire, it is represented by *Pagiophyllum* (*Hirmeriella*) *kurii*, *P. (H.) masculosum* and the shoots *Brachyphyllum crucis* with their so-far unnamed male cones. Also possibly belonging here are *Brachyphyllum ardenicum*, *Genitzia rigida*, *Pagiophyllum insigne* and *P. ordinatum*.

Pinaceae

Today representatives of the Pinaceae are the most common conifers in the Northern Hemisphere. They include pines, larches and cedars. For many years, the fossil record of the family was thought to extend back to the Late Triassic Epoch but most of these early records are now thought to be spurious (Millar, 1998). Harris (1979a) suggested that the Yorkshire Jurassic fossil *Pityocladus scarburgensis* and its probable female cone scales, *Schizolepis liasokeuperanus*, might belong to the Pinaceae, but he also noted several differences from living members of the family. Morgans also reported species of the wood genera *Cedroxylon* (recorded as *Cedroxylon* spp.) that bear some similarity to the Pinaceae.

Podocarpaceae

The Podocarpaceae is regarded by many botanists as the most primitive living conifer family and it may be significant that the oldest known examples are Early Triassic in age, hence older than any known example of other conifer families with living representatives. The female cone *Scarburgia blackii* (and its probable male cone *Pityanthus scalbiensis*) and *S. hillii* belong here.

Podozamitaceae

The Podozamitaceae is a family of Mesozoic conifers with cycad-like leaves, and includes *Lindleycladus lanceolatus* in Yorkshire.

Taxaceae

The earliest member of this family was found in the Lower Jurassic Series of Sweden; today it includes the yew. Some botanists separate this group from the conifers because, although the foliage is conifer-like, the ovules are quite different, being borne singly at the ends of shoots and partly surrounded by a fleshy fruit-like structure called an aril. In Yorkshire, the family includes *Marskea jurassica*, and possibly *Elatocladus punctatus*, *E. ramosus* (which might be linked to the ovuliferous dwarf shoot *Poteridion hallei*), *Torreya gracilis* and *T. valida*.

Taxodiaceae

Today the Taxodiaceae has a scattered distribution, with each of the seven genera restricted to a particular continent. It includes the Californian redwoods and the dawn redwood, *Metasequoia*, which was described as a fossil before being found living in a remote part of China. In Yorkshire, *Elatides williamsonii*, *E. thomasii* and possibly *Pagiophyllum fragilis* and *Elatocladus laxus* are thought to belong here. Morgans (1999) also reported taxodiacean wood

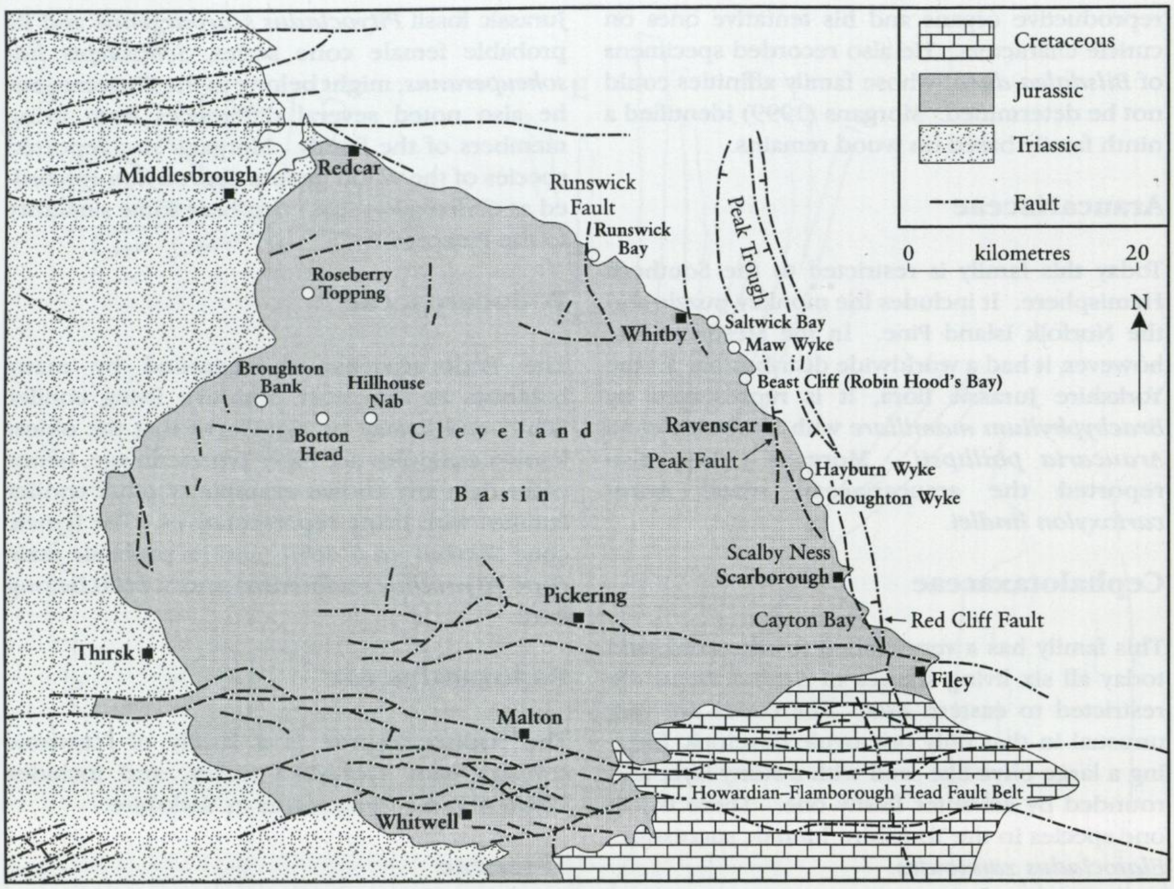


Figure 3.12 The Cleveland Basin, showing the position of the GCR sites for the Yorkshire Jurassic floras. (After Rawson and Wright, 1995.)

of the genera *Taxodioxylon* and *Xenoxylon*.

Cupressaceae

Morgans (1999) reported the fossil wood genus *Cupressinoxylon*, which probably belongs to this family.

PALAEOBOTANICAL SITES IN THE YORKSHIRE JURASSIC SUCCESSION

Any study of Yorkshire Jurassic plants soon reveals that there are many professionally collected specimens with no labels or, even worse, with incorrect labels. There have also been comparatively few accounts that list species by localities. Thomas (1913) and Black (1929) were the first. Spicer and Hill (1979) attempted to quantify data from the Broughton Bank locality using 'Principal Components Analysis'. The new field guide to Yorkshire Jurassic plant fossils gives lists for only four sites. Even in his monograph, Harris does not always document all the known sites for many species. Therefore, in order to provide species lists here it proved necessary to look at all the original papers, the field notes of Harris and Hill (archived in the Natural History Museum, London), and the collections in the Natural History Museum and the National Museums and Galleries of Wales. Even these lists (Table 3.1) should not be regarded as complete, because further collecting will inevitably yield new records or even new species.

Although Harris never produced floral lists for the any of the large number of sites from which he collected, he summarized his views on the distribution of plants within the succession (Harris, 1952a). The flora is distributed more or less evenly over the whole area although the composition of individual plant beds may differ quite considerably. Floral change is commonly attributable to fluctuation rather than to 'sufficiently final' events that may form the basis of a zonation. Harris recognized five ranges of species, and van Konijnenburg-van Cittert (1971) added a sixth.

1. Species ranging through the whole succession with no striking change in abundance, e.g. *Brachyphyllum mamillare* and *Coniopteris hymenophylloides*.
2. Species common in the lower three formations but absent in the Scalby Formation, e.g. *Equisetum columnare*.
3. Species confined to the 'Lower Deltaic Series' (= Saltwick Formation), e.g. *Spenobaiera pecten*.
4. Species common in both the 'Lower and Upper Deltaic Series' (= Saltwick and Scalby Formations) but rare in between, e.g. *Baiera furcatas*, *B. gracilis*, *Pachypteris lanceolata*, *Ptilophyllum pectinoides* and *Zamites gigas*. Some, such as *Stenopteris nana* and *Pseudoctenis oleosa*, are rare in the Lower and Upper Deltaics and so far unknown in between.
5. Species more or less abundant in the 'middle divisions' (Sycarham–Gristhorpe Members), but rare or absent below and above, e.g. *Ptilophyllum pecten*, *Weltrichia pecten* and *Williamsonia leckenbyi*.
6. Species characteristic of the Scalby Formation that are rare or absent from the lower beds, e.g. *Czekanowskia blackii* and *Ginkgo huttonii*.

Harris' view was that the entire flora should be treated as a single entity. He identified five types of fossiliferous beds although he stressed that they intergrade (Harris, 1952a):

1. Autochthonous beds where plants are preserved in the position of growth. The vast majority are of stands of *Equisetum*, sometimes with vertical sandstone casts of the stems formed when the swampy places in which they grew were suddenly overwhelmed by sand through the diversion of a river (e.g. Beast Cliff). More frequently they consist of beds of truncated roots, the upper parts having been eroded by river action (e.g. Cloughton Wyke, Gristhorpe). Many of the very thin coal seams probably represent the accumulated remains of *Equisetum* stems in a marsh because they yield cuticles attributable to the genus by the million. The thicker coal seams differ in being formed of logs of coniferous trees, a varying amount of *Equisetum* and leaves. Such deposits were allochthonous although the plant material may not have been transported far.
2. Lagoonal and sluggish river channel beds in which the prevailing sediment is fine mud (e.g. Gristhorpe and Broughton Bank).
3. River channel beds that have a higher proportion of water-worn plants (e.g. Whitby Long Bight plant bed).
4. Drifted accumulations in which the prevailing sediment is sand and all but the smallest plants are severely water-worn (e.g. Black's drifted plant bed at Scalby Wyke).
5. Redeposited plant beds where the characteristic fossils are tough cuticles that were often already partially macerated at the time of deposition. Reworking would have only involved plants from slightly older sediments because all of the erosion channels in the Middle Jurassic succession are shallow.

Based partly on these factors, 12 sites have been chosen from the 500 or so known, for several reasons. All yield good assemblages of a reasonably large number of species, and all are sufficiently different from each other to warrant inclusion. They also incorporate sites from the entire known stratigraphical range of plant fossils in the region. Some, such as Scalby Ness, are classic sites from which fossil plants have been collected since the beginning of the 19th century. Others, such as Hillhouse Nab, have only been known for a comparatively short time. All yield compression fossils that often give excellent cuticles, spores and pollen. Three dimensionally preserved specimens are rarely encountered, but have been found recently in the Runswick Bay locality. The general location of these sites in the Cleveland Basin is shown in Figure 3.12.

WHITBY–SALTWICK (NZ 901 115–NZ 916 109)

Introduction

The cliffs south of Whitby have been the focus of palaeobotanical research for many years, and have yielded some of the best-preserved fossils of the Yorkshire Jurassic strata. Many of the best

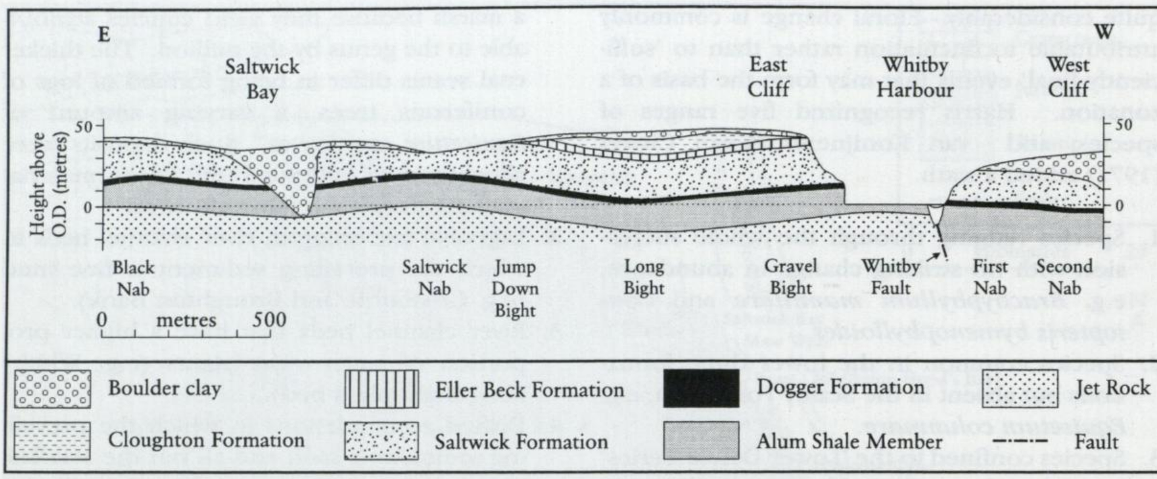


Figure 3.13 Schematic view of the cliffs between Whitby and Saltwick, showing the main stratigraphical units exposed. (Redrawn from Rawson and Wright, 1992.)

museum specimens of Middle Jurassic plant fossils originated from these cliffs. The specimens came from a lens within the channel-fill sandstone of the Saltwick Formation. Of the numerous species recorded, particularly noteworthy are the spectacular examples of bennettitalean reproductive organs such as those of *Williamsonia* and *Weltrichia*.

The earliest illustrated records are those of Young and Bird (1822, 1828). The specimens listed by Brongniart (1828a) as coming from Whitby almost certainly originated here, and Phillips (1829, 1835, 1875), Lindley and Hutton (1837), Yates (1855), Carruthers (1870a), Nathorst (1880) and Seward (1897a) described and figured plant fossils from this succession. Seward (1900a) reviewed the 19th century palaeobotany of the Whitby Plant Beds. According to Harris (1961a), the only Yorkshire Jurassic plant fossil Seward ever collected came from here! Many of the specimens used by Nathorst (1909, 1911) in his revision of the structure of bennettitalean flowers were from these beds, as were the ginkgoalen foliage described by Thomas (1913) and the equisetalean stems described by Erdtman (1921). More recently, the Whitby plant fossils were included in Harris' revision of all Yorkshire Jurassic floras (Harris 1941a, 1945b, 1946a–c, 1948, 1949a, 1951, 1952a, 1953), which culminated in his five monographs (1961a, 1964, 1969, 1979a; Harris *et al.*, 1974). Kendall (1948, 1952), one of Harris' students, also published on a number of conifers from Whitby, and specimens from there have been used to study the in-situ spores recovered from fern sporangia (van Konijnenburg-van Cittert, 1978).

Description

Stratigraphy

The stratigraphy of the Middle Jurassic strata near Whitby has been summarized by Rawson

Table 3.2 Location of in-situ plant beds identified by T.M. Harris (in manuscript) along the cliffs between Whitby and Saltwick.

Whitby Haggerlyth	54° 29' 25", 0° 38' 28"
Whitby Jumpdown Bight	54° 29' 18", 0° 35' 30"
Whitby Long Bight Plant Bed	54° 29' 19", 0° 36' 0"
Whitby Long Bight fallen blocks	
Whitby Rail Hole Bight	
Whitby Spittal Beck just below G.L.	54° 28' 32", 0° 35' 50"
Saltwick *Equisetum* and *Coniopteris* Beds	54° 29' 0", 0° 35' 6"
Saltwick *Matonidium* Bed	54° 28' 59", 0° 34' 52"
Saltwick Waterfall Bed	54° 28' 59", 0° 34' 52"
Saltwick *E. laterale* Bed above Waterfall Bed	54° 29' 11", 0° 35' 52"

Figure 3.14 *Solonites vimineus* (Phillips) Harris. These very long unbranched leaves are typically 150–200 mm long and usually less than 1 mm wide. The leaves often appear in spreading out masses, as shown here, and occasionally are found in bundles of 10–15 attached to small shoots that are covered in scales. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.14865, Saltwick Formation, south of Whitby, × 0.8. (Photo: J.H. A. van Konijnenburg-van Cittert.)

and Wright (1992, 1995), although neither provides a detailed stratigraphical section. A schematic view of the cliffs is shown in Figure 3.13. The main exposure consists of fine-grained sandstones of the Saltwick Formation, which cut down into mudstones of the Dogger Formation. In his unpublished notebooks, Harris identified ten places at this site from which he collected plant fossils (see Table 3.2). The classic Whitby Plant Bed, which has yielded most of the museum-quality material, is towards the base of the Saltwick Formation and is seen best at Long Bight. Higher in the section there is also a bed rich in bennettitalean remains; this is known as the *Zamites* Bed at Jump Down Bight.

Palaeobotany

Over 90 species have been reported from Whitby (Table 3.1, Figure 3.14). The numerous records of species from West Cliff, High Whitby or near the Fog Signal are not listed here because these parts of the coast are not within the GCR site. Sometimes, however, locality details are not precise enough to be certain whether the specimens were collected from within the site. In these cases the species records have been included.

The site is particularly rich in ferns, bennettites and conifers (16, 24 and 18 recorded species, respectively). There is also an abundance of equisetalean remains, especially of the stems *Neocalamites nathorstii*. In contrast, there are relatively few species of cycads and pteridosperms and only one of *Caytonia*.

Nineteen species were based on type specimens from here, mainly from the Long Bight exposure or from loose blocks on the beach. These are *Annulariopsis simpsonii*, *Neocalamites nathorstii*, *Nilssonia thomasii*, *Pseudoctenis herriesii*, *Stenopteris nana*, *Cycadolepis hypene*, *C. thysanota*, *Otozamites anglica*, *O. gramineus*, *O. simpsonii*, *Weltrichia setosa*, *W. sol*, *W. spectabilis*, *W. whitbiensis*, *Williamsoniella papillosa*, *Eremetophyllum whitbiensis*, *Ginkgo whitbiensis*, *Czekanoswkia furcula* and *Inxostrobus whitbiensis*.

Interpretation

The fact that so many type specimens are from this section of coast is partly because the plant assemblage is especially diverse and partly because collecting has been undertaken here from the earliest days of palaeobotanical study. Only one other Yorkshire Jurassic site included in the GCR has more species, namely the Gristhorpe Bed at Red Cliff.

Although much of the material that has been found originated from fallen blocks, it has been possible to use evidence of association to relate separate organs to the same parent plant. The linking of two groups of bennetitalean organs in this material has been particularly important. The classic example was based on the materials in the *Zamites* Bed at Whitby, where the fronds *Zamites gigas* are closely associated with the female flower *Williamsonia gigas* and the male flower *Weltrichia sol*. It was recognized from an early date that they almost certainly belonged to the same plant (Young and Bird, 1822; Yates, 1855; Carruthers, 1870b; Seward, 1897a; Nathorst, 1909, 1911). Another well-documented example in the main Whitby Plant Bed is the association noted by Nathorst (1909) of the fronds *Ptilophyllum pectinoides* (Nathorst identified them in error as *P. pecten* – see Harris, 1969) and the female flowers *Williamsonia hildae*. Harris (1969) also linked to the same plant the male cone *Weltrichia whitbiensis* and the scale leaves *Cycadolepis hypene* on the combined evidence of association and similarity of cuticles. Cridland (1957) and Harris (1969) reported the close association of the pollen-producing *Williamsoniella papillosa* (here in its type locality), a hairy scale leaf identified as *Cycadolepis* sp., and the leaf *Nilssoniopteris major*, all of which are now regarded as having belonged to the same plant. Other proposed connections are between the frond *Otozamites beanii* and the male flower *Weltrichia setosa*; and between the frond *O. gramineus*, the male flower *W. spectabilis* and the scale leaves *Cycadolepis spheniscus* (Harris, 1969). Hence Whitby has played a central role in the development of the taxonomic concept of the Bennettitales, which is one of the most important groups of Mesozoic plants throughout the world. It is anticipated that further examination of associated organs in the fallen blocks will yield additional evidence of botanical affinities.

Whitby is the only known locality for unequivocal specimens of another type of bennettitalean male flower, *Weltrichia setosa*. Harris (1969) reported a fragment from Cloughton Wyke that could belong to this species but it is too poorly preserved to be sure.

The plant beds have also proved important for the study of fossil conifers (Harris, 1979a). The taxodiacean *Elatides thomasii*, which is a characteristic species of the lower Saltwick Formation, is particularly abundant here and often has attached male and female cones. In addition, there are abundant examples of (?)taxodiacean foliage *Elatocladus ramosus* and *Torreya gracilis*, this being the only known locality for the latter. The Taxaceae conifers are represented by *Marskea jurassica* with several attached female cones and one male cone, and *Poteridion hallei*, for which this is the only known locality. A third family of conifers, the Podozamitaceae, is also abundant here as the foliage species *Lindleycladus lanceolatus*.

The Czekanowskiales are not particularly common or diverse at Whitby, although there are some fragments of foliage that have yielded well-preserved cuticles (*Czekanoskia furcula* – see Harris, 1974a). More significantly, this is the only known locality for *Ixostrobus whitbiensis*, which Harris *et al.* regarded as a czekanowskialean male reproductive organ.

The ferns, although represented by a diversity of species, are not especially abundant here. The most complete record is in Harris (1961a). The most notable occurrence is a bed rich in well-preserved matoniacean fronds, *Matonidium goeppertii* at Saltwick. Van Konijnenburg-van Cittert (1978) used specimens of *Todites denticulatus* from Whitby in her study of in-situ osmundaceous fern spores.

It might be thought that this well-studied assemblage would yield some valuable information about the ecology of the early Middle Jurassic Epoch. Using the published records alone presents serious difficulties in developing such a study, as so much of the material came from fallen blocks that cannot always be accurately placed within the local lithostratigraphy. Nevertheless, there is considerable scope here for such work through additional fieldwork.

Conclusions

The cliff section between Whitby and Saltwick is one of the classic localities for the Yorkshire Jurassic flora, with a long history of investigation stretching over nearly two centuries, and providing a unique insight into the vegetation growing in Britain 170 Ma ago. It has yielded over 90 plant species, two of which are unique to the locality, and it is the type locality for 19 species. The coastal section has provided particularly important information about the structure of bennettitalean reproductive organs and yields numerous examples of conifer shoots with cones still attached. It is an outstanding site for its superlative plant remains and, particularly, their bearing on bennettitalean history. It is a valuable locality that will no doubt yield many more exciting discoveries.

RUNSWICK BAY (NZ 809 170)

Introduction

Three-dimensionally preserved plant fossils have been known from the Yorkshire Jurassic succession since Young and Bird (1822) described

Figure 3.15 Cliffs at Runswick Bay. The fossiliferous ironstone occurs in the undercliff, which appears to have slipped from the main cliff behind it. The photograph was taken in 1980 just prior to the excavations that were made there. (Photo: C.J. Cleal.)

them from the ironstone seams (sideritic sandstone beds) in the cliff at Runswick Bay (Figure 3.15). Others were later labelled as coming from 'Saltwick' and 'Hawsker'. Interestingly, Chapman (1973) suggested that these plant fossils were found on stones collected from the beach for the Tyne Iron Company. This parallels the much earlier discovery and collecting of the Tertiary pyritized fruits and seeds on the beach at Sheppey (see Chapter 5). Other specimens were collected by Yates (1855), Williamson (1870) and Halle in 1910 (Hill *et al.*, 1985). Thomas (1915) described some of Yates's specimens in the Paris Museum as male flowers of *Williamsonia gigas*, later transferred by Harris (1969) to his new species *Weltrichia sol*. In this work Harris also stated that the beds from which the ironstone casts were collected are no longer known. The discovery in 1980 of an in-situ sideritic sandstone bed at Runswick Bay yielding three-dimensionally preserved plants was followed up by extensive collecting and subsequent publication of the flora by Hill *et al.* (1985) and Hill (1990).

There are over 30 species described from the site, of which about five are new, and many show previously unknown anatomical details. The most important of these are a new species of the cycad male cone *Androstrobus* (*A. balmei*), the bennetite 'flower' *Williamsonia gigas* and the male cone of the conifer *Elatides thomasii*.

Description

Stratigraphy

The stratigraphy at this site is summarized in Figure 3.16. The main plant bed (the Wrack Hills plant bed) is within the Saltwick Formation (Aalenian). Hill *et al.* (1985) based their dating on the occurrence of abundant, relatively unfragmented, plant remains and fossils of the freshwater mussel *Unio*. They showed that the Saltwick Formation here overlies the Dogger Formation, which itself rests upon Lower Jurassic Alum Shale. Their excavations also led them to deduce that the fossil-bearing undercliff region had slipped from the main cliff some distance behind it.

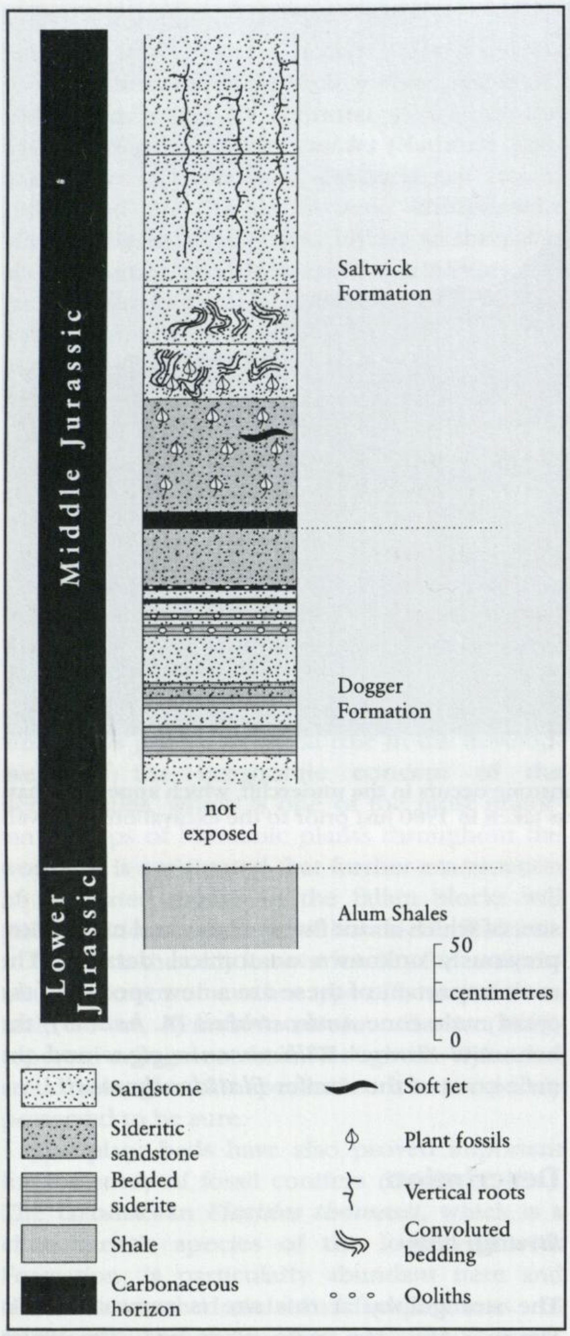


Figure 3.16 The succession through the Dogger and Saltwick Formations at Runswick Bay, showing the position of the main plant beds. (After Hill *et al.*, 1985.)

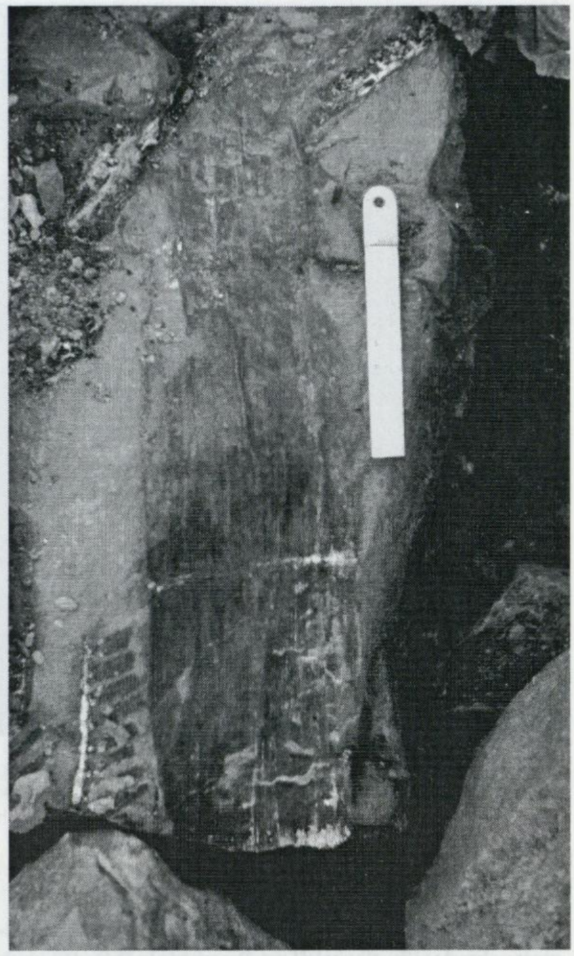


Figure 3.17 Stem of the horsetail *Equisetum beanii* (Bunbury) Harris from Runswick Bay. The ruler is 130 mm long. (Photo: R. Williams.)

Palaeobotany

There are two kinds of preservation of plant fossils at the Runswick locality. The more commonly found compressions are present in the basal claystones, but of far more importance are the three-dimensionally preserved organs in the sideritic sandstone. The uncompressed state of the plants must be due to early diagenetic carbonate precipitation.

Hill *et al.* (1985) described 31 species of plant fossils, representing what they thought to be 23 whole plant species in the sideritic sandstone (a more complete list of the 34 species that have been found at this site is given in Table 3.1; see also Figures 3.17 and 3.18). Cycad remains include leaves that have been tentatively referred to *Nilssonia tenuinervis*, male cones to *Androstrobus* and a fragment of the female cone *Beania*. The reproductive organs retain not only their original form, but also considerable amounts of structural and microscopic detail. Hill (1990) subsequently described the ultra-

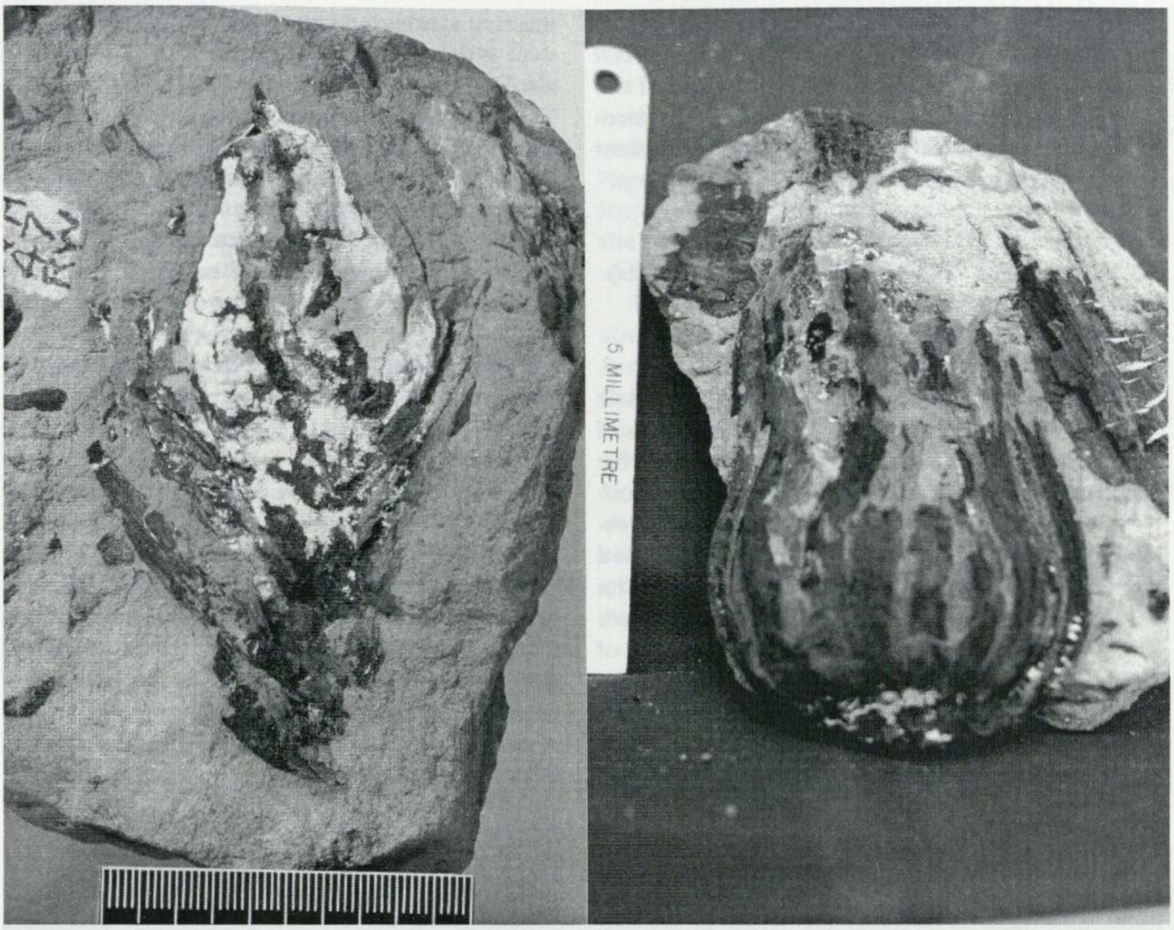


Figure 3.18 The female *Williamsonia flower* (left, scale graduated in mm) and male *Weltrichia* flower (right, scale graduated in 5 mm intervals) of the *Williamsonia gigas* plants from Runswick Bay. The female flower is preserved in longitudinal section, the male flower shows the outer surface. (Photos: R. Williams.)

structure of in-situ pollen that he had extracted from his new species of male cycad cone *Androstrobus balmei*.

Hill *et al.* collected about 30 specimens of *Williamsonia gigas* (Figure 3.18) out of the 200 they saw. They appear to represent a developmental sequence from relatively small, immature specimens to larger, presumably more mature, specimens in which the gynoecium reaches up to 8 cm long and the base of the corona is up to 26 mm wide. This collection prompted a new restoration of a relatively mature 'flower' or 'fruit' in which the surface of the corona and mamilla is composed of modified interseminal scales that lie adpressed to the surface.

Interpretation

The species diversity at Runswick Bay is much less than at many of the other Yorkshire Jurassic sites, such as Broughton Bank and in the Gristhorpe Bed at Cayton Bay. Nevertheless, the three-dimensional preservation gives the specimens unique value for the Yorkshire Jurassic fossil material. This new locality does not fit with the site location described by Yates, nor is it certain whether it is the ironstone bed from where Williamson (1870) described *Williamsonia* and *Zamites gigas*. It may be that there is more than one ironstone band or that such plant fossil lenses were distributed throughout the area. In time, other localities might well be discovered, but for now the potential value of this site is immense.

Conclusion

Runswick Bay is the most important Middle Jurassic site in Britain for three-dimensionally preserved plant fossils. These give much needed morphological information about the plants growing in this country about 170 Ma ago. Of especial interest is the evidence provided of the detailed structure of fructifications of the bennettitaleans, one of the most important plant groups of that time.

ROSEBERRY TOPPING (NZ 579 126)

Introduction

This is a locality famous for its Middle Jurassic plant bed, which has yielded a prolific flora of some 70 species. It is particularly important for well-preserved specimens of *Pachypteris papillosa*, which show the plant to have had xeromorphic characters and to be probably adapted to salt marsh conditions, in contrast to the majority of species in the flora, which were either freshwater marsh plants or inhabitants of dry land.

Plant fossils were first described from Roseberry Topping by Thomas (1913, 1915) when mining operations caused part of the massive sandstone cap to slip downhill, carrying with it the underlying beds to form a scree (see also Thomas and Bose, 1955). However, it was Tom Harris who made a major impact on the study of the site, especially with his work on the bennettites, cycads and corystosperms (Harris, 1946b, 1949a, 1951, 1964, 1983; Thomas and Harris, 1960). Van Konijnenburg-van Cittert (1975b, 1989) has also studied the ferns found here.

Description

Stratigraphy

This isolated hill (Figure 3.19) has a cap of massive sandstone underlain by shales. On the north side of the hill, Thomas (1913, 1915) described the fossiliferous beds as '8–10 feet' (*c.* 2.7–3.3 m) of black and yellow shales immediately beneath the sandstone. Here they were said to be conformable with those below but thinning out northwards. The fossiliferous bed is part of the Saltwick Formation and therefore of early Aalenian age.

Figure 3.19 Roseberry Topping. View towards the characteristically cone shaped outlier of Middle Jurassic rocks. The plant-bearing beds are exposed in the face on the north-west side. (Photo: D.J. Batten.)

Palaeobotany

About 70 species have been recorded from Roseberry Topping although most are very limited in their distribution both horizontally and vertically. Working along the section can, therefore, give new plant species. The exception to this is the abundant *Equisetum beani*, which occurs throughout the section. A full list of the known species found here is given in Table 3.1 (see also Figure 3.20).

Many of the plants are beautifully preserved and can easily be removed from the surface of the rock without chemical treatment. Thomas (1913) stated that cuticles of *Zamites*, *Anomozamites*, *Ctenozamites* and *Ctenis* are preserved in this way. Then in 1915, Thomas described the compound leaves of what is now called *Pachypteris papillosa* from a thin bed almost entirely composed of this species. Large numbers were extracted from this bed without any treatment and from the main escarpment at Little Roseberry where the bulk of the bed was exposed.

Figure 3.20 *Ginkgo whitbiensis* Harris. A characteristically small leaf with blunt apices to its lobes. Its veins are obscure. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.1468, Saltwick Formation, Roseberry Topping, ×2. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

In contrast to *Pachypteris papillosa*, good hand specimens of *P. lanceolata* (Figure 3.21) are very rare. However, small fragments are common, chiefly occurring in sandstones along with driftwood and other tough leaves such as *Pagiophyllum*. At Roseberry Topping several leaves have been found together, in contrast to the coastal sections where it is only ever found as fragments.

The bennettite *Otozamites penna* is locally abundant in the basal black coaly clay. The cycad *Pseudoctenis lanei* is also locally abundant. Other species found here that are worth mentioning are the very rare *Dicksonia kendalliae* (two specimens known to date), which has this as its type locality, abundant *Nilssonia kendalliae*, which also has this as it type locality, abundant *Ctenis kanehanai*, and locally frequent *Cladophlebis aktashensis* and *Pseudoctenis oleaosa*.

Van Konijnenburg-van Cittert (1975b, 1989) used specimens of *Dicksonia kendalliae*, *Eboracia lobifolia* and *Marattia anglica* from here in her studies of in-situ fern spores.

Interpretation

This flora shows large variation in content both vertically and laterally. This suggests that the lagoon in which the sediments were deposited received the remains of plants that were growing in different communities at different times.

The distribution and sometimes great abundance of *Pachypteris papillosa* is of outstanding importance. It is characteristic of the Aalenian strata above the Dogger and is often associated with *Brachyphyllum expansum*, suggesting that both species required the same ecological conditions. *P. papillosa* leaves have very thick cuticles and Harris (1964) suggested that they were thick and succulent, with tough skins and soft interiors. The stems were also fleshy and rotted easily, having only thin layers of xylem and firm tissues in the phloem and outer cortex. Harris (1983) used specimens from here in his interpretation of *P. papillosa* as a large shrub that formed mangrove-like thickets along tidal rivers or on salt marshes, probably growing between high and low tide marks. This is supported by their association with the marine microfossils *Tasmanites* and dinoflagellate cysts.

P. papillosa is associated here with the pollen-organ *Pteroma thomasii*, which Harris (1964) thought belonged to the same plant.

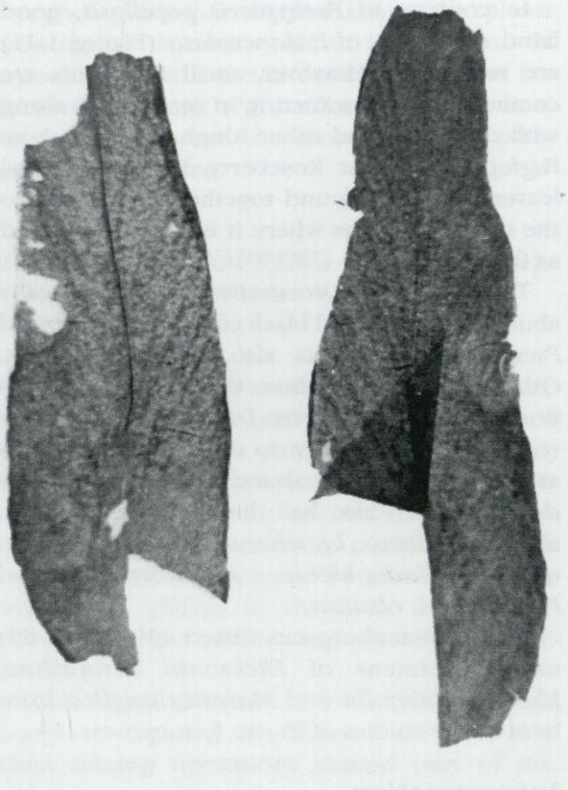


Figure 3.21 *Pachypteris lanceolata* Brongniart. These are upper and lower cuticles of a pinnule of this corystosperm leaf. Large numbers of leaf and stem fragments come from a thick (up to 3 m) band of dark shale, within which there are bands of almost pure leaves with comparatively little sediment between them. National Museums and Galleries of Wales, Cardiff, specimen 98.24.G6, Saltwick Formation, Roseberry Topping, × 3. (From Cleal and Thomas, 1999; photo: B.A. Thomas.)

This plant is now thought to belong to the Corystospermaceae, a peltasperm family that is better known from the southern high latitudes such as in South Africa (e.g. Anderson and Anderson, 1983).

Pachypteris lanceolata (Figure 3.21) was probably an abundant plant inland that sometimes grew close to water bodies where its intact leaves could become incorporated into sediment. The rest of the common or abundant species either grew in fresh water or were brought down from the river banks.

The Roseberry Topping floras have also been important for improving the understanding of Mesozoic cycad biology. As at Broughton Bank and Marske Quarry, the cycad fronds *Pseudoctenis lanei* are associated here with fragments of the massive and more compact pollen-producing cone *Androstrobus prisma* (Thomas and Harris, 1960). This constant association, together with a similarity in epidermal structure between the leaf and the exposed part of the microsporophyll, suggests that they were both borne by the same parent plant species. Both organs are very like the corresponding organs of such recent cycads as *Zamia* and *Encephalartos*, so it is possible that the whole plant was closely similar to these genera. The cones are quite different from those that Harris (1961b) thought were attached to his *Beania* tree (*Androstrobus manis* Harris), which were stalked and more slender (Harris described the latter as being more like catkins). Roseberry Topping has also yielded the best and in some cases only known examples of *Nilssonia kendalliae*, *Ctenozamites cycadea*, *Ctenis kanebarii* and *Pseudoctenis oleosa*.

Conclusion

Roseberry Topping is a nationally important locality for well-preserved plant remains that help us to interpret the early Middle Jurassic floral ecology of this part of Yorkshire. It has proved particularly important for studies on fossil cycads and corystosperms, which were important groups of plants growing in Britain 170 Ma ago. It has great potential for future research.

BROUGHTON BANK (HASTY BANK) (NZ 568 035)

Introduction

Broughton Bank (often referred to in the literature as 'Hasty Bank'; Figures 3.22 and 3.23) has yielded an extensive flora of 87 species, and is important for the number of reproductive organs that are associated with the more common shoots and leaves. Cuticles are well preserved here, providing important evidence for linking different plant organs together, which in turn helps in the development of part- or whole-plant reconstructions.

Alum workers first made the exposure at Broughton Bank during the last century, but it was not until the 1920s that Hamshaw Thomas and Maurice Black discovered it to be an important plant fossil locality. It was longer still before Mabel Kendall (1952) published the first record of plant fossils found here, including

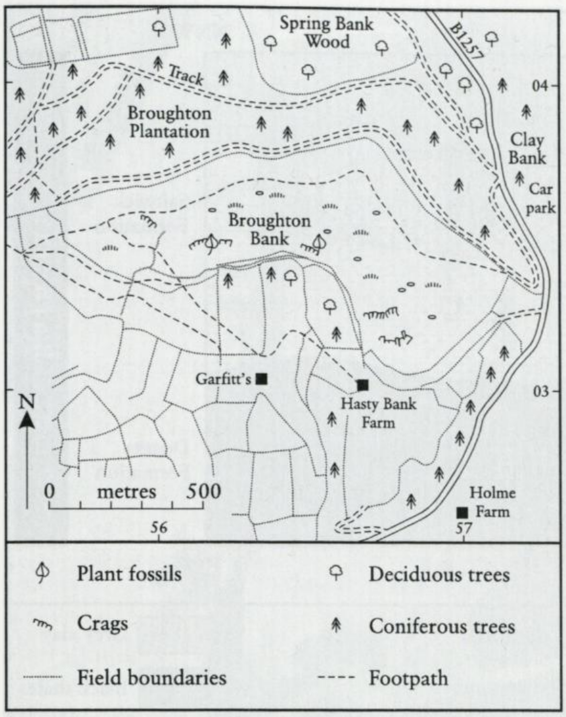


Figure 3.22 Location of the Broughton Bank GCR site. (After van Konijnenburg-van Cittert and Morgans, 1999.)

descriptions of fragments of conifer foliage. Tom Harris was actively collecting from here for some time in the 1940s and 1950s, and some specimens were published by him (Harris, 1950, 1952b, 1953). However, it was not until he published his main series of monographs on the Yorkshire Jurassic floras (Harris, 1961a, 1964, 1969, 1979a; Harris *et al.*, 1974) that he documented any of his finds from here. Hill and van Konijnenburg-van Cittert (1973) and Hill (1974) gave lists of the taxa then known to occur at Broughton Bank. In recent years, van Konijnenburg-van Cittert (1975a,b, 1989, 1996) has carried out research on the flora here, especially on the ferns and their spores. Spicer and Hill (1979) investigated the plant palaeoecology of the site in an attempt to establish what controlled the variations in the composition of the flora across the site.

Description

Stratigraphy

The exposure at Broughton Bank extends over 100 m and is up to 7 m thick. The plant-bearing

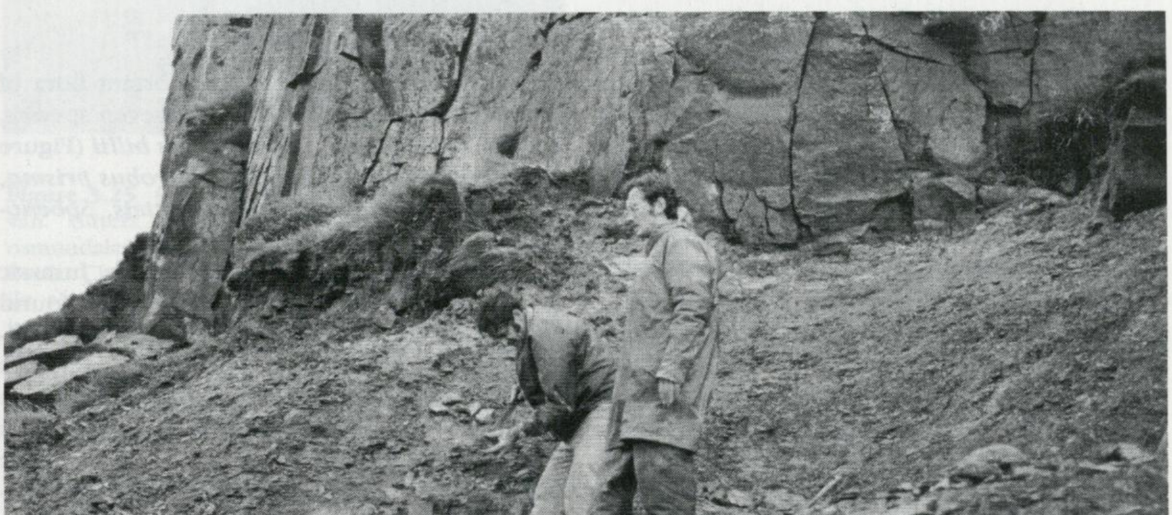


Figure 3.23 Collecting from the plant bed at Broughton Bank. (Photo: J.H.A. van Konijnenburg-van Cittert.)

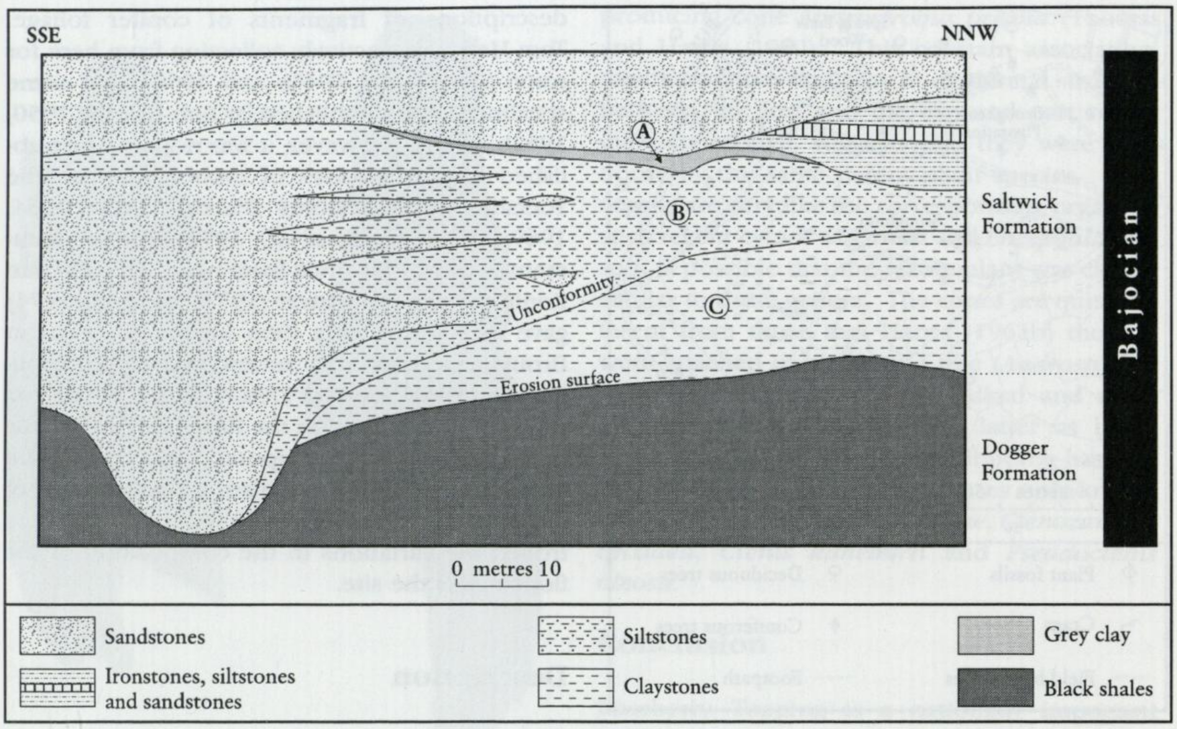


Figure 3.24 Schematic section of the exposure at Broughton Bank, showing the three main plants beds (A–C). Redrawn from Spicer and Hill (1979).

rocks are at the base of the Saltwick Formation and are, therefore, of early Aalenian age. Here at Broughton Bank the Saltwick Formation was deposited in an eroded depression of the lower Aalenian Dogger Shales.

Harris, in his unpublished notebooks, identified three plant beds here, shown in Figure 3.24 as A–C. The basal mudstones overlie marine shales containing animal fossils and marine algae, which suggest the region was sometimes flooded by sea water during this period of deposition. Above the mudstones is a siltstone layer that Hill (1974) suggested was the slow part of a river channel. A sandstone-filled erosion channel immediately to the south-east of the siltstone is probably the main river channel. The top dark clay layer is relatively thin and narrow, and lenticular sandstones that form the cliffs at the top of the bank cover the fossiliferous beds.

There is also a leaf coal above the capping sandstone that has yielded abundant plant fragments (mostly cuticles). The flora of this leaf coal includes abundant bennetitaleans, and the conifer *Marskea jurassica* is also present. It is, therefore, rather different from the main Broughton Bank flora below.

Palaeobotany

This locality has a large and important flora of about 90 species (Table 3.1). For seven species, it is the type locality: *Osmundopsis hillii* (Figure 3.25), *Pteroma thomasii*, *Androstrobus prisma*, *Hastystrobus muirii*, *Paracycas cteis*, *Sphenobaiera gyron* and *Palissya harrisii*.

All the major groups of Yorkshire Jurassic plants, except the lycopsida, have been found here and most are represented by well-preserved specimens yielding good cuticles and/or spores. The most common species are pteridophytes, the *Caytonia* leaf *Sagenopteris colpodes*, cycads and the seed fern *Pachypteris papillosa*. There are only small numbers of bennettites, ginkgos and conifers. Because this is a relatively new locality, very few type species have been described from it. Harris described his *Cycadites cteis* from here, and van Konijnenburg-van Cittert (1968, 1975a) described both the small cycad cone *Androstrobus major*, and the marattialean fern *Angiopteris blackii*, which has been suggested to be intermediate between older genera and living *Angiopteris*.

Figure 3.25 *Osmundopsis hillii* van Konijnenburg-van Cittert. This exceptionally rare fertile osmundalean fern is known only from Broughton Bank. Clusters of sporangia replace the normal sterile segments of the fern, which when found are known as *Cladophlebis harrisii* van Cittert. Natural History Museum, London, specimen V.60955, Saltwick Formation, Broughton Bank, × 7.2. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

Hill (1987) also studied *Angiopteris blackii* from Broughton Bank and showed it to have localized dead areas, most probably caused by a rust fungus. The ferns also showed tilting of sporangia in about one-third of the specimens, which Hill interpreted as being produced by currents acting on the waterlogged, somewhat decayed material, before or during the early stages of burial. Similar post-mortem changes occurred in the related fern *Marattia anglica* (Figure 3.26). Both species are more likely to have been susceptible to post-mortem changes than to have decayed during long-distance transportation.

Van Konijnenburg-van Cittert (1975b, 1989) also used specimens of *Coniopteris murrayana*, *Dicksonia kendalliae* and *Marattia anglica* from here in her studies of in-situ spores of these species.

Muir (1964) studied the palynology of this locality. She identified four ecological groups of palynomorphs, representing species that were living on the lowland swamps, in the lowlands but not in the swampy areas, in the hinterland, and growing both in the hinterland and in the drier lowland areas.

Interpretation

This is a very rich assemblage of nearly 90 species, with many ferns and cycads, which makes it different from that of the Saltwick Formation on the coast. *Equisetum columnare* occurs *in situ* here, in contrast to its obviously drifted nature at most other localities.

The presence of relatively large and well-preserved pieces of *Pachypteris lanceolata*, in association with the male fructification *Pteroma thomasii*, suggests that they were preserved close to their original position of growth. Harris suggested that *Pachypteris* grew in a salt marsh environment at sea level. The consistent association of *Pachypteris*, *Cladophlebis harrisii* and the cycad *Nilssonia kendalliae* with the microfossils *Tasmanites* and dinoflagellate cysts strengthens this idea and suggests that all were early colonizers of channel banks close to the sea. In contrast, the fragmentary nature of the conifers *Marskea jurassica* and *Bilsdalea dura* suggests that these species lived some distance inland.

As at Roseberry Topping, the pteridosperm leaf *Pachypteris lanceolata* is closely associated here with the pollen organ *Pteroma thomasii* (for which this is the type locality) and both are now usually attributed to the same parent plant (Harris, 1964). Harris (1983) also used specimens from here in his interpretation of *P. papillosa* as a large shrub with succulent young stems, which formed mangrove-like thickets along tidal rivers.

Broughton Bank has also played an important role in the study of Mesozoic cycads. The male

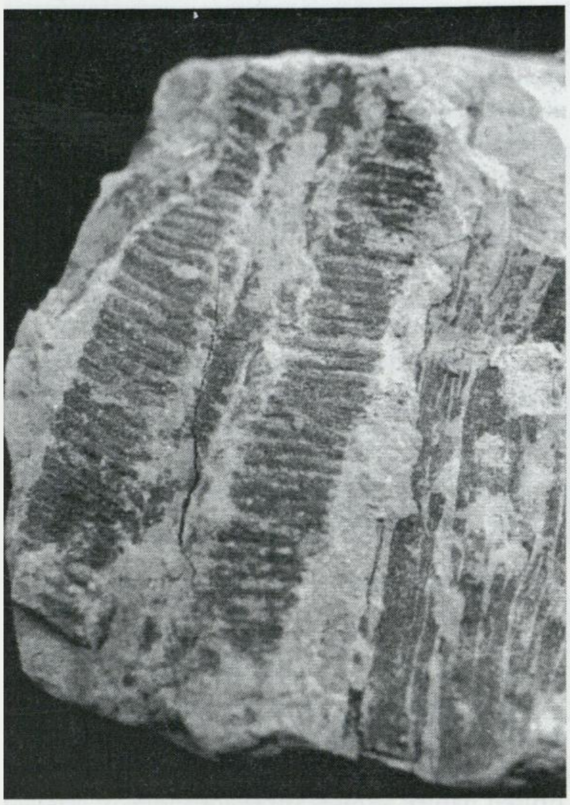


Figure 3.26 *Marattia anglica* (Thomas) Harris. Pinnae and leaf fragments of this Marattiaceae fern are quite common at Broughton Bank, although a complete leaf has yet to be found. Pinnae can reach 300 mm in length and 15–25 mm in width and have entire margins. Veins depart perpendicularly from the midrib at about 10–12 per 10 mm. More than half the specimens found at Broughton Bank are fertile like the one illustrated here. The elongated synangia (fused clusters of sporangia) are about 5–7 mm across. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.2703, Saltwick Formation, Broughton Bank, × 1.8. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

cone *Hastystrobus muirii* is as yet known only from two specimens from this site (van Konijnenburg-van Cittert, 1971). It is a small cone, about 20 mm long and 7 mm across, with spirally arranged microphylls whose entire lower surface was probably covered with sporangia. Its pollen compares closely to the common dispersed pollen genus *Eucommiidites troedssonii* Erdtman. Pollen referable to this genus have also been found in the micropyles of the gymnosperm seeds *Spermatites* and *Allicospermum*. Van Konijnenburg-van Cittert suggested that *Hastystrobus* belongs to the cycads because this is the only group that has the whole lower surfaces of its micosporophylls covered with sporangia.

Although not as diverse as in some of the other Yorkshire Jurassic sites, there have been some important bennettite discoveries at Broughton Bank. Most notable has been some finely preserved examples of the female flower *Williamsonia hildae*, which have revealed a number of crucial features of the peduncle and the perianth scales (Harris, 1969).

Conifers are also not particularly rich at this site, but it is the best-known locality for *Brachyphyllum crucis*. Harris (1979a) showed that many of these have undamaged apices where the leaves become progressively shorter, suggesting that the shoots had been shed deciduously. There are also good examples of juvenile shoots of *Geinitzia*, suggesting that the mature tree produced the occasional juvenile shoot, as happens in some modern conifers, such as *Juniperus sabina*. There are abundant shoots of *Elatides thomasii*, sometimes with attached male or female cones. Fragments of *Marskea jurassica* and *Bilsdalea dura* are also found here.

This is the only site where the Yorkshire Jurassic flora has been the subject of a multivariate statistical analysis. Quantitative data on species abundance were analysed by Spicer and Hill (1979) using 'Correspondence Analysis' and 'Principal Component Analysis'. The main component of the pattern of distribution was apparently controlled by lithology, with two main assemblages being recognized.

1. The Siltstone Assemblage characterized by *Marattia anglica*, *Nilssonnia syllis* and *Nilssoniopteris vittata*.
2. The Claystone Assemblage characterized by *Clathropteris obovata*, *Cladophlebis harrisii*, *Nilssonia tenuinervis*, *Pseudoctenis lanei*, *Ctenozamites cycadea*, *Sphenobaiera gyron*, *Brachyphyllum crucis*, *B. mamillare* and *Hirmeriella* sp..

Spicer and Hill also recognized associations between biologically related but physically separated organs. Correspondence Analysis revealed that many of the components of the '*Williamsonia hildae*' plant, as reconstructed by Harris (1969), were found close to one another (i.e. the leaf *Ptilophyllum pectinoides*, the perianth scales *Cycadolepis hypene*, the male flowers *Weltrichia whitbiensis*, and the stem *Bucklandia pustulosa*). Only the female flower (*Williamsonia hildae*) did not occur in this association, but this flower is always rare as a fossil.

In view of the abundance, diversity and fine preservation of the plant fossils found here, it is perhaps surprising that there has been so little published work on the flora. There is clearly considerable scope for further investigation of this important flora.

Conclusions

Broughton Bank is an important locality for the Yorkshire Jurassic flora, which has yielded a large number of species of many groups of plant fossils. Cuticles and spores are well preserved, which makes the specimens valuable research material. It has already proved of great importance in the study of fossil cycads and of the extinct group of plants called the corystosperms. It is a site of undoubted potential for helping to improve the understanding of the plant life that was growing in Britain 170 Ma ago.

HILLHOUSE NAB (SE 659 993)

Introduction

Hillhouse Nab has yielded a distinctive Middle Jurassic flora from the Aalenian Saltwick Formation. The flora is dominated by conifers and differs from others of similar age, indicating that it originated from a drier, less waterlogged habitat. A thin coal in the section yields a different flora again.

Harris discovered the plant bed at Hillhouse Nab (Figure 3.27) in about 1950 and mentioned the locality in his species accounts in *The Yorkshire Jurassic Flora* (Harris, 1961a, 1964, 1969, 1979a; Harris *et al.*, 1974) and in his discussion of *Matonia braunii* (Harris, 1980). No published description of the site exists so the observations below are largely based on Harris' manuscript description, which is housed in the Palaeontology Department of the Natural History Museum, London.

Description

Stratigraphy

Based on Harris' unpublished notes, the stratigraphy at Hillhouse Nab is as shown in Figure 3.28. The basal sandstone was reported as extending for about 500 m, thinning towards the edges, but Harris recorded that he only collected from the plant bed over about 70 m. This bed is about 2 m thick. It overlies a pale yellow sandstone and is in turn overlain by 10 cm of crumbly coal composed mainly of fusainized wood fragments. Above the coal are a few metres of grey clays that weather to a bright yellow.

The basal sandstone is over 2 m thick; its base is not exposed. At the top of the sandstone the lithology changes to a micaceous sandy siltstone and for the first 1 m it alternates unevenly between fine sandstone and grey or brown micaceous siltstones and there are lenses of hard sandstone. The plants occur in the silty layers.

Palaeobotany

The complete list of species is given in Table 3.1. There are lenses within the silty layers with each having a single species in great abundance. The best of these gave *Phlebopteris braunii*, the stems of *Pachypteris papillosa*, *Pseudotorellia tibia* or *Equisetum* sp. with stems about 3–5 mm wide and pronounced nodes. Many of the other species are widespread although often rather fragmentary. Conifers are especially common here, including *Cyparissidium rudlandicum*, *Brachyphyllum crucis* and *B. mamillare*.

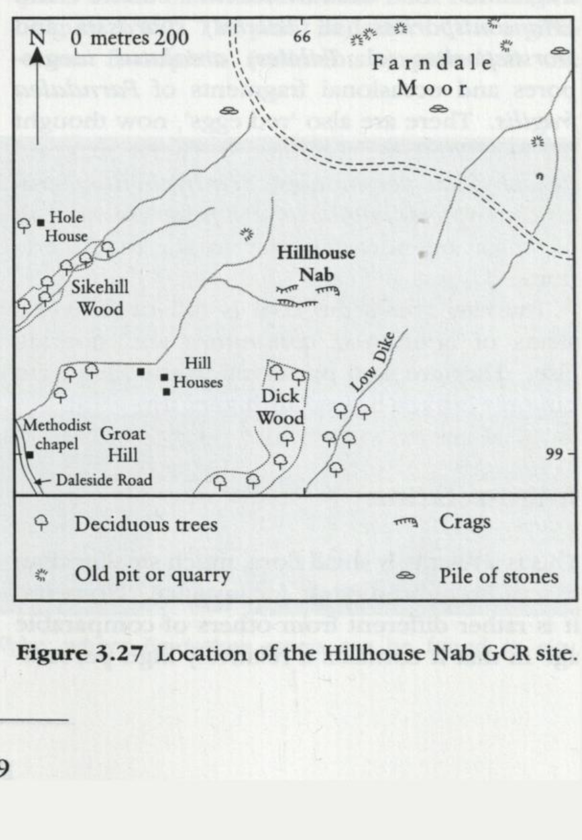


Figure 3.27 Location of the Hillhouse Nab GCR site.

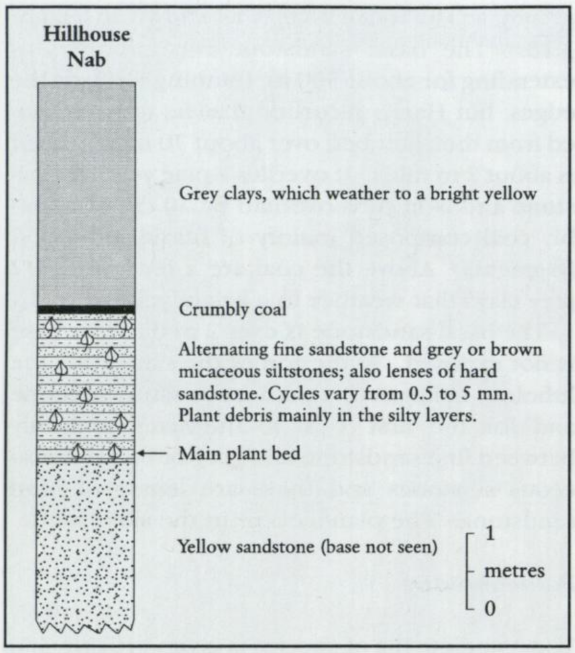


Figure 3.28 Stratigraphical section at Hillhouse Nab, based on manuscript notes by T.M. Harris.

The coal has a small flora of megaspores and leaf cuticles quite different from those of the plant bed. Although there are many fragments of fusain, the coal itself is not fusainized because it dissolves on maceration. It yields many small fragments of *Czekanowskia* cuticle and *Erlansonisporites* (al. *Triletes*) *sparassis* and *Horstisporites* (al. *Triletes*) *areolatus* megaspores and occasional fragments of *Farndalea fragilis*. There are also 'red eggs', now thought to be clitellate cocoons. There was no *Ptilophyllum pectinoides*, *Brachyphyllum crucis*, *Pachypteris papillosa* or *Equisetum* spp., all of which are normally easy to see in macerations.

The clay above the coal is full of flattened stems of *Equisetum columnare* and nothing else. They are well preserved in the first 2 cm but only broken bits occur higher up.

Interpretation

This is a relatively small flora, much smaller than that of Broughton Bank, for instance. However, it is rather different from others of comparable age in that it contains a relatively high percentage of conifers. This indicates that the flora was at least partly derived from a drier, less waterlogged, environment than the others. Significant among these conifers are the remains of foliage called *Elatides thomasii* Harris, which occurs with abundant male and female cones indicating that it belonged to the Taxodiaceae.

The stems of *P. papillosa* are particularly well preserved at the Hillhouse Nab GCR site. They gave Harris (1983) plenty of material for his interpretation of them as the young succulent stems of large shrubs that formed mangrove-like thickets along tidal rivers. Harris (1980) also used the rich source of *Matonia braunii* to redescribe the species, consider the overall status of the Yorkshire Jurassic Matoniaceae, and review the earlier descriptions of the family. The species had previously only been collected as occasional specimens at Saltwick and from the Gristhorpe Bed.

Harris stressed in his manuscript that *Equisetum columnare* was absent in the plant bed below the coal and that he did not encounter any suggestion of vertical roots. He suggested that the water level must have been consistently too high for *Equisetum* to invade, being at least 1 m deep and often more than this, implying deposition in open water into which came fragments of plants from the surrounding area. The coal would have been formed from a mass of plant debris that accumulated in the water body rather than from in-situ Carboniferous-type swamp vegetation.

This is the only known British locality for Jurassic macrofossils of the unusual ginkgophyte foliage *Pseudotorellia tibia*, although dispersed cuticles of another species of the same genus have been found elsewhere (Harris, 1974a). It is similar in leaf shape to *Eretmophyllum* but has a significantly different epidermal structure and provides further evidence for the diversity of the ginkgoaleans in Mesozoic vegetation.

Conclusions

Hillhouse Nab is an important locality for its conifer-dominated flora, which complements those at Broughton Bank and Roseberry Topping. The rich lenses of individual species offer good opportunities for future detailed studies. The inclusion of the coal seam in the short sequence at this GCR site also gives an unrivalled opportunity for future palaeoecological research.

HAYBURN WYKE (TA 011 969)

Introduction

The Hayburn Wyke plant beds have long been known to yield a diverse and well-preserved fossil flora of Aalenian age. It is a key Yorkshire Jurassic plant fossil locality with unique floral elements, especially of cycads. The marchantialean liverwort ***Hepaticites haiburnensis*** is known only from this locality.

Hayburn (or 'Haiburn') Wyke is a small bay near Cloughton (Figures 3.29 and 3.30), and is an important source of plant fossils from the Saltwick Formation (the 'Lower Deltaic Series' of earlier authors). The earliest records seem to be by Phillips (1829) and Lindley and Hutton (1837). Leckenby (1864) also collected from here and some of his specimens were mentioned by Phillips (1875) (Leckenby's specimens are stored in the Sedgwick Museum, Cambridge). The 19th century records were summarized by Seward (1900a). Hamshaw Thomas collected extensively from the section in the early 20th century, although does not appear to have published descriptions of this material. Harris (1944a, 1945a, 1948, 1949a,b, 1950, 1951, 1952a, 1953) and Bose (1955) have described various species of bennettite, ginkgophyte, czekanowskialean and conifer foliage. However, the full spectrum of the flora at Hayburn Wyke was not revealed until the publication of Harris' monograph on the Yorkshire Jurassic floras (1961a, 1964, 1969, 1979a; Harris *et al.*, 1974).

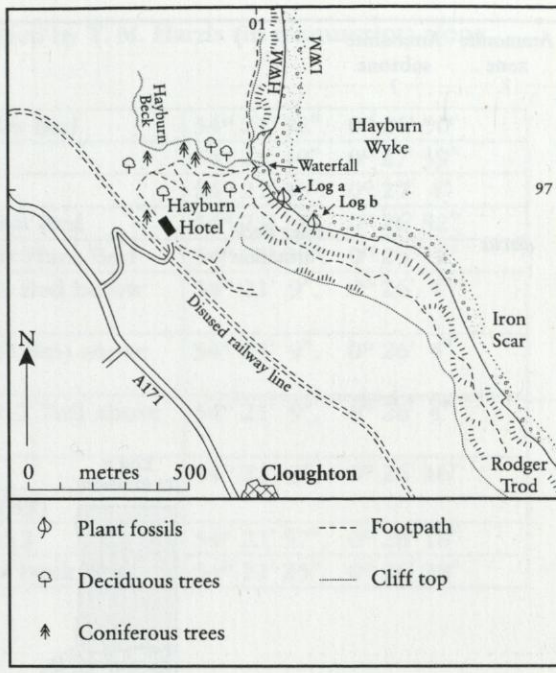


Figure 3.29 Location of the Hayburn Wyke GCR site. Redrawn from van Konijnenburg-van Cittert and Morgans (1999).

Description

Stratigraphy

The section exposed at Hayburn Wyke includes parts of the Saltwick and Eller Beck Formations (Figure 3.31). The plant beds are in the argillaceous floodplain sediments exposed in the

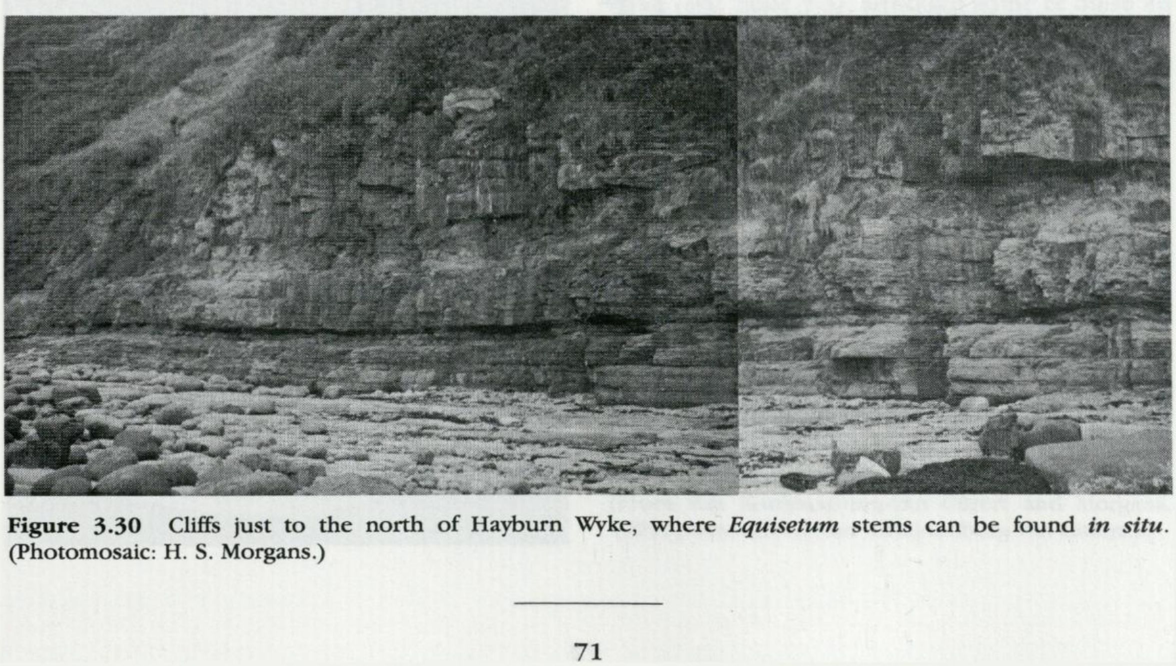


Figure 3.30 Cliffs just to the north of Hayburn Wyke, where *Equisetum* stems can be found *in situ*. (Photomosaic: H. S. Morgans.)

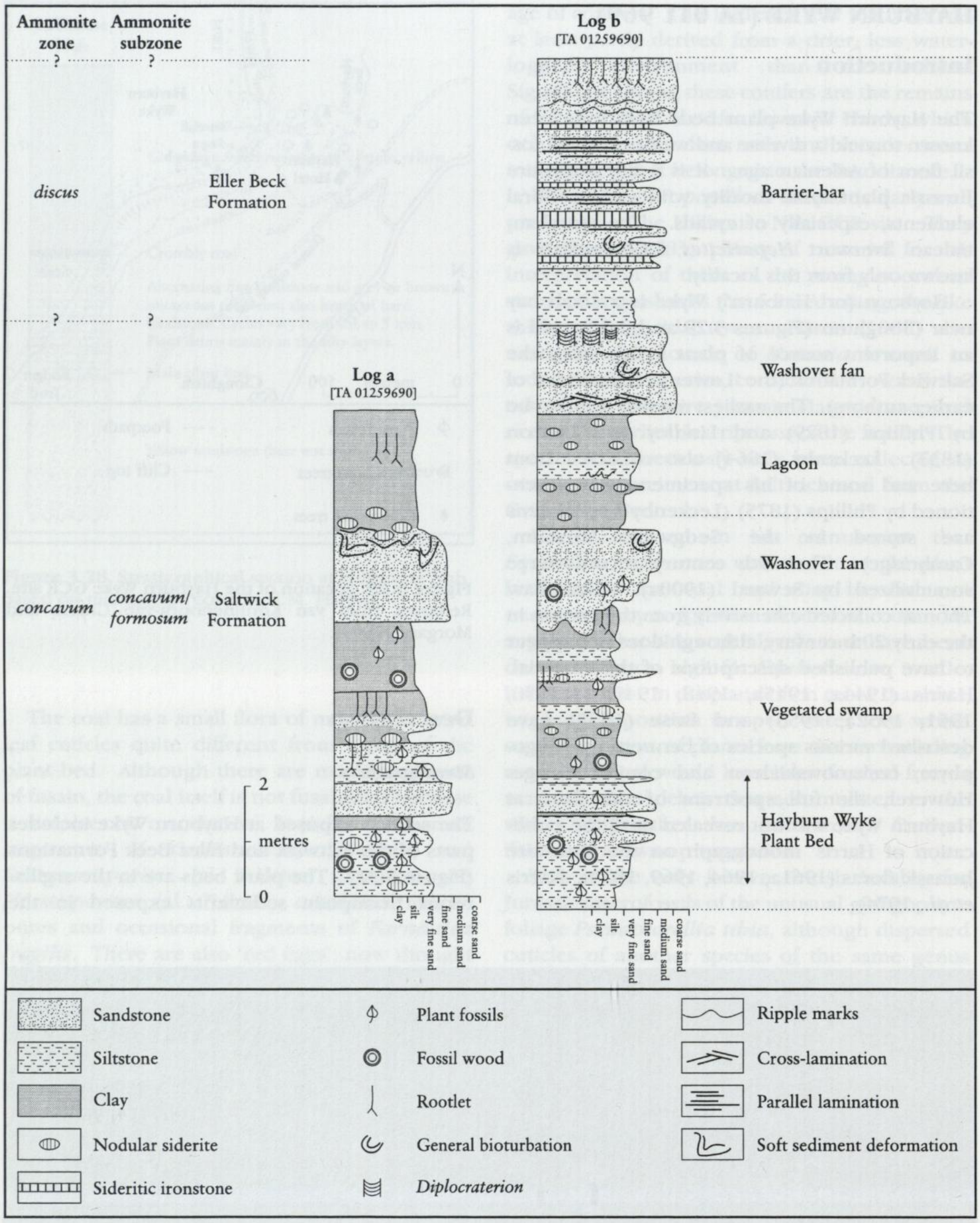
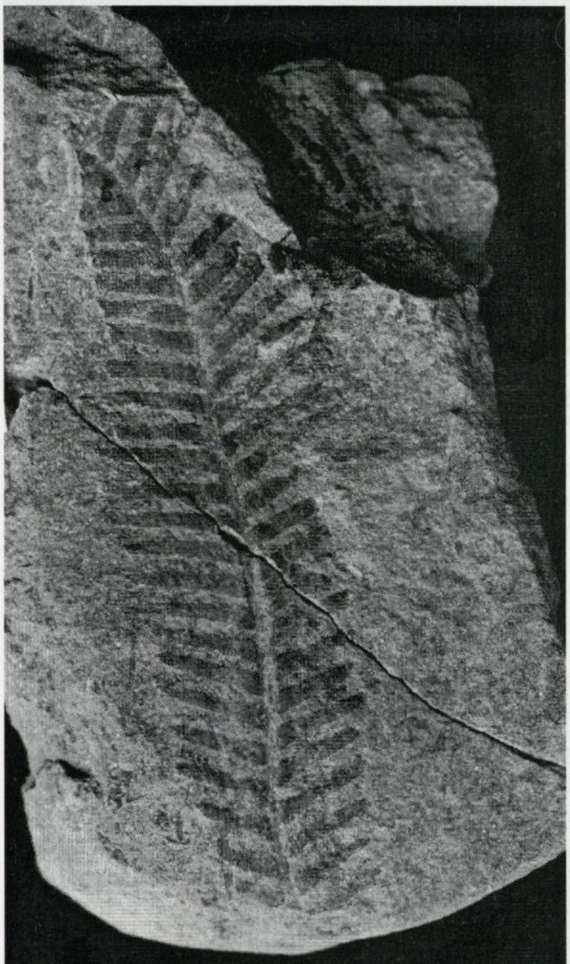


Figure 3.31. Stratigraphical section exposed at Hayburn Wyke, showing position of main plant beds. The locations of the logs are shown in Figure 3.29. (After van Konijnenburg-van Cittert and Morgans, 1999.)

Table 3.3 The locations of the plant beds identified by T. M. Harris (in manuscript) along the coast at Hayburn Wyke

Lower Deltaic Series (= Saltwick Formation)	Hayburn Beck *Zamites* Bed	54° 21' 32", 0° 26' 50"
	Hayburn Beck Bed 1	54° 21' 40", 0° 27' 39"
	Hayburn Beck Bed 2	54° 21' 35", 0° 27' 4"
	Hayburn Wyke *Zamites* Bed	54° 21' 27", 0° 26' 32"
	Hayburn Tindall Point Plant Bed	54° 21' 25", 0° 26' 12"
	Hayburn *Phlebopteris* Bed below Iron Scar	54° 21' 9", 0° 26' 4"
Sycarham Series, Middle Deltaic Series (= Sycarham Member of Cloughton Formation)	Hayburn Wyke 25 ft (*c*.8m) above Iron Scar	54° 21' 9", 0° 26' 4"
	Hayburn Wyke 5 ft (*c*. 2.7m) above Iron Scar	54° 21' 9", 0° 26' 4"
	Hayburn Gorse Bed	54° 21' 3", 0° 26' 16"
	Hayburn Gorse Bed (B5)	
	Hayburn Thomas Bed 2	54° 21' 57", 0° 28' 18"
	Hayburn–Top of Eller Beck Bed	54° 21' 25", 0° 26' 28"



centre of the small bay. The succession dips gently southwards, the Eller Beck Formation reaching beach level at Iron Scar. The exposure is scattered over the rocky beach and often covered by landslip. The sandy units contain fragmentary plant remains, many of which are charcoalified. The finer-grained beds contain much abundant, more diverse, and better-preserved plants. Van Konijnenburg-van Cittert and Morgans (1999) have provided details of the field geology of this site.

Harris' unpublished notebooks refer to 12 separate plant beds in the vicinity of Hayburn Wyke (see Table 3.3), although some of these lie in the Cloughton Formation and are beyond the boundaries of the GCR site. The principle source of plant fossils is the main Hayburn Wyke Plant Bed, which probably corresponds to the Hayburn Beck and *Zamites* Beds of Harris.

Figure 3.32 *Otozamites gramineus* (Phillips) Phillips. The leaves of this bennettitalean can be up to 300 mm long and 50–70 mm wide, and are composed of slender pinnae in which the upper angles of their bases are enlarged as auricles. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.6432, Saltwick Formation, Hayburn Wyke, × 0.9. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

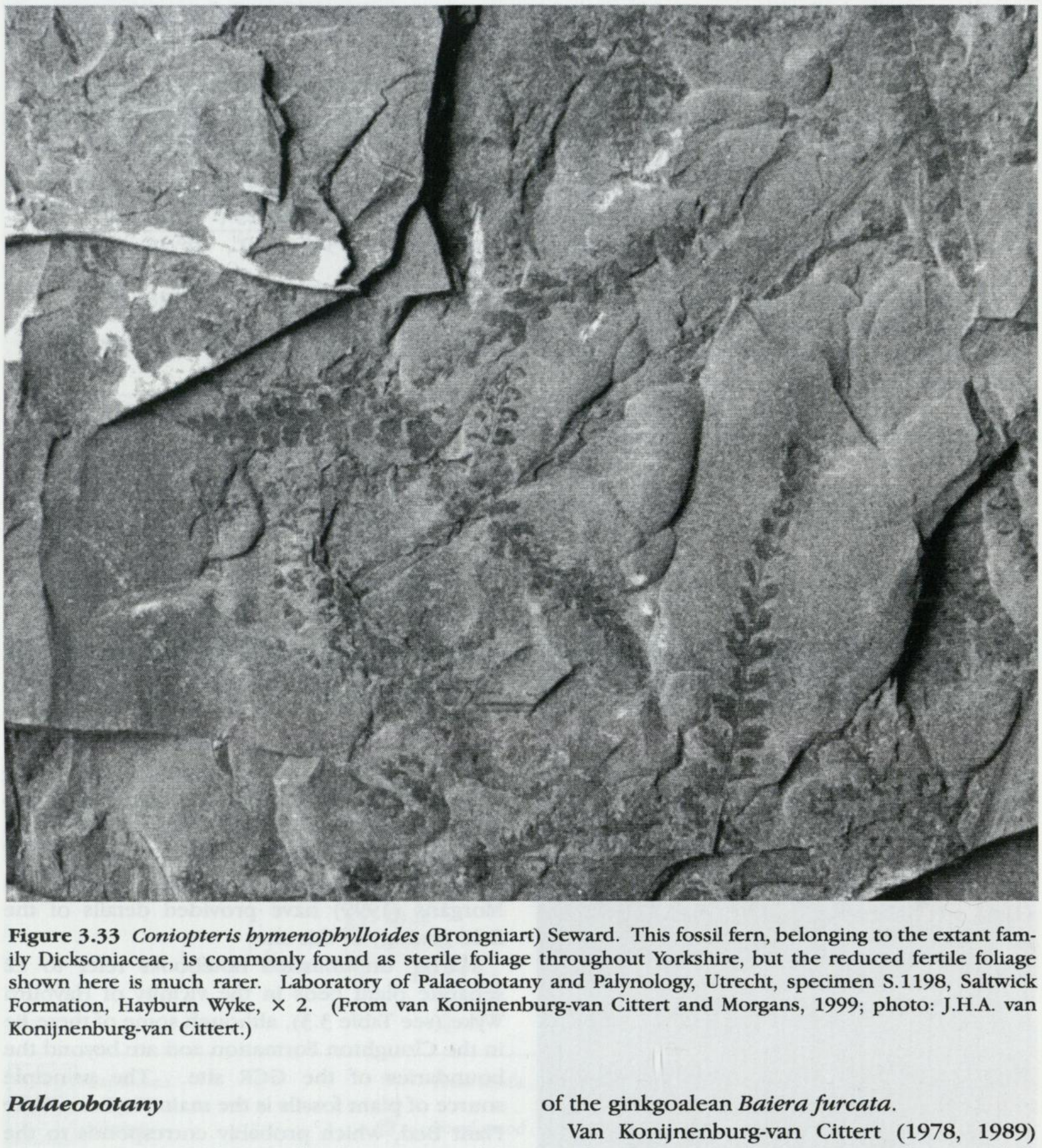


Figure 3.33 *Coniopteris hymenophylloides* (Brongniart) Seward. This fossil fern, belonging to the extant family Dicksoniaceae, is commonly found as sterile foliage throughout Yorkshire, but the reduced fertile foliage shown here is much rarer. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.1198, Saltwick Formation, Hayburn Wyke, × 2. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

Palaeobotany

The complete list of about 60 plant species that have been found at Hayburn Wyke is given in Table 3.1. It includes the marchantialean liverwort *Hepaticites haiburnensis* for which this is the type locality. The 12 ferns include *Cladophlebis haiburnensis*, which was first described from here by Lindley and Hutton. There are relatively few cycads and pteridosperms, although there are 11 bennettites, of which *Bucklandia gigas*, *Otozamites leckenbyi*, *O. mimetes*, *O. parallelus*, *O. tenuatus* (see also Figure 3.32), and *Weltrichia sol* were first described from here. The site is also the locality of the ginkgoalean *Baiera furcata*.

Van Konijnenburg-van Cittert (1978, 1989) used specimens of *Coniopteris hymenophylloides* (Figure 3.33), *C. murrayana*, *C. simplex* and *Todites princeps* from Hayburn Wyke in her studies of in-situ spores of these species. Morgans (1999) has described charcoalified conifer wood from floodplain mudstone and crevasse-splay sandstones at the site as *Cedroxylon* spp., *Cupressinoxylon* spp., *Taxodioxylon* spp. and *Xenoxylon phyllocladoides* Gothan, 1906.

Interpretation

There are several horizons at Hayburn Wyke that

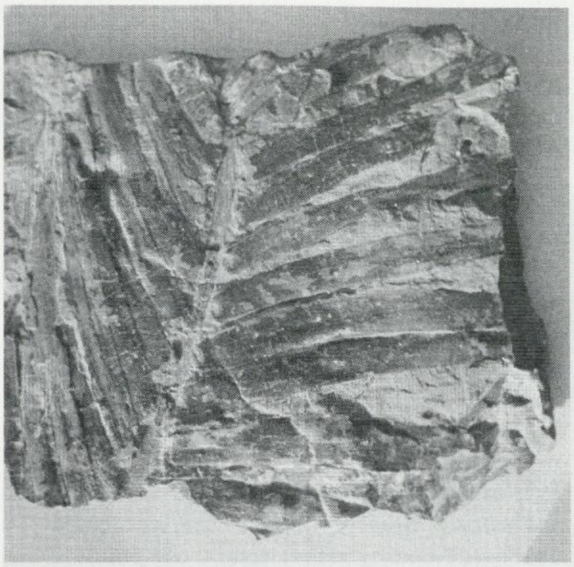


Figure 3.34 *Zamites gigas* (Lindley and Hutton) Morris. This common bennettite leaf is typically 300 mm long and 120 mm wide with large pinna that are parallel-sided and tapering in their upper third towards an acute apex. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.1319, Saltwick Formation, Hayburn Wyke, × 0.25. (Photo: J.H.A. van Konijnenburg-van Cittert.)

yield different assemblages. The *Zamites* Bed is the richest and most important although it shows intense localization, both vertically and horizontally. Ferns are frequently common with *Clathropteris obovata*, *Coniopteris bella*, *C. hymenophylloides*, *C. murrayana*, *C. simplex*, *Matonidium goeppertii* and *Phlebopteris woodwardii*. The pteridosperm *Pachypteris lanceolata* is also common in places. At one point the only gymnosperms found by Harris (1969) were great numbers of *Zamites gigas* leaves (Figure 3.34), a few pieces of *Williamsonia* (*Bucklandia*) stem, a few *Williamsonia gigas* flowers and a few good specimens of *Weltrichia sol*, suggesting that these three organs were parts of a single plant species.

In contrast, the *Equisetum* bed, which is just above the Iron Scar (Figure 3.29), is only rich in *Coniopteris simplex*, possibly reflecting a very local plant community immediately surrounding a small lagoon.

Conclusion

The Hayburn Wyke plant beds contain an important and rich flora including several species that were first described from here and the only known occurrence of the liverwort *Hepaticites haiburnensis*. A reassessment of the species content of the various horizons should reveal valuable ecological information.

BOTTON HEAD (NZ 596 020)

Introduction

Botton Head is located near Ingelby Greenhow, in the North Yorkshire Moors National Park and is about 4 km from Broughton Bank. This locality in the Aalenian Saltwick Formation is a comparatively recent find. Preliminary investigations have revealed a reasonably large flora with many good gymnosperm reproductive organs. The site has great potential for future studies on gymnosperm evolution and taxonomy.

There is no published account of the palaeobotany of this site, and the following assessment of its significance is based on manuscript notes by Dr Christopher Hill, deposited with fossil plants from the site, in the Natural History Museum, London. Other manuscripts held by the Museum deal with the palynoflora (J.E. John) and megaspores (A. Leitch).

Description

Stratigraphy

The beds, like those at Broughton Bank and Roseberry Topping, belong to the Saltwick Formation. They are composed of claystones, siltstones, sandy siltstones and sandstones overlying the black shales of the Dogger succession (Figure 3.35). The sediments were deposited after the first erosion phase of channel activity in the area and, therefore, yield an interestingly different assemblage from those of the other two sites. There are no marked channel deposits and for some of the time conditions favoured coal formation.

The plant beds are about 2 m thick and extend more than 1 km laterally. The principal bed is above the main sandstone, and is overlain by a micaceous and carbonaceous siltstone with rootlets, followed by a thin layer of dark grey claystone. Like the beds at Broughton Bank and Roseberry Topping, they are near the base of the Hayburn Formation but, unlike the beds at the other two sites, they indicate deposition in an

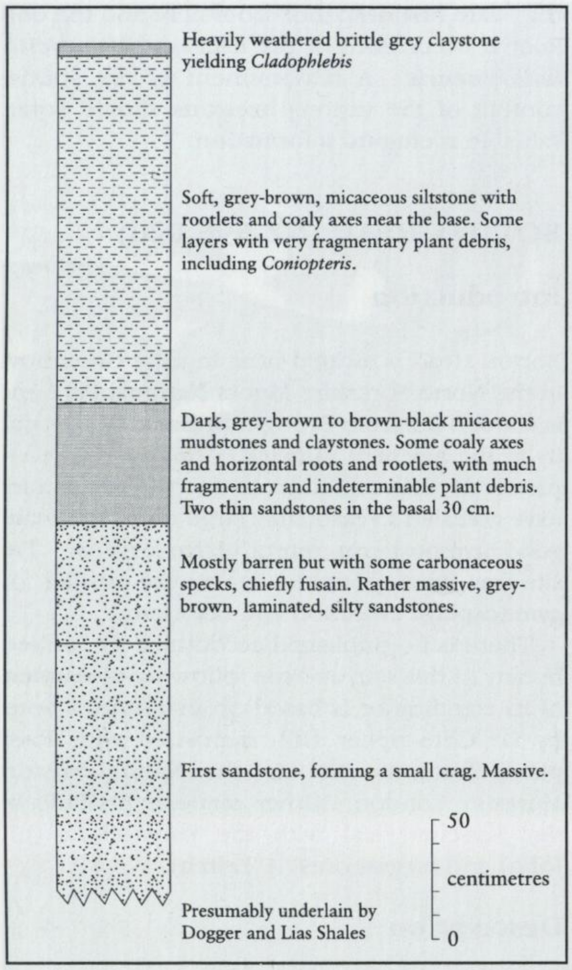


Figure 3.35 Stratigraphical section for the Botton Head GCR site. (After C. Hill, in manuscript).

overbank swamp environment with no marked channel association.

Palaeobotany

The complete list of species recovered from this site is given in Table 3.1. The principal plant bed contains a relatively low abundance of pioneer plants, such as *Pachypteris papillosa* and ferns, a relatively greater number of bennettites, and some conifers such as *Marskea* and *Bilsdalea*. These assemblages are more characteristic of a mature, fairly stable sedimentary environment.

There is considerable lateral variation in the composition of the flora. In some places the grey and grey-brown shales are about 0.15 m thick and incorporate in the top 0.1 m an *Equisetum columnare* rhizome bed about 200 mm thick.

The coaly layer is rich in bennettites, such as *Nilssoniopteris*, *Pterophyllum*, *Zamites* and *Otozamites*, together with pieces of *Equisetum columnare* and *Ptilophyllum hirsutum*.

Interpretation

A flora such as this, which is rich in bennettites and conifers, is characteristic of a more mature 'top set' phase of fluvio-deltaic activity than is found at Broughton Bank and Roseberry Topping. The composition of the coaly layer suggests that it formed by the accumulation of pieces of plants from the surrounding vegetation. The fragmentary pieces of *Equisetum columnare* must similarly have come from a water-side colony rather than from plants growing on site. The depth of water must have been too great to permit colonization by horsetails.

Conclusions

The Botton Head flora is dominated by conifers and bennettites. A number of their reproductive organs have yet to be described. The variation in composition offers future possibilities for discovering associations of vegetative and reproductive organs that might indicate natural affinities. A detailed study of the plant fragments and spore content of the coaly layer might also reveal a better understanding of the delta vegetation that surrounded the area of deposition.

BEAST CLIFF (ROBIN HOOD'S BAY) (TA 002 996–TA 005 988)

Introduction

A number of plant-bearing horizons crop out along this stretch of the coast within the Saltwick and Cloughton Formations. Many species that are seldom found at the other Yorkshire Jurassic localities occur here. Approximately 60 species have been recorded from Beast Cliff (Figure 3.36), including some notable rarities.

The site has long been known as a source of Jurassic plant fossils. Halle (1913) and Kendall (1913) recorded examples of in-situ *Equisetum* in the cliffs at Robin Hood's Bay. Wilson and Yates (1953) described some dicksoniacean ferns and Harris (1946a, 1949a,b, 1951, 1952b, 1953) described bennettite fronds and scale

Figure 3.36 View across Robin Hood's Bay towards Beast Cliff. (Photo: H.S. Morgans.)

leaves from here. Fragments of the conifer *Brachyphyllum* were described by Kendall (1947). However, it was not until Harris (1961a, 1964, 1969, 1979a; Harris *et al.*, 1974) published his monographs on the Yorkshire Jurassic floras that the full importance of the site became evident.

Description

Stratigraphy

Vertical variation is well marked in the coastal exposures of the Saltwick Formation (Aalenian), which is seen clearly in the channel sandstone deposits. In the Beast Cliff sections there are large composite bodies of multiple channel origin, while mixed sand–silt channel fills in the upper part suggest tidal influence (Livera and Leeder, 1981). Basal loading and soft sediment deformation is also common towards the top. This, together with other upward trends of fewer root beds and increased amounts of drifted plant remains, indicates a change from a well-drained floodplain complex to a saturated swampy environment drained by smaller, mixed-load channels. Thin coal seams seen in the cliffs represent the accumulation of plant debris, notably *Equisetum*, in relatively small, shallow lagoons.

The Eller Beck Formation (Bajocian) represents an inundation and marine transgression that resulted in a sequence that begins in basal ironstones and proceeds upwards into shales and medium-grained sandstones. However, the succeeding Cloughton Formation (also Bajocian in age) marks a return to non-marine conditions, with root beds that indicate fresh water and dense colonization by plants. Further root beds and thin coal seams indicate more, well-developed stands of *Equisetum*.

Harris (in manuscript) listed 12 main plant beds at Beast Cliff; these are shown with other beds in Table 3.4. Most are in the Saltwick Formation, but one (the Petard Point Bed) is in the Cloughton Formation.

Palaeobotany

The list of about 70 plant species found at Beast

Table 3.4 The locations of the plant beds identified by T. M. Harris (in manuscript) at Beast Cliff.

Lower Deltaic Series (Saltwick Formation)	Coal 1 in cliff foot	54° 23' 47", 0° 28' 11"
	North *Ptilophyllum* Bed	54° 23' 37", 0° 28' 4"
	Coal 4 in cliff foot	54° 23' 38", 0° 28' 4"
	Solonites Bed (fallen block below Ashyard Farm)	54° 23' 36", 0° 28' 0"
	Fern Bed	54° 23' 30", 0° 57' 56"
	E. beani Bed (fallen)	54° 23' 26", 0° 27' 28"
	Coniopteris tatugensis Bed (fallen)	54° 23' 18", 0° 27' 44"
	Rocky Point *Ptilophyllum* Bed	54° 25' 17", 0° 26' 54"
	Elatides and *Neocalamites* Bed (fallen)	54° 22' 33", 0° 27' 12"
	Ptilophyllum Bed (near Petard Point in cliff foot)	54° 22' 19", 0° 26' 52"
	Otozamites Bed	54° 23' 41", 0° 28' 5"
	Equisetum Bed	54° 22' 0", 0° 26' 47"
	Red House Plant Bed (fallen)	54° 21' 46", 0° 26' 40"
	Ripple-marked sandstone	54° 21' 42", 0° 26' 41"
	Otozamites Bed	54° 22' 14", 0° 26' 48"
Middle Deltaic Series (Cloughton Formation, Sycarham Member)	Shale 1 over Eller Beck Bed (EBB)	54° 23' 41", 0° 28' 7"
	Shale and Coal 3 over EBB	54° 23' 36", 0° 28' 7"
	Shale 5 over EBB	54° 23' 27", 0° 27' 59"
	Shale 6 over EBB	54° 23' 26", 0° 27' 58"
	Shale 7 over EBB	54° 23' 17", 0° 27' 52"
	Petard Point Plant Beds, black shale over EBB (upper and lower)	54° 22' 16", 0° 26' 54"
	A above EBB	54° 22' 8", 0° 26' 53"
	B above EBB	
	C above EBB	
	D above EBB	
	E above EBB	54° 21' 50", 0° 26' 45"
	F above EBB	
	G above EBB	

Cliff is included in Table 3.1. It is the only known locality for *Bennetticarpus diodon*, and the type locality for another eight species: *Schizoneura stenophylla*, *Ctenis exilis*, *Deltolepis calyptra*, *D. mitra*, *Nilssonia syllis*, *N.* sp. B of Harris (1969), *Cycadolepis sphenis-cus* and *Marskea jurassica*. However, this does not provide a complete picture because the various plant beds at Beast Cliff reveal different assemblages of species. One of the best known of these is the *Equisetum* Bed in the cliff, known also from a number of such localities in the area (Halle, 1913; Kendall, 1913). Here *Equisetum columnare* can be found with erect unbranched stems preserved as three-dimensional casts that are typically 40–50 mm wide. Harris (1961a) described the stems as gregarious (occurring 0.1–0.2 m apart and always broken off at the same level between 0.05 and 0.1 m from the base). They probably grew in a pure stand rooted in peaty silt in a pool. When the pool was suddenly overwhelmed with silt the plants died and the stems broke off, allowing sediment to invade their hollow interiors. The rhizomes and peaty soil around them formed a thin coal seam with the roots preserved in the silt beneath. Cone fragments have been found in association with the stems. It is not yet known whether they were borne terminally or on the tips of branches. Fragments of the fern *Dicksonia mariopteris* are also present in the *Equisetum* Bed, presumably representing plants that were growing around the edge of the *Equisetum* stand.

Harris (1961a) has described two other

members of the Equisetales from Beast Cliff. *Neocalamites nathorstii* stems and leafy twigs occur together with the conifers *Elatides thomasii* and *Elatocladus ramosus*. This is the only known locality for the few specimens of *Schizoneura stenophylla*, which Harris found in 1957 in a fallen block of clay-ironstone near Prospect House (Harris, 1961a). *Schizoneura* is a common genus of the Permian of Gondwana, although the type species is widespread in the Triassic rocks of Europe. This is the only unequivocal record of the genus in Jurassic strata.

The *Otozamites gramineus* Bed contains a large flora. Harris claimed that it was not known before he began his work on the Yorkshire floras. He found the bed to be accessible for only a few metres horizontally and when exposed again, it (or perhaps another bed at about the same horizon) had a different flora (Harris, 1969). *O. gramineus* is common and found together with the scale leaf *Cycadolepis spheniscus*, here at its type locality. The two occur together at four locations, so most probably belong to the same plant (Harris, 1969). The gynoecium *Bennetticarpus litchi* also occurs here associated with *O. gramineus*, but elsewhere *B. fragrum* occurs with this leaf, hence creating a problem because the case for biological linkage is as good for either. The ferns *Cladophlebis haiburnensis*, *Kylikipteris arguta*, *Klukia exilis* and *Aspidistes thomasii* are common, as is the cycad leaf *Nilssonia syllis,* which is found in association with the scale leaf *Deltolepis mitra*, known only from this locality. The two are, therefore, presumed to come from the same plant (Harris, 1964). The conifer shoot *Marskea jurassica* is found here with cones attached.

Other interesting associations have been encountered at Beast Cliff. In sandstone at the foot of Rocky Point, a bennettitalean bud was found in association with plentiful *Ptilophyllum pectinoides* leaves where nothing could be determined. It consists of closely overlapping *Cycadolepis hypene* scales that Harris (1969) suggested enclosed the female flower *Williamsonia hildae*. The bud was at the top of a slender stem, *Bucklandia pustulosa*, which also bore a *Ptilophyllum pectinoides* leaf. All these cases of associated specimens are immensely valuable in showing how otherwise biologically isolated organs originated from the same parent plant.

The Fern Bed has yielded *Coniopteris burejensis*, *C. concinna*, *C. murrayana* and the common *Todites princeps*. Van Konijnenburg-van Cittert (1978, 1989) has described the in-situ spores of the last three species from specimens collected here.

The type locality for the rare pteridosperm *Ctenis exilis* is Harris' Bed A where he found three more or less complete pinnae and many minute cuticle fragments.

Interpretation

There is clearly considerable potential for further work at Beast Cliff, Harris having only scratched the surface of its palaeobotanical interest. It has already been shown that species occur here that are rare or absent from most of the other Yorkshire Jurassic localities. These include *Schizoneura stenophylla*, *Dicksonia mariopteroides*, *Coniopteris burejensis*, *Ctenis exilis*, *Nilssonia syllis*, *Deltolepis mitra* and *Paracycas cteis*. The Beast Cliff plant beds therefore seem to represent habitats that were different from those indicated by other sections in the Yorkshire Jurssic. Further discoveries of unusual plants can thus be expected in the future.

The large number of different assemblages at Beast Cliff reflects changing environments of sedimentation. The shallowest conditions permitted *Equisetum* to flourish and spread across the lagoons. Sudden influxes of sediment into these lagoons would have killed the entire stand, leading to rotting of the apical parts of stems and sand filling their hollow centres. Renewed colonization could have been initiated by survivors around the fringes of the lagoons if the depth of water was right. If it was too deep then *Equisetum* would have been restricted to the fringes, behind which would have been ferns, cycads and bennettites.

The large assemblage found in the *Otozamites gramineus* Bed suggests that there was a diverse local flora. However, although *O. gramineus* is common and found together with some of its reproductive organs, the associated plants in the various fossiliferous lenses vary greatly. This suggests that *Otozamites* colonized the fringes of the lagoon whereas the surrounding plants had no particular spatial arrangements. Fern remains are common but they are different from the species encountered in the Fern Bed, which presumably represents a very local assemblage.

The association of the equisetalean *Neocalamites nathorstii* with the conifers *Elatides thomasii* and *Elatocladus ramosus* suggests that they were growing together, probably some way up the river system inland. The conifer shoot *Marskea jurassica*, being found here with attached cones, had probably not travelled far before being incorporated into the sediment.

Conclusion

Beast Cliff has yielded a range of plant fossil assemblages with many species that are relatively rare in the Yorkshire Jurassic succession. The association of leaves with reproductive organs provides vital evidence for reconstructing whole plants. The many different assemblages were preserved in several different ways, showing how they can be related to sedimentation. The *Equisetum* stands preserved in growth position are important examples of in-situ fossilization.

MAW WYKE (HAWSKER BOTTOMS) (NZ 942 082)

Introduction

Maw Wyke is an outstanding locality for the study of Middle Jurassic fossil ferns, having yielded particularly fine examples of *Coniopteris*, *Cladophlebis* and *Phlebopteris*, including fertile specimens essential to systematic studies. Most of the genera recorded have extant relatives.

This important palaeobotanical site has received relatively little attention in the literature. There are hardly any references to plant fossils from it other than the records in Harris (1961a, 1964, 1969, 1979a; Harris *et al.*, 1974) of specimens coming from Hawsker (fallen blocks at Widdyfield), Hawsker Cliff, or Hawsker *Otozamites gramineus* Bed. Morgans (1999) described conifer wood from 'between Hawsker Bottoms and Castle Chamber', but this is outside the GCR boundary. It is nevertheless clear that the site has considerable potential importance, especially for the study of Jurassic ferns.

Description

Stratigraphy

The plant bed at Maw Wyke is a lenticular body of shale within the Saltwick Formation, and is thus of Aalenian age. Further details of the geology can be found in Cox and Sumbler (in press, in the site report for 'Hawsker Bottoms').

Palaeobotany

Only about 20 species have been recorded from Maw Wyke (Table 3.1), among which are the common cycad leaf *Nilssonia tenuinervis*, the rare *Stenopteris nana*, four bennettite leaf species and the 'flower' *Williamsonia gigas*, two species of the ginkgoalean leaf *Sphenobaiera*, two czekanowskialean leaf species and two species of conifer shoot. However, the main significant elements are six species of fern, many specimens of which are well preserved and often fertile. Diligent, responsible, collecting should yield more records.

Interpretation

The assemblage is an unusual one for the Yorkshire Jurassic strata. None of the ferns is rare, but there is a much higher percentage of them than at any other site. This suggests that the local flora included an extensive fern sward around the area of deposition, which was most probably a closed shallow lagoon. *Williamsonia gigas* and *Zamites gigas* are both present, confirming their biological relationship (van Konijnenburg-van Cittert and Morgans, 1999) and suggesting that the parent plants grew amongst the fern sward. The common czekanowskialean leaf *Solonites vimineus* is present, implying that it also grew in the vicinity. The other plants are a mixture of common and rare species. The rarest are the cycad *Stenopteris nana* and the ginkgophyte *Sphenobaiera ophioglossum,* which are only recorded from here and Whitby–Saltwick. There are none of the commoner conifer species, suggesting that there was no input from the rivers that would have been carrying such fragments from further inland.

Conclusion

This is a nationally important site for the study of Middle Jurassic ferns. The plant assemblage contains a much higher proportion of ferns than is usual for Yorkshire Jurassic floras. In addition, the preservation is unusually good, with well-preserved reproductive structures (sporangia) being common. There is considerable potential for further work here, especially pertaining to the palaeoecology of this unusual assemblage.

RED CLIFF (GRISTHORPE BAY/ CAYTON BAY) (TA 083 842)

Introduction

This site (Figure 3.37) is probably the most famous Middle Jurassic plant locality in the world. Its prolific flora has been the centre of attention for geologists ever since the early days of Williamson, Phillips, and Young and Bird. Over 100 taxa have been described from these beds in the Cloughton Formation (Bajocian), of which nearly 30 are type species. The best-known member of this flora is *Caytonia*, whose parent plant has been reconstructed using specimens from this site.

The fossiliferous deposits are sometimes referred to as the 'Cayton Bay plant beds', but they are more correctly referred to as the 'Gristhorpe plant beds'. They crop out in an extensive foreshore exposure (Figures 3.38 and 3.39) and, although usually only accessible at low tide, have been collected from many times over the years. As Harris (1969) stated, 'its flora though large must be one of the best known [in the world]'. Young and Bird (1822, 1828) were the first to figure and describe material from

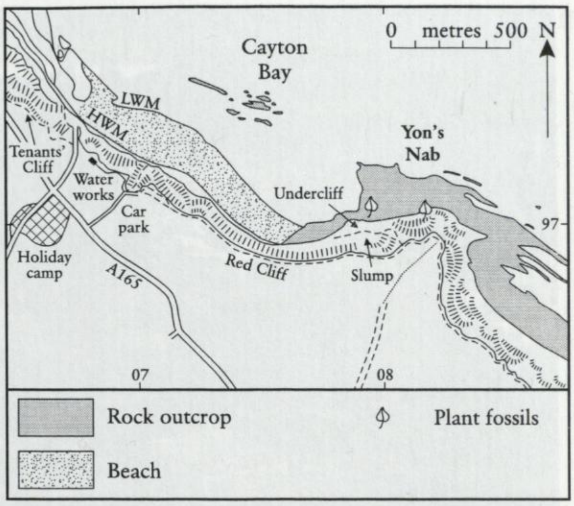


Figure 3.37 Map of the foreshore exposures of the Gristhorpe plant beds at Red Cliff. (After van Konijnenburg-van Cittert and Morgans, 1999.)

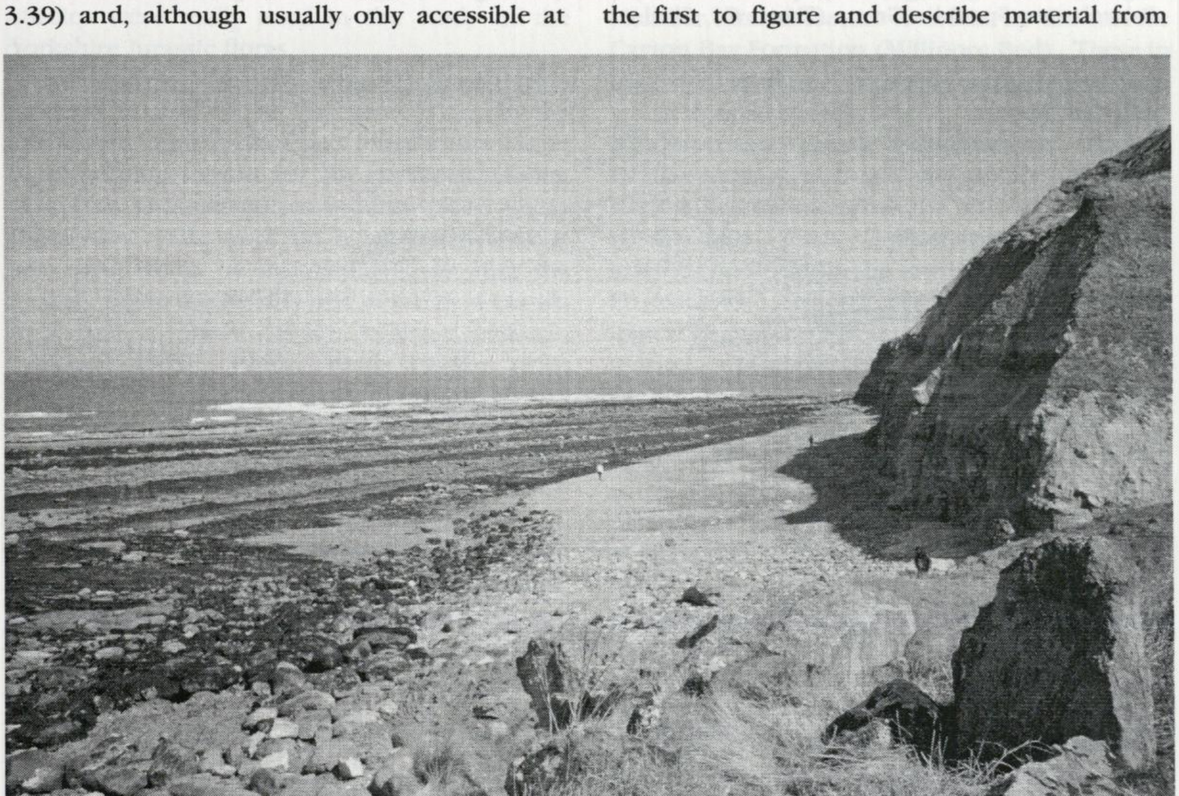


Figure 3.38 Cayton Bay, near Scarborough. The fossiliferous beds are on the foreshore (Photo C.J. Cleal.)

Figure 3.39 Collecting from the plant bed at Cayton Bay during the 1994 field meeting of the Linnean Society Palaeobotany Specialist Group (Photo: C.J. Cleal.)

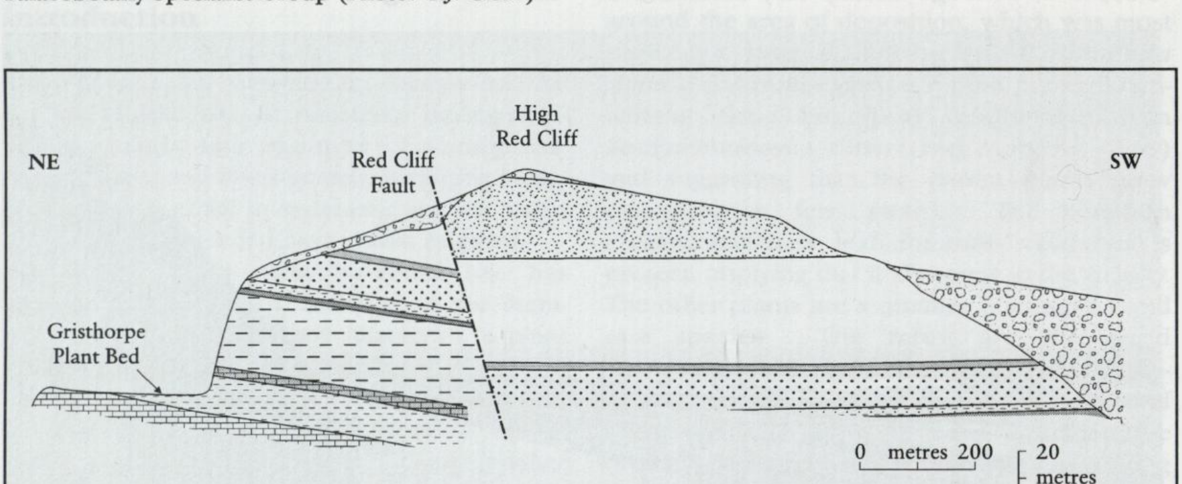


Figure 3.40 Cliff section at Red Cliff showing the position of the Gristhorpe Plant Bed. (After Rawson and Wright, 1992.)

Table 3.5 The locations of the plant beds identified by T.M. Harris (in manuscript) at Red Cliff (Gristhorpe Bay).

Gristhorpe Member	Gristhorpe Bed	54° 14' 34", 0° 20' 31"
	Black layer below Gristhorpe Bed	
	Black layer above Gristhorpe Bed	
Lebberston Member	Millipore Bed	54° 14' 34", 0° 20' 15"
	Yons Nab Marine Series	54° 14' 33", 0° 20' 15"
Sycarham Member	5 m below Millipore Bed	54° 14' 36", 0° 20' 12"
Scalby Formation	Black's Upper Estuarine Plant Bed in Grey Limestone	54° 14' 26", 0° 20' 9"
	Bed above channel	
	Hill's *Haiburia blackii* Bed in Cliff	
	Kendall's cliff foot bed in Upper Estuarine	54° 14' 11", 0° 19' 37"
	Mell-Casty Hill (1)	54° 14' 13", 0° 19' 47"
	Mell-Casty Hill (3)	54° 14' 11", 0° 19' 42"
	Mell-Casty Hill (4)	

here, shortly followed by Phillips (1829, 1835, 1875) and Lindley and Hutton (1837). Significantly, Lindley and Hutton showed that cuticles were still preserved in these fossils, although it was nearly a century before cuticle studies were really used in the study of the Yorkshire Jurassic floras.

Interest in the site waned significantly towards the end of the 19th century and by the early 20th century its exact location seems to have become forgotten. As explained earlier, Hamshaw Thomas rediscovered the plant bed in the 1920s. His work on a small ovuliferous structure, which he named *Caytonia* after the locality, made the locality one of the best known in Yorkshire. Harris (1941b, 1942a–c, 1943a,b, 1944a,b, 1945c, 1946a, 1948, 1949b, 1951, 1952a,b) later described or redescribed many of the species, and they formed a major part of his monograph (Harris, 1961a, 1964, 1969, 1979a; Harris *et al.*, 1974). Kendall (1947, 1948) described a number of conifers from the bed. More recent studies have been by van Konijnenburg-van Cittert (1968, 1981, 1989) and Morgans (1999), who included the site in a field guide to the Yorkshire Jurassic floras (van Konijnenburg-van Cittert and Morgans, 1999).

Description

Stratigraphy

Immediately north of Yons Nab, the Cloughton Formation is exposed at low tides as landward dipping beds (Figure 3.40). The succession is shown in Figure 3.41, including the position of the main plant bed. The oldest beds exposed (only at the lowest tides) belong to the Sycarham Member, and these are overlain by the marine Cayton Bay Formation (Millipore Bed). These in turn are overlain by the Gristhorpe Member, which represents a return to marshy, delta-top conditions and paralic sedimentation. Stacked tabular sheet sandstones with poorly developed channelling characterizes the unit, with burrows of the trace fossil, Diplocraterion, indicating marine conditions in the lower sandier horizons. Hancock and Fisher (1981) reported a palynological change up through the member in which marine dinoflagellate cysts, gave way to acritarchs and leiospheres, and finally tasmanitids. They suggested that this indicates gradual shallowing of a sublittoral environment, which coincided with an increase in the amount of plant material being deposited and preserved.

Harris, Kendall and Hill all collected extensively from the exposure, and several different plant beds were identified (Table 3.5), although the classic Gristhorpe Plant Bed, which is approximately 0.5 m thick and exposed continuously for over 100 metres, is the most prolific. It occurs near the base of the Gristhorpe Member and represents a channel abandonment facies (Livera and Leeder, 1981). It consists of three layers: a basal claystone rich in plant debris; a soft, grey-white claystone yielding the best

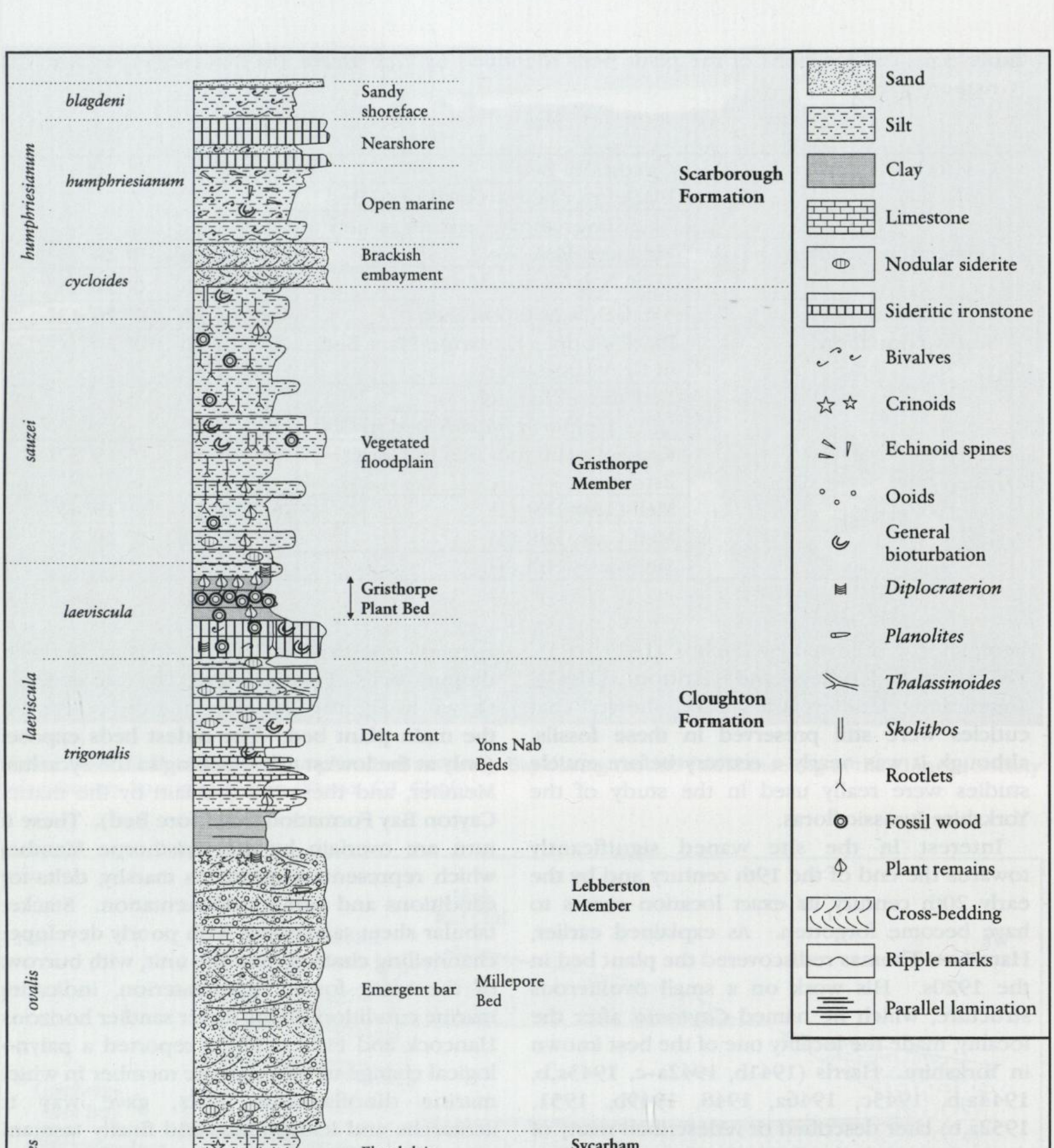


Figure 3.41 Stratigraphical section through the Gristhorpe Plant Bed and associated strata, exposed at Red Cliff. (After van Konijnenburg-van Cittert and Morgans, 1999.)

specimens; and an overlying hard, micaceous silty claystone in which U-shaped burrows of *Diplocraterion* indicate marine influence. The composition of the flora and the preservation of the plants changes laterally every few metres.

The best-preserved leaves and fructifications occur in pale grey to white clays while the more fragmentary plants tend to be common in medium to dark grey siltstones.

Palaeobotany

The complete list of species is given in Table 3.1 (see also Figures 3.42–3.45). It includes representatives of all the major plant groups known to be present in the Yorkshire Jurassic succession (bryophytes, horsetails, clubmosses, ferns, caytonias, 'pteridosperms', cycads, bennettites, ginkgophytes, czekanowskiaeans and conifers).

The Gristhorpe Bed is the type and only known locality for *Androstrobus manis*, *Otozamites thomasii*, *Bennetticarpus diodon* and *Elatocladus zamioides*. It is also the type

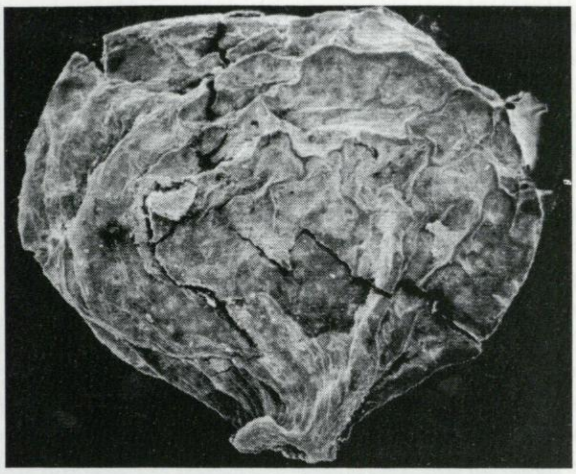


Figure 3.42▲ *Caytonia sewardii* Thomas. This seed-bearing organ was edible, like berries, since coprolites have been found containing their chewed up remains. The mouth of this cupule has its lip curving up to the left and is itself to the left of the broken stalk. Gristhorpe Plant Bed, Gristhorpe Member, Cloughton Formation, Red Cliff, × 20. (From Cleal and Thomas, 1999; photo: B.A. Thomas.)

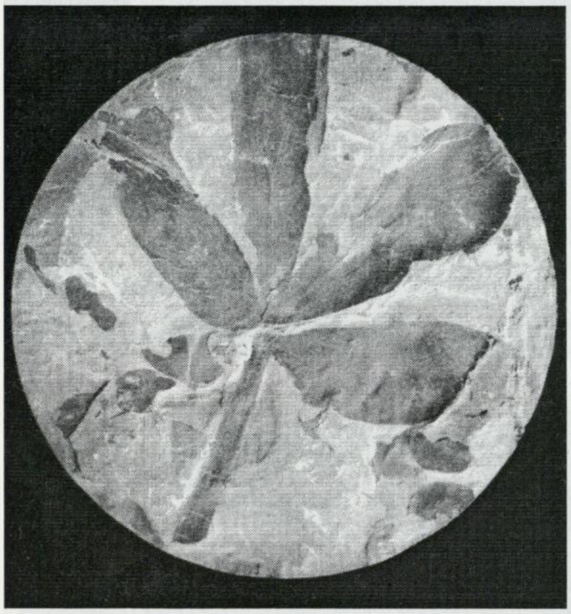


Figure 3.43▲ *Sagenopteris colpodes* Harris. This is an aggregate of two very similar species that differ only in size. The specimen shown here has a complete 'large' leaf with a petiole and four lanceolate leaflets and fragments of 'small' leaves. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.9639. Gristhorpe Plant Bed, Gristhorpe Member, Cloughton Formation, Red Cliff, natural size. (Photo: J.H.A. van Konijnenburg-van Cittert.)

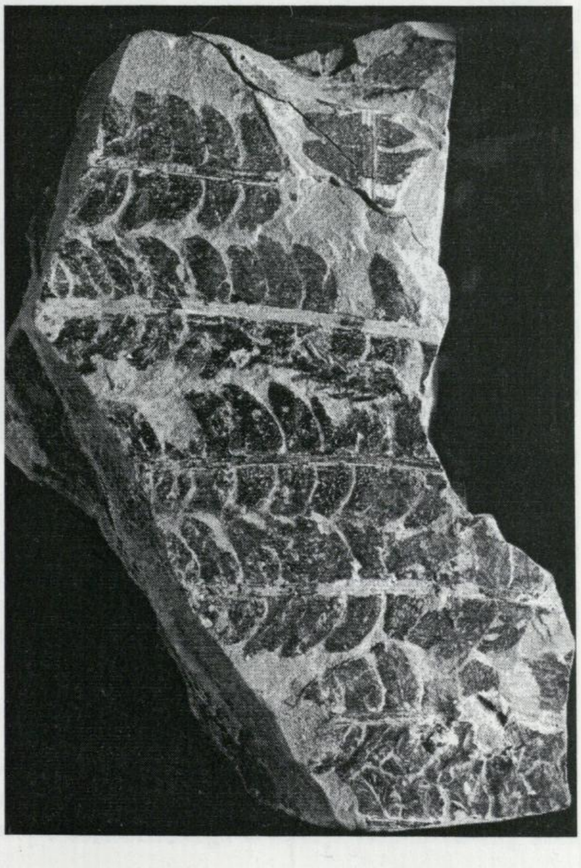


Figure 3.44▸ *Cladophlebis denticulata* (Brongniart) Nathorst. This is the sterile foliage of the osmundaceous fern *Todites denticulatus*, which only differs in being covered in sporangia. Both have a twice-divided frond with sharply toothed pinnules. National Museums and Galleries of Wales, Cardiff, specimen 98.24.G5, Gristhorpe Plant Bed, Gristhorpe Member, Cloughton Formation, Red Cliff, natural size. (From Cleal and Thomas 1999; photo: B.A. Thomas.)

Figure 3.45 *Elatides williamsonii* (Lindley and Hutton) Nathorst. Conifers belonging to this genus are thought to belong to the living family Taxodiaceae. This species is one of the commonest fossils in the Gristhorpe Plant Bed and is recognized by its spirally arranged, 6–12 mm long falcated leaves. Both male and females cones are borne terminally. Female cones, like the one shown here, are oval, 40–60 mm long and 20–25 mm broad, with spirally arranged cone scales. National Museums and Galleries of Wales, Cardiff, specimen 84.27G.361, Gristhorpe Plant Bed, Gristhorpe Member, Cloughton Formation, Red Cliff, × 1.5. (From Cleal and Thomas, 1999; photo: B.A. Thomas.)

locality for another 33 species: *Hepaticites arcutus*, *H. hymenoptera*, *H. wonnacottii*, *Aspidites thomasii*, *Todites thomasii*, *Amphorispermum pullum*, *Caytonanthus arberi*, *C. onocodes*, *Caytonia nathorstii*, *C. sewardii* (Figure 3.42), *Sagenopteris colpodes* (Figure 3.43), *S.*

phillipsii, *Ctenis reedii*, *C. sulicaulis*, *Ctenozamites leckenbyi*, *Androstrobus szei*, *A. wonnacottii*, *Deltolepis crepidota*, *Nilssonia tenuicaulis*, *Pseudoctenis locusta*, *Stenopteris nitida*, *Anamozamites nilssonii*, *Cycadolepis nitens*, *C. stenopus*, *Otozamites beanii*, *Williamsoniella coronata*, *Eremetophyllum pubescens*, *Czekanowskia microphylla*, *C. thomasii*, *Solonites vimineus*, *Geinitzia divaricum*, *G. rigida*, *Masculostrobus harrisii* and *Pagiophyllum insigne*.

Van Konijnenburg-van Cittert (1981, 1989) described the in-situ spores of *Coniopteris hymenophylloides*, *C. murrayana*, *Dicksonia mariopteris*, *Eboracia lobifolia*, *Kylikipteris arguta*, *Todites denticulatus*, *T. princeps*, *T. thomasii* and *T. williamsonii* from specimens collected here. Some specimens of the fern *Phlebopteris polypodioides* have recognizable fungal spots on their pinnae (Harris, 1961a). Morgans (1999) has recently described pyritised conifer wood from wood-rich layers as *Cupressinoxylon* spp. and *Xenoxylon phyllocladoides* Gothan 1906.

Interpretation

The Gristhorpe Bed contains the most diverse assemblage of plant fossils in the whole of the Yorkshire Jurassic succession. It has yielded an enormous amount of material and many accounts have been written of specimens found here. One of the best-known studies is that by Thomas (1925) on a small ovuliferous structure, which he named *Caytonia* after the locality, as noted above. This made Gristhorpe one of the best-known palaeobotanical localities in Yorkshire, particularly because Thomas argued that *Caytonia* might be an ancestral angiosperm. His reconstruction of the plant was based on the constant association of these ovuliferous structures with the male fructification *Caytonanthus* and the palmate leaf *Sagenopteris*. He thought *Caytonia* was a carpel enclosing ovules and possessing a stigmatic lip on which he had observed pollen. His work generated much interest in the plant, but Harris (1951, 1958) subsequently showed *Caytonia* to be an open pteridosperm cupule rather than a closed carpel. Pollen gained entry to the ovules through a canal below the lip; hence the grains observed by Thomas were those that had failed to enter the cupule rather than become successfully attached to a stigma. This revelation did not diminish interest in the site, and the *Caytonia* plant remains one of the best known of the now-extinct Mesozoic gymnosperms.

Two other important associations recorded from the Gristhorpe Bed have had important consequences for reconstructing Mesozoic plants. The most widely quoted is that of the cycad leaf *Nilssonia compta*, the ovuliferous cone *Beania gracilis* and the pollen-producing cone *Androstrobus manis* (Harris, 1941b, 1942b, 1964). This was used by Harris (1961b) to reconstruct the *Beania* tree (see Figure 3.7), a distinctive Jurassic cycad that is quite different from living cycads. Many palaeobotanists place this plant in its own family, the Nilssoniaceae, and it has played an important role in attempts to unravel the early evolutionary history of the cycads.

Four gynoecia, surrounded by persistent, narrow, inwardly curved bracts called *Bennetticarpus diodon* have been collected from the Gristhorpe Bed and nowhere else. It is, therefore, a very rare plant organ, particularly in view of the fact that it comes from what Harris (1969) has described as 'one of the most collected plant beds in the world'. Harris also recovered the scale leaf *Cycadolepis stenopus* from shale bearing the locally abundant bennettitalean leaf *Anomozamites nilssonii* (both species having this as their type locality) and suggested the two belonged together. Although the scales are twice as long as any previously described specimens, they are half the size of *B. diodon*. Nevertheless, similarity of epidermal structure is highly suggestive of the two being biologically linked. Unfortunately the base of *B. diodon* is unknown, although if it were complete it would have to be referred to either *Williamsoniella* or *Wielandia*. Indeed it was just for such uncertainty that the genus *Bennetticarpus* was created.

The number of species known from this site must, in part, be a result of excellent local conditions for preservation. The change in lithology from the basal claystone to the softer grey-white claystone is accompanied by a change in the quality of the plants preserved. Indeed one of the notable features of collecting in the Gristhorpe Bed is the softness of the shale and the beautiful appearance of the black plant remains. It would be interesting to know if there is any corresponding change in species content between the two claystone bands.

The assemblage is interpreted as having been deposited in a lagoon. The flora surrounding it must have been diverse for such a varied fossil assemblage to have been preserved. It includes the most diverse pteridophyte flora of any of the Yorkshire sites, although unusually, no horsetails have been recorded. Instead the rare lycophyte *Lycopodites falcatus* is present as are three species of the very rare thalloid liverwort genus *Hepaticites*. Like the liverworts, *Lycopodites* was probably a creeping plant so there must have been open ground for them to spread over. Where this might have been is a difficult question to answer. It is unlikely that it was around the lagoon because such an area would probably have been quickly colonized by ferns and gymnosperms. Perhaps *Lycopodites* and the liverworts grew on the levee banks and were washed in when parts of the bank collapsed or were eroded away. It is highly likely that the assemblage overall consists of the remains of a flora that was being carried to the site of deposition by a river system, although the good state of preservation of the plant remains suggests that they did not travel a great distance. Limited transport would have reduced damage to specimens and also permitted different organs of the same plant to become entombed together. Transportation over longer distances would have caused leaves and seeds to become separated because of their different buoyancy and waterlogging characteristics. The association of the leaves, female and males organs of *Caytonia*, and of the conifer *Elatides williamsonii* with female cones and seeds strongly suggests that the parent plants must have been growing not far from the lagoon.

Conclusion

The Gristhorpe Bed is the most famous locality in the British Jurassic succession and is widely known internationally. It has yielded a large and well-researched flora including the 'type' material for 37 species. The site has proved enormously valuable for linking dispersed organs biologically, which in turn has helped in developing whole-plant reconstructions. The most famous of these are the *Caytonia* and *Beania* plants. Even though so much appears to be known about the assemblage there is still considerable potential for further research into whole-plant reconstructions and palaeoecological interpretations.

CLOUGHTON WYKE (TA 010 951)

Introduction

The beds of the Cloughton Formation (the 'Middle Deltaic Formation' of earlier authors) exposed in Cloughton Wyke are well known for their abundant well-preserved plant fossils. Over 70 species have been recorded. Common genera include the bennettitaleans *Ptilophyllum* and *Otozamites* and the fern *Coniopteris*. Among the more important members of the flora are *Beania mamayi* and *Androstrobus wonnacottii*, the female and male cones of *Nilssonia tenuinervis*. These three taxa have enabled a reconstruction of the parent cycad to be made. The site is of national importance, especially for systematic studies of gymnosperms.

The site has long been the subject of palaeobotanical research. Leckenby (1864) collected plant fossils from the Cloughton Wyke exposure in the early 19th century and many were figured and described by Phillips (1829, 1835). Later, Nathorst (1880) and Halle (1911) sampled here;

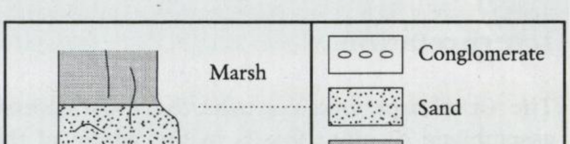


Figure 3.46 Stratigraphical section through the Cloughton Formation exposed at Cloughton Wyke. (After Livera and Leeder, 1981.)

their collections now being housed in the Natural History Museum, Stockholm. It is the type locality for a species of the ginkgophyte leaf genus *Eretmophyllum*, which was erected by Thomas (1913), and Kendall (1947, 1948) described shoots of the conifers *Brachyphyllum* and *Pagiophyllum* from here. However, the most extensive studies on the site were those of Harris (1943b, 1946a,b, 1948, 1951, 1952a,b, 1953), culminating in his monographs (Harris, 1961a, 1964, 1969, 1979a; Harris *et al.*, 1974). More recently, the palaeobotany of the site has been investigated by van Konijnenburg-van Cittert (1981, 1987) and Morgans (1999).

Description

Stratigraphy

The stratigraphy of the section at Cloughton Wyke is summarized in Figure 3.46. It begins with a hardground that is overlain by a storm-derived conglomerate and beach deposits. This is interpreted as the Millipore Bed (within the Cayton Bay Formation), which was probably deposited as a southerly migrating strand line (Livera and Leeder, 1981). The overlying Yons Nab Beds, which comprise the lowest part of the Gristhorpe Member, are exposed in the low cliff and are interpreted to represent part of a system of sand ridges separated by lagoonal deposits. In the centre of the wyke, the overlying beds are exposed in the cliffs and the rock platform. The lowest part consists of well-bedded mudstones, and siltstones with thin coals. The lowest coal was probably formed from drifted plant material. Fragments of *Equisetum* are found associated with some of the bedding planes showing root penetration. Surfaces showing burrows of the trace fossil *Diplocraterion* are also present.

Two metres of sandstones dominate the middle part of the member. These display a wide range of sedimentary features, including horizontal to wavy lamination, wave-ripple cross-lamination, planar lamination and small-scale trough cross-lamination. The upper part of the Gristhorpe Member consists of about 7 m of channel sandstones, siltstones and mudstones with rootlet beds. These include the major lacustrine plant-rich beds at Cloughton Wyke. Above are sheet sands/sandstones of crevasse-splay origin, which dominate the middle part of the Gristhorpe Member (Livera and Leeder, 1981).

Harris (in manuscript) listed 17 separate plant fossil localities at Cloughton Wyke; these are summarized in Table 3.6.

Table 3.6 The locations of the plant beds identified by T.M. Harris (in manuscript) at Cloughton Wyke.

Black Shale B	54° 20' 21", 0° 25' 45"
Black Shale A	54° 20' 25", 0° 25' 51"
Equisetum Bed in waterfall	54° 20' 25", 0° 25' 51"
3 ft 6 ins [=1.1 m] shaley sandstone	54° 20' 26", 0° 25' 51"
Solonites Bed	54° 29' 28", 0° 25' 42"
Eretmophyllum Bed	54° 20' 31", 0° 25' 45"
Fern Bed	54° 20' 36", 0° 25' 40"
Pachypteris Bed (10 ft [=3 m] sandstone)	54° 20' 36", 0° 25' 43"
Equisetum laterale Bed (9 ft [=2.7 m] sandstone)	54° 20' 37", 0° 25' 43"
quinqueloba Bed	
Coal Bed	54° 20' 40", 0° 25' 43"
Neocalamites Bed	
2 ft 6 ins [= 0.8 m] Drifted Plant Bed	54° 20' 50", 0° 25' 47"
Phlebopteris Bed (fallen)	54° 20' 51", 0° 25' 48"
Base of Millipore Bed	54° 20' 54", 0° 25' 49"
Otozamites bunburyanus Bed	54° 20' 55", 0° 25' 49"
Zamites Bed	54° 20' 54", 0° 25' 49"
15 ft [= 5 m] below Millipore Bed	54° 20' 55", 0° 25' 49"
(*Otozamites beanii*) *Nilssonia* Bed	54° 20' 56", 0° 25' 49"

Palaeobotany

The Cloughton Wyke plant beds have yielded 73 taxa (see Table 3.1; Figure 3.47). Remains of ferns, cycads, bennettites and conifers are especially common, but bryophytes, clubmosses, horsetails, caytonias, pteridosperms, ginkgophytes and czekanowskias have also been found. It is the type locality for 12 species: *Coniopteris margaretae*, *Bucklandia pustulosa*, *Cycadolepis eriophous*, *C. hallei*, *Nilssoniopteris pristis*, *Pterophyllum thomasii*, *Ptilophyllum pecten*, *Weltrichia pecten*, *Classostrobus cloughtonensis*, *Hirmeriella kendalliae*, *Pagiophyllum ordinatum* and *Trulla nitens*. For *Coniopteris margaretae*, *Cycadolepis eriophous* and *Classostrobus cloughtonensis* it is the only known locality. As with many other palaeobotanical sites in the Yorkshire Jurassic succession, however, a simple compilation of species tells only part of the story of the plant diversity at Cloughton Wyke. The different plant beds found by Harris (in manuscript) vary in content and importance, reflecting differences in both source vegetation and taphonomic histories. The *Solonites* Bed is the most significant and certainly contains the largest number of species (identified by an 's' on Table 3.1). It is most probably a lagoonal deposit incorporating the many species that grew around the edge of the water and in the near vicinity. *Solonites vimineus*, from which the bed takes its name, is very abundant; so common in some places that its matted leaves form a paper coal (Harris, 1974a). The bryophyte *Hepaticites arcutus* occurs here, and there are large numbers of pteridophyte remains, including the relatively rare *Lycopodites falcatus*, and *Kylikpteris arguta* (the spores of which have been described by van Konijneburg-van Cittert, 1989). A number of important gymnosperms have also been found, including cycad cones and leaves; bennettite flowers, leaves and scale leaves; and conifer shoots with cones.

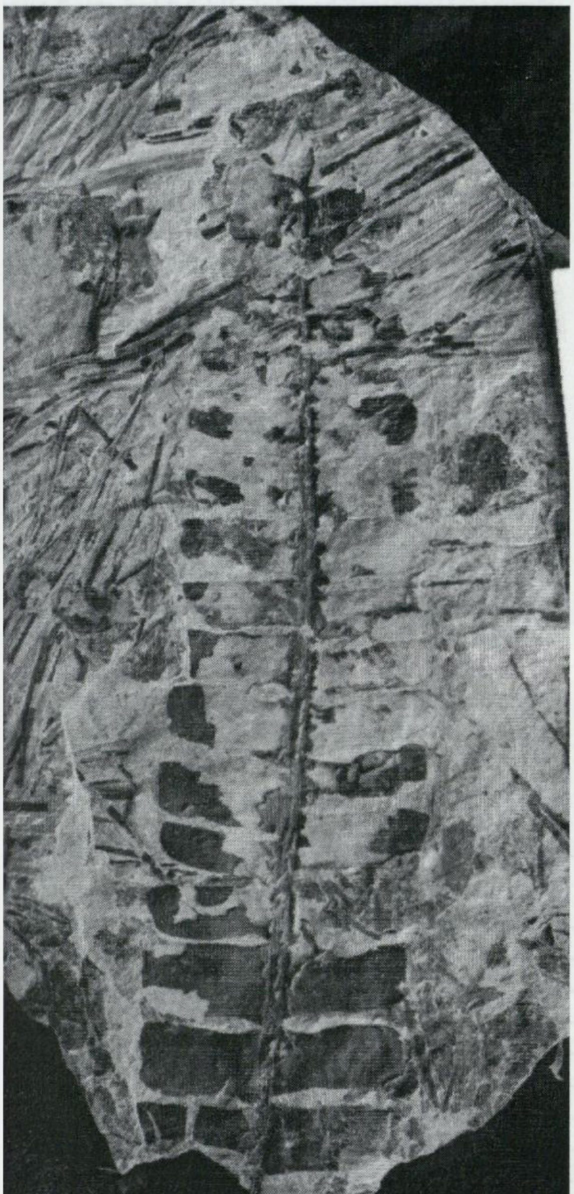


Figure 3.47 *Anomozamites nilssonii* (Phillips) Harris. These bennettitalean leaves are typically 150 mm by 30 mm and divided into square-cut segments that have minutely dentate ends. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.3085, Cloughton Formation, Cloughton Wyke, × 1.5. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

The *Nilssonia* Bed (discovered in the late 1940s or early 1950s by Wayne Fry and Serge Mamay) also contains abundant cycad remains, but this time it is the leaf *Nilssonia tenuinervis* (the only species here) and associated cones and bud scales.

The other beds yield much poorer assemblages although a few important finds have been made in them. For instance, the only remains of the fern *Coniopteris margaretae* have been found in the *quinqueloba* Bed of Harris along with *C. simplex*, *C. murrayana*, *Hepaticites arcutus*, *Lycopodites falcatus*, *Nilssoniopteris pristis* and *Ginkgo longifolius*. Van Konijnenburg-van Cittert (1987) reported abundant conifer remains from a loose block that probably originated from this bed.

The *Zamites* Bed, which is just above the Millipore Bed, is thought to be an autochthonous assemblage in which *Zamites gigas* is present along with masses of isolated leaves of *Pagiophyllum masculosum*, which in turn is associated with ovuliferous cone scales (*Hirmeriella kendalliae*) and huge numbers of *Classopollis* pollen grains.

Van Konijnenburg-van Cittert (1981, 1989) described the in-situ spores of *Coniopteris margaretae*, *C. hymenophylloides*, *C. simplex*, *Klukia exilis*, *Kylikipteris arguta* and *Todites denticulatus* from specimens collected from the Cloughton Wyke plant beds, and Morgans (1999) has recently described fragments of *Cupressinoxylon* spp. from woody horizons.

Interpretation

The Jurassic flora at Cloughton Wyke provides an important complement to the more diverse asssemblages from the Cloughton Formation at Red Cliff. Although there are some species unique to the site (*Coniopteris margaretae*, *Cycadolepis eriophous*) it is especially valuable for the associations of different plant organs, which help in the development of whole-plant reconstructions. For instance, abundant *Solonites vimineus* leaves in the *Solonites* Bed are associated with ovules of *Leptostrobus cancer*, which Harris has shown to occur together in six other Yorkshire localities. These are presumed to be biologically linked to the same czekanowskialean parent plant. There are some capsules here with relics of seeds and, although no complete seeds have yet been found, Harris suggested that a special search might prove worthwhile. In the same bed there are also associations between the cycad leaf *Nilssonia tenuinervis* and its supposed cone *Androstobus wonnacottii*; the bennettite leaf *Ptilophyllum pecten* and its supposed stem *Bucklandia pustulosa*; and *Cycadolepis stenopus*, the biologically related leaf *Pterophyllum thomasii* and the cones *Williamsonia leckenbyi* and *Weltrichia pecten* (numerous here in its type locality). There are also fine specimens of the conifer *Elatides williamsonii*, frequently with intact seeds.

The *Nilssonia* Bed is important because of the association of three cycad organs: the leaf *Nilssonia tenuinervis* (the only *Nilssonia* species present), the cone *Beania mamayi* and the bud scale *Deltolepis calyptra*. Harris found the scales only after a deliberate search, illustrating how important it is to realize which associated organs are worth looking for in any one site.

Van Konijnenburg-van Cittert (1987) collected good shoots of *Pagiophyllum masculosum* from the foot of the cliff to the south of the *quinqueloba* Bed. In close association was a female cone, *Hirmeriella kendalliae*, and three small pollen-producing cones, which she called *Classostrobus cloughtonensis* after the *Classopollis* pollen that it contained and the site from which it was recovered. This suggests that these organs can be linked to form the basis of a whole-plant reconstruction for one of the cheirolepidiacean conifers in the Yorkshire Jurassic strata.

An accumulation of abundant leaves almost entirely referrable to the pteridosperm *Pachypteris lanceolata* is present in the aptly called *Pachypteris* Bed. Although it has yet to be investigated in detail, a thorough search of this bed might well yield associated organs. The bennettite scale leaf *Cycadolepis eriphous* was found in fallen blocks along with *Otozamites mimetes*; this would also merit further investigation for evidence of additional association.

Cope *et al.* (1980a) interpreted the Millipore Bed as having been deposited as a southerly migrating strand line over the Sycarham Member and the overlying Yons Nab Beds as part of a prograding system of sand dune ridges separated by silt-dominated lagoonal deposits. They suggested that the environment was equally influenced by tides and waves. A thin coal with poor root foundation that can be seen in the basal shales was most probably formed by plant remains drifting into a lagoon. This lagoonal interpretation is supported by palaeobotanical data, the assemblages of well-preserved plants suggesting minimal transportation from a surrounding vegetation.

The *Solonites* Bed is the main plant bed at Cloughton Wyke. It contains a third of the species recorded for the site, which is more of a mixture of plants than is found in the other beds. Hence it is possible that some of these, such as *Otozamites beanii*, were not part of the immediate vegetation but were brought into the lagoon by a river. The lagoons must have gradually filled with sediment, *Equisetum* eventually colonizing the shallows and giving rise to beds now dominated by this pteridophyte.

Conclusion

Cloughton Wyke is a nationally important site for plants fossils of the Cloughton Formation. Within the varied assemblages there are many examples of organ associations that provide evidence for whole-plant reconstructions of the cycad *Nilssonia*, the bennettites *Ptilophyllum* and *Pterophyllum*, the czekanowskia *Solonites*, and the conifers *Elatides* and *Pagiophyllum*. It is also the type locality for 13 species, one of which, *Cycadolepis eriophous*, is known only from here.

SCALBY NESS (TA 037 911)

Introduction

The plant beds of the Scalby Formation contain an important flora, well known for its outstanding examples of ginkgoalean remains. The most significant is *Ginkgo huttonii*, here at its type locality. It is a good example of a 'living fossil', being closely similar to the only extant species, *Ginkgo biloba*, the maidenhair tree. The Scalby

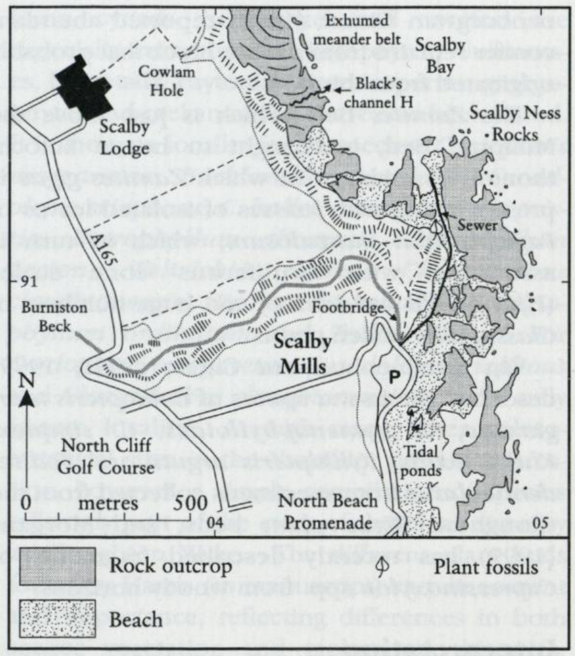


Figure 3.48 Location of the Scalby Ness GCR site. (After Van Konijnenburg-van Cittert and Morgans, 1999)

Figure 3.49 The Middle Jurassic *Ginkgo*-rich plant beds at Scalby Ness. (Photo: J.H.A. van Konijnenburg-van Cittert.)

Ness site is also the type locality for six other species of plant fossils.

Fossil plants have been collected, studied and described from this locality from the earliest days of investigations on the Yorkshire Jurassic flora. W.C. Williamson collected specimens of *Ginkgo* from here and these were illustrated in Lindley and Hutton's *Fossil Flora of Great Britain* (1831–1837). Subsequent studies have been carried out by Phillips (1875), Black (1929), Harris (1946b, 1948, 1961a, 1964, 1969, 1979a; Harris *et al.*, 1974) and Morgans (1999).

Description

Stratigraphy

The Scalby plant beds are part of the Scalby Formation (Bathonian), which overlies the thick marine Scarborough Formation (Figure 3.50). The exact age of the Scalby Formation has been debated for many years although Hogg (1993) recently dated it as late Bathonian, *discus* Zone on the basis of a sparse dinoflagellate cyst assemblage. It is fluvio-deltaic in origin although the actual type of depositional environment has been the subject of much discussion and disagreement. The lower division, the Moor Grit Member, consists of foreset deposits of a prograding delta front, channel fills of a braided river system and a deltaic distributary system. The upper division, the Long Nab Member, comprises delta-top deposits, a meander belt complex crossing an alluvial plain, and a saline-influenced delta plain system with smaller sinuous channels, some of which may have been tidal (Nami and Leeder, 1978; Leeder and Nami, 1979).

The plant fossils are found just above the base of the Long Nab Member at a number of places in the immediate vicinity of Scalby Ness where the gentle seaward dip brings these silty shales to the base of the cliff (Table 3.7). They constitute the Scalby Plant Bed. Nearby at Scalby Wyke the plant bed is a few metres from the base of the Long Nab Member and exposed on the shore under flat sandstone reefs. It is full of water-worn fragments suggesting that it is a drifted plant bed in a channel infill. In contrast, the Plant Bed at Scalby Ness is full of plants at various levels in what is interpreted as a river channel. The fragmentary nature of the plant remains and the fact that they are spread along the bedding planes indicate that they have drifted (Black, 1929). However, the fact that most of the fossils are well preserved indicates that they were not carried very far before becoming trapped in the river sediments.

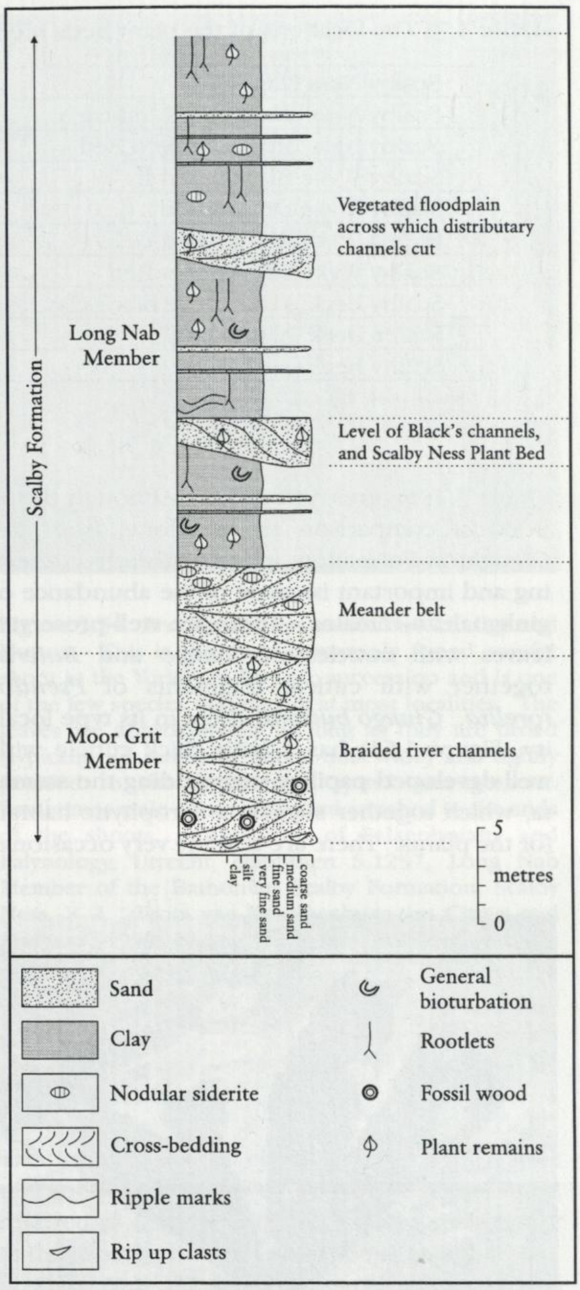


Figure 3.50 Stratigraphical section through the Scalby Formation, Scalby Ness GCR site. (After Van Konijnenburg-van Cittert and Morgans, 1999.)

Palaeobotany

Fifteen species are known from Scalby Ness

Table 3.7 The locations of the plant beds identified by T.M. Harris (in manuscript) at Scalby Ness.

Scalby Ness Plant Bed	54° 18' 14", 0° 24' 18"
Scalby Ness *Ginkgo* Bed in beach	54° 18' 20", 0° 24' 17"
Scalby Ness Brown *Ginkgo* Bed	54° 18' 21", 0° 24' 30"
Scalby Wyke Black's Bed E	54° 19' 2", 0° 24' 50"
Scalby Wyke Drifted Bed	54° 19' 0", 0° 25' 0"
Scalby Wyke Black's Bed G	54° 18' 57", 0° 25' 0"
Scalby Wyke *Otozamites* Bed	54° 18' 21", 0° 24' 36"
Scalby Beck, sand above black clay	54° 18' 13", 0° 24' 36"
Scalby Beck, black clay	
Scalby Beck sandy layer	54° 18' 14", 0° 24' 35"

(Table 3.1; Figures 3.51–3.54). Although this is poor in comparison to the floras from the Cloughton Formation, it is particularly interesting and important because of the abundance of ginkgoalean remains. There are well-preserved leaves with cuticles of *Ginkgo* and *Baiera*, together with cuticle fragments of *Pseudotorellia*. *Ginkgo huttonii* (here in its type locality; Figure 3.51) has a fairly thick cuticle with well-developed papillae surrounding the stomata, which together suggest a xerophytic habitat for the plants. There are also the very occasional

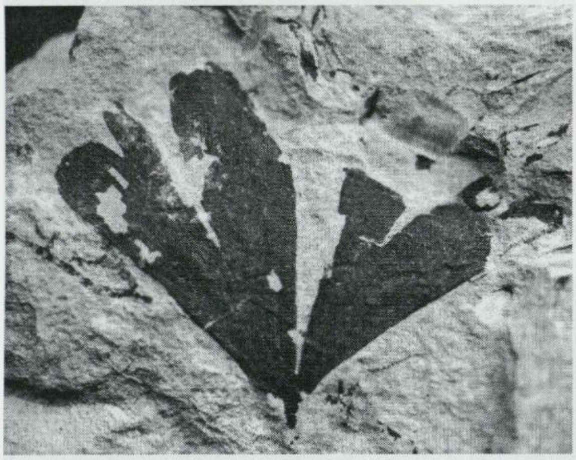


Figure 3.51 *Ginkgo huttonii* (Sternberg) Heer. This ginkgoalean leaf is the most common plant fossil at Scalby Ness, which is also its type locality. The leaf is characteristically deeply divided into six segments with rounded apices. Associated seeds found at Scalby Ness are attributed to the same plant that bore these leaves. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.3037, Long Nab Member of the Bathonian Scalby Formation, Scalby Ness, × 1.2. (From van Konijnenburg-van Cittert and Morgans, 1999; Photo: J.H.A. van Konijnenburg-van Cittert.)

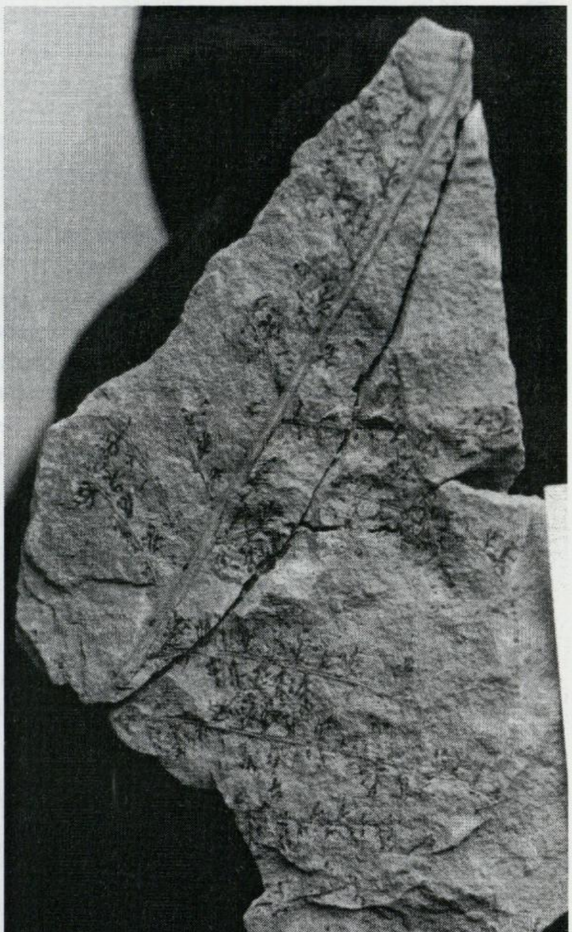


Figure 3.52 *Coniopteris bella* Harris. This fern, belonging to the extant family Dicksoniaceae, is characterized by its rounded leaf segments. It is relatively common at Scalby Ness but less so in the Gristhorpe Plant Bed at Cayton Bay (Red Cliff). Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.3031, Long Nab Member of the Bathonian Scalby Formation, Scalby Ness, natural size. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

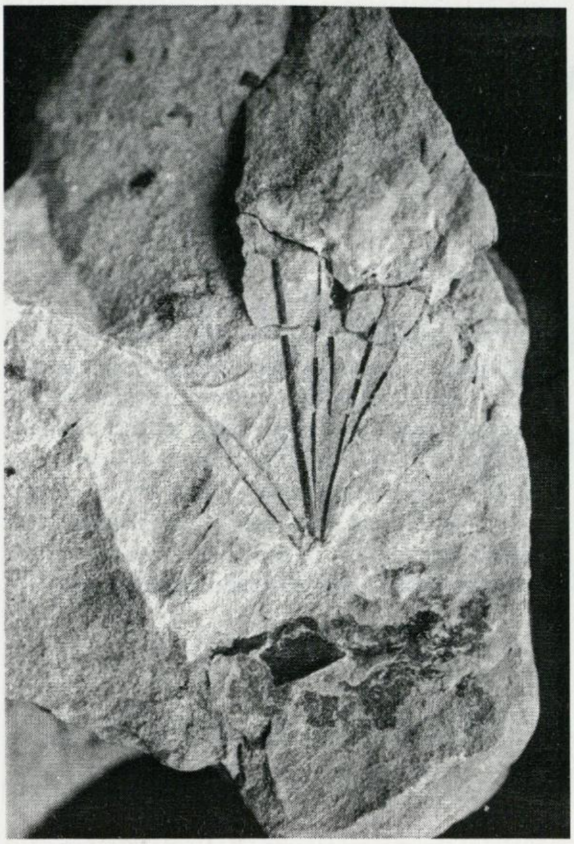


Figure 3.53 *Czekanowskia blackii* Harris. This species, which is locally common at Scalby Ness, is characterized by having five to eight leaves attached to each short shoot. Each leaf can be up to 150 mm long and normally forks twice. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.1292, Long Nab Member of the Bathonian Scalby Formation, Scalby Ness, × 2. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

Figure 3.54 *Brachyphyllum mamillare* Lindley and Hutton. This is the most commonly found conifer shoot in the Yorkshire Jurassic succession and is one of the few species that occurs at most localities. The leaves are approximately as long as they are broad (typically 1.5 mm long and 2 mm wide) and tightly pressed to the stem in a spiral arrangement. Sometimes male cones are found attached to the ends of the shoots. Laboratory of Palaeobotany and Palynology, Utrecht, specimen S.1257, Long Nab Member of the Bathonian Scalby Formation, Scalby Ness, × 2. (From van Konijnenburg-van Cittert and Morgans, 1999; photo: J.H.A. van Konijnenburg-van Cittert.)

seeds, bud scales and male cones, which have been attributed to *G. huttonii*.

Other species that are relatively common are *Coniopteris bella* (Figure 3.52), *Zamia gigas*, *Otozamites graphicus* and *Czekanowskia blackii* (here at its type locality; Figure 3.53). There are also the interesting conifers *Cyparissidium blackii* (foliage), *Pityanthus scalbiensis* (male cone) and *Scarburgia hillii* (female cone), this being the type locality for the last two.

Morgans (1999) has recently described charcoalified fragments of conifer wood from meandering channel sandstones comprising the overlying Long Nab Member as *Cedroxylon* spp. and *Cupressinoxylon* spp..

Interpretation

This is one of the classic sites for Mesozoic ginkgophytes. The well-preserved leaves here, referred to *G. huttonii*, bear a striking similarity to those of the living *G. biloba*. More significant, however, are the closely associated seeds and pollen organs that compare well with those of the living tree. Not all fossil ginkgoaleans are quite so similar to the modern form (Hori *et al.*, 1997). It is clear that there was a considerable diversity in this group in the Mesozoic Era. Nevertheless, the fossils from the Scalby Ness *Ginkgo* Bed strongly support the idea of *Ginkgo biloba* being a 'living fossil'.

Harris (1979a) took *Cyparissidium blackii*, *Pityanthus scalbiensis* and *Scarburgia hillii* to be parts of one plant species, which he assigned to the extant Southern Hemisphere family Podocarpaceae. This suggests a cosmopolitan history for the family, as also inferred from the widespread distribution of podocarp-like pollen grains in Mesozoic and Tertiary deposits of the Northern Hemisphere, particularly in Russia. The cone is much larger and more developed than those of living podocarps, which suggests that the modern cones, which often comprise just one or two cone scales, are probably reduced.

The presence of well-preserved plant organs shows that they were not carried far, if at all, before becoming trapped in the sediment. Consistent with this interpretation are the associations of *Ginkgo* leaves with what are probably the seeds and pollen organs of the plant, and the conifer *Cyparrisidium blackii* with its male fructification *Pityanthus scalbiensis* and its female cone *Scarburgia hillii*. These characters of the assemblage are consistent with the idea that a delta marsh flora is represented, as suggested by Hemingway (1974). In contrast, the water-worn fragments that dominate the nearby Scalby Wyke plant bed suggest that it is a bed of drifted plants that settled with fine clastic sediments in an abandoned channel.

Conclusions

The main significance of the plant bed lies in the abundance of ginkgoalean remains. It is the type locality for *Ginkgo huttonii* and the seeds, scales and male cones referable to this species. Although some 170 Ma old, these fossils are very similar to the living maidenhair tree, *Ginkgo biloba*. Much has also been learned about the evolutionary history of the Podocarpaceae from the shoots and cones collected here.