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

GCR Editor: D. Palmer

JOINT NATURE CONSERVATION COMMITTEE

Chapter 6

The Cretaceous palaeobotany of Great Britain

B.A. Thomas and D.J. Batten

INTRODUCTION

The Upper Cretaceous Series of Britain consists almost exclusively of the distinctive calcareous marine deposits known as 'Chalk', which contain no identifiable plant macrofossils. However, the Lower Cretaceous rocks of southern Britain consist of terrestrial or shallow marine clastic sequences that contain a good macrofloral record. It is best illustrated by the Wealden flora, although there are other localities along the south coast of England and on the Isle of Wight (see Luccombe Chine and Hanover Point GCR site reports). Similar floras are known from several parts of continental Europe (Belgium, France, Germany, Spain and Portugal) although some of these are not strictly contemporaneous.

HISTORY OF RESEARCH

The British Wealden flora has been studied intermittently since the early part of the 19th century. Mantell (1822) was the first to report that plant fossils occurred in Wealden deposits but the specimens were not described for another two years (Stokes and Webb, 1824). Later, Mantell (1833) himself figured and described plant fossils from the Tilgate Forest, and also referred to them in his synoptic paper on the palaeontology of Sussex (Mantell, 1835). Fitton (1836) described further remains from the Wealden rocks of south-east England, including the first reference to *Tempskya* stems. Other records were documented by Brown (1851), Topley (1875), Carruthers (1870a; in Dixon, 1878) and Peyton (1883). Bristow (1869) reported the presence of Wealden plants on the Isle of Wight.

The next major contribution was by Albert Seward (1894, 1895, 1913), who described most of the then-available specimens, principally in the collections of the British Museum (Natural History), and produced what was for many years the definitive account of this flora. However, as with his work on the Yorkshire Jurassic floras (see Chapter 3), a major weakness of his work was his failure to realize the important role that cuticle studies could play in improving the understanding of the plants.

A significant development was by R. Holden (1914), who prepared cuticles from bennettite foliage from the Wealden near Hastings and showed its importance in taxonomic work on these fossils. It was, however, many years before there were any further major developments in the study of the Weald floras. The recent growth in interest in them has arisen mainly from the activities of Ken Alvin, Joan Watson and their co-workers, who started to revise the flora during the 1960s using modern techniques, especially cuticle analysis. The results of this work have been published in numerous papers (e.g. Alvin, 1974, 1983; Alvin *et al.*, 1978, 1981, 1994; Watson, 1977, 1983; Watson *et al.*, 1987, 1988; Skog, 1986). Watson has also been publishing monographs on various plant groups in the Wealden flora (Watson, 1969; Watson and Batten, 1990; Watson and Sincock, 1992). This work on the macrofossils has been complemented by analyses of the palynology of these deposits by Norman F. Hughes (e.g. Hughes, 1958, 1976; Hughes and Croxton, 1973) and David J. Batten (e.g. 1968, 1973, 1975, 1982, 1998), which have helped to widen the perspective of both the vegetation and the environment of southern England during much of the Early Cretaceous Epoch. Finally, Tim Oldam (1976) investigated the dispersed cuticles found in the Wealden plant debris beds.

Plant fossils tend to be rare in the Lower Greensand but have nevertheless attracted some attention because of their fine preservation. Mantell (1822) and Fitton (1836) made passing references to petrified wood from here, but the first macrofossil to be described in detail was a petrified conifer cone from Lyme Regis, *Pinostrobus oblongus* (Lindley and Hutton, 1834), later redescribed by Williamson (1887). Mantell (1833, 1835, 1851) made further references to wood in these deposits, and later (Mantell, 1844, 1846) described fossil cones. By 1854 Morris was able to list six fossil plant species from the Lower Greensand in his *Catalogue of British Fossils*. Mackie (1862) described the famous 'Dragon tree' from the Lower Greensand of Kent as a possible monocotyledon, although it was later shown by Marie Stopes (1911) to be a conifer. However, the most important contributions in the 19th century were by Carruthers (1866, 1867b, 1869, 1870a) who described several cones and stems from the Lower Greensand deposits of southern England. Berry (1911) included a list of 17 species from this succession in his summary of Lower Cretaceous floras.

The fossil wood from the Lower Greensand was first described in detail by Barber (1898) and then in a number of papers by Stopes (1911, 1912). Her work culminated in the catalogue of the Lower Greensand plant fossils in the then British Museum (Natural History), which to this day remains the definitive account of these floras (Stopes, 1913, 1915). In 1918, she described a bennettite cone from the Lower Greensand, and another from the Gault of Folkestone. However, her now-famous book on birth control, *Married Love*, was also published in 1918, and this effectively marked the end of her palaeobotanical work (Andrews, 1980). Since then, little work has been done on the palaeobotany of the Lower Greensand, although a study on the wood is currently being finalized by Mark Crawley, formerly of the Natural History Museum, London.

PALAEOGEOGRAPHICAL SETTING

The palaeogeography of the Early Cretaceous world is summarized in Figure 6.1. Most of the land was still joined together in the supercontinent of Pangea, although the beginnings of some of today's oceans, such as the North Atlantic, were apparent. One of the most notable features of the Early Cretaceous Epoch was that arid and semi-arid conditions had not only spread through most of the low latitudes but also into some parts of the middle latitudes of both the Northern and Southern hemispheres. Britain was in middle latitudes at the time and the climate was hot to very warm. Rainfall varied and sometimes there were periods of severe drought, especially in the Wessex Basin (Allen, 1998).

As in the Jurassic Period, the Early Cretaceous Epoch was a time of 'greenhouse' conditions, with a relatively low climatic gradient between the equator and the poles. This led to relatively low levels of vegetational provincialism over the globe. The plant macrofossil record of the equatorial zone is generally very poor. Palynological studies have suggested that a restricted vegetation prevailed, comprising mainly cheirolepidiacean conifers and matoniacean ferns (Doyle *et al.*, 1982). Three floristic zones have been recognized (Meyen, 1987; Vakhrameev, 1991): the Notal Palaeoarea in southern middle and high latitudes (Australia, India, southern Africa); the Europe (or Eurosinian) Palaeoarea in northern middle latitudes (USA, much of Europe and China); and the Siberia Palaeoarea in northern high latitudes (Siberia, north-east Canada). According to this scheme the British floras clearly belong to the Europe Palaeoarea.

During the first part of the Cretaceous Period

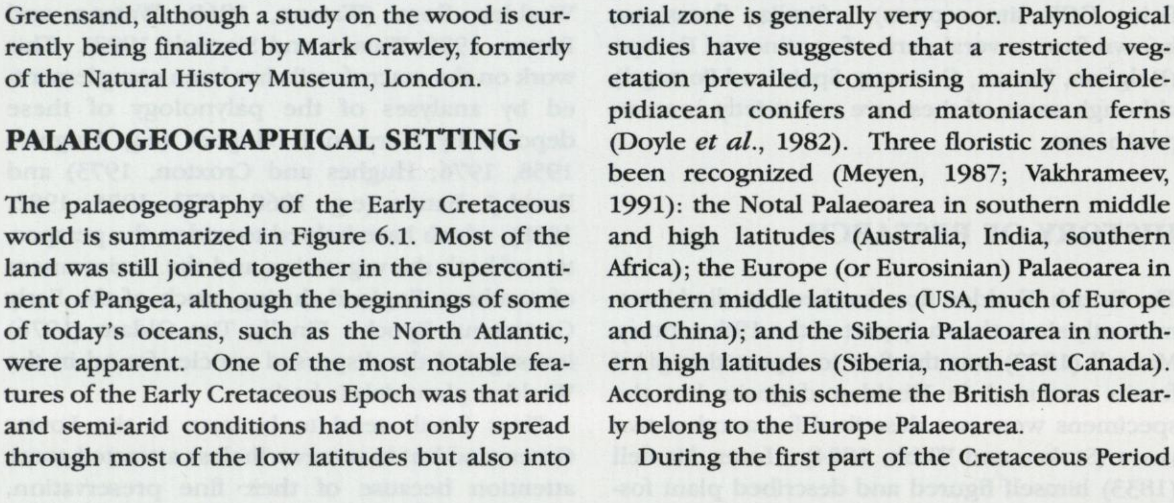

Figure 6.1 Palaeogeography of the Early Cretaceous world, showing main areas of land and mountains (based on Smith *et al.*, 1994). Also shown are the main palaeofloristic areas (based on Meyen, 1987 and Vakhrameev (1991).

(Berriasian to Hauterivian), central southern and south-eastern England was part of an area of coastal mudflats with lagoons and sandy rivers (Figure 6.2) (Allen, 1976, 1981). This supported the varied vegetation that forms the classic Wealden floras of south-east England. The fossils reveal important environmental information. A few plants are relatively well known in terms of growth habit, internal structure and reproductive biology. The vast majority of species are, however, less well known, with many being represented by one or only a small number of fragments. Unless they show special morphological or structural characteristics, they are of little value for environmental interpretations. The most reliable characters, according to Watson and Alvin (1996), are as follows:

1. Charcoal, which is accepted as a reliable indicator of wildfire that most probably started by lightning strike.
2. Xeromorphy, whose significance is far from clear. Xeromorphic characters, including thick-walled epidermis and hypodermis, thick and shiny cuticles, epicuticular wax, papillae and trichomes, salt glands, sunken stomata, small leaves and photosynthetic stems, are all found in Wealden plants. They can indicate either dry conditions or physiological adaptations for water uptake, transportation or loss. They are prevalent in the gymnosperms and especially in the conifers. However, all conifers living today have xeromorphic characters regardless of the climate in which they live, so not much can be read into their abundance in the Wealden.
3. Growth rings, which indicate seasonal environments; these are usually alternations of warm and cold or wet and dry. Ring patterns observed in Wealden woods are most probably the result of alternating wet and dry conditions.

Batten (1975, 1998), Allen (1976) and Watson and Alvin (1996) have given summaries of the Wealden flora and interpreted the environments in which its various components grew. Allen (1976) interpreted the lower Hastings Beds as coastal mudplains with lagoons, sandy watercourses and coalescent alluvial fans that were subject to wet and dry seasons. Batten (1968, 1973, 1975, 1982) used palynological and palynofacies data including, with co-workers (Batten and Eaton, 1980; Batten and Lister, 1988a,b), the distribution of dinoflagellate cysts to interpret the depositional environments and composition

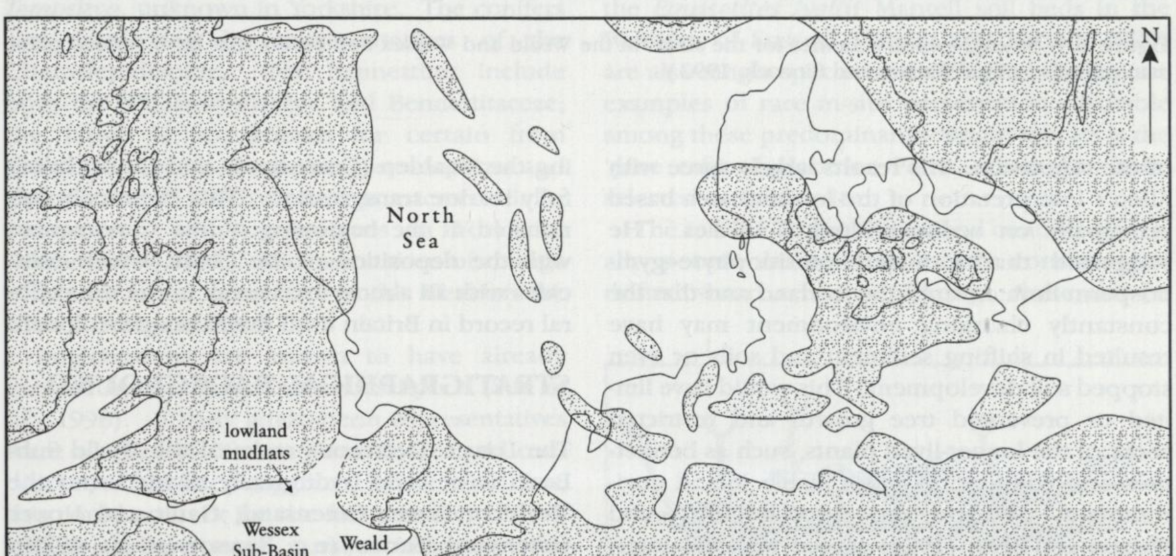

Figure 6.2 Palaeogeography of north-western Europe during the Berriasian Age, showing areas of lowlands where the 'Wealden' deposits typically developed. Scale: 1 cm = *c.* 100 km (After Batten, 1996.)

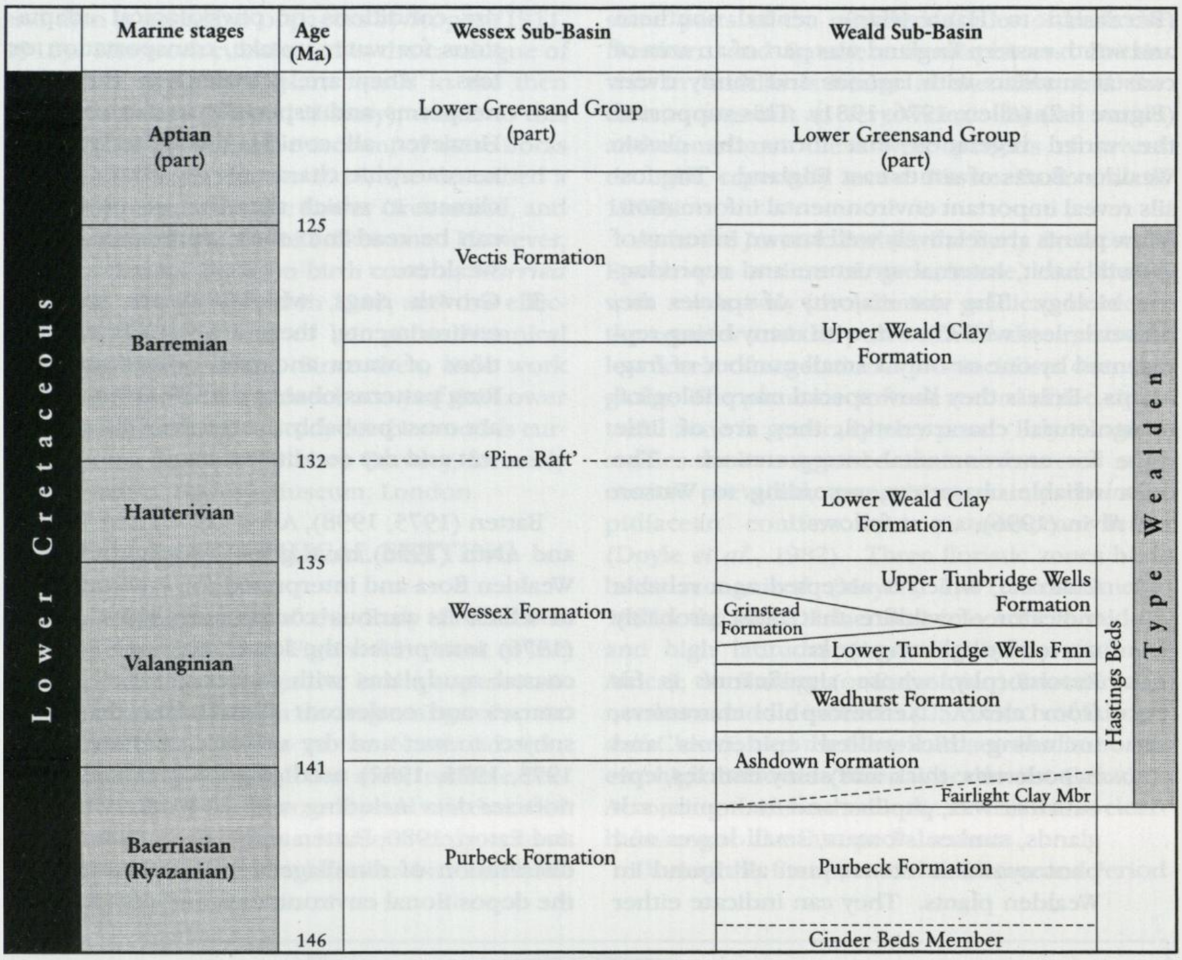

Figure 6.3 Stratigraphical schemes for the strata in the Weald and Wessex Sub-Basins that have yielded plant macrofossils. (After Watson and Sincock, 1992.)

of the vegetation. His results largely agree with Allen's interpretation of the lowland area based principally on sedimentological studies. He suggested that a mixed pteridophyte–gymnosperm flora covered the lowland and that the constantly changing environment may have resulted in shifting sediment and soils or even stopped soil development. This would have limited or prevented tree growth and restricted some of the longer-lived plants, such as bennettites and conifers, to more stable inland environments. Watson and Sincock (1992) and Watson and Alvin (1996) agreed with this interpretation, believing there to be bennettitaleans, cycads, perhaps some conifers and ferns in a number of distinct communities requiring different microclimate and edaphic conditions.

Later in the Early Cretaceous Epoch, there is evidence of rising sea levels, the deposits overlying the Wealden (Greensands and Gault) being fully marine transgression. This eventually culminated at the beginning of the Cenomanian with the deposition of the Chalk, which coincides with an almost total break in the macrofloral record in Britain until the Palaeocene Epoch.

STRATIGRAPHICAL BACKGROUND

The Lower Cretaceous rocks of the Weald Sub-Basin have been traditionally divided into the Wealden, Lower Greensand, Gault and Upper Greensand 'Series' (e.g. Rawson *et al.*, 1978). The Wealden succession is divided into the Hastings Group and the Weald Clay Formation, the former comprising several formations (Figure 6.3), the latter being composed of Lower and Upper divisions. Much of the material described by the earliest workers (e.g. Mantell, 1822; Stokes and Webb, 1824) originated from inland exposures in quarries in the Wadhurst and Tunbridge Wells formations, which are Valanginian in age (e.g. Watson and Sincock, 1992). However, the coastal exposures, including all those covered in this volume, are in the underlying Ashdown Formation and thus somewhat older (late Berriasian–early Valanginian).

The rather different successions that are exposed on the Isle of Wight are divided into the Wessex and Vectis Formations, Lower Greensand Group, and Gault and Upper Greensand Formations (Figure 6.3). The famous 'pine raft' at Hanover Point is in the upper Wessex Formation and thus post-dates the palaeobotanical sites of the Weald Sub-Basin. The stratigraphically highest flora, from Luccombe Chine, is in the Lower Greensand and Aptian in age.

EARLY CRETACEOUS VEGETATION

Although the plant groups present in the Wealden floras are broadly the same as those seen in the Yorkshire Jurassic succession (see Chapter 3), the proportions are somewhat different. They are particularly rich in horsetails, ferns, bennettites and conifers. The commonest ferns belong to the Matoniaceae, although there are also the remains of the enigmatic tree fern *Tempskya*, unknown in Yorkshire. The conifers are dominated by representatives of the Cheirolepidiaceae. The bennettites include both the Williamsoniaceae and Bennettitaceae; the latter is not known for certain from Yorkshire. Cycads, caytonias, corystosperms and ginkgos are all relatively rare as macrofossils by comparison with occurrences in Yorkshire (Vakhrameev, 1991). Reconstructions of a range of plants found preserved in the Wealden are shown in Figure 6.5.

Angiosperms are known to have already evolved by the Early Cretaceous Epoch (Sun *et al.*, 1998). If early angiosperm representatives were adapted to life in upland and/or arid conditions, as has been suggested by some authors, this could account for the fact that they do not appear to have made a major impact on the mudflats of southern England during deposition of the Wealden succession. Hill (1996) has described just one possible example (*Bevhalstia*) from the Wealden Clay, although its systematic position is somewhat in doubt (Figure 6.4).

CRETACEOUS PALAEOBOTANICAL SITES IN BRITAIN

The most important Cretaceous palaeobotanical sites in Britain are in the Ashdown Formation of the Weald Sub-Basin (Figure 6.3). The flora is large, varied and well preserved in mudplain deposits that indicate deposition close to the position of growth. Today, the only site still yielding material is at Covehurst, a coastal exposure to the east of Hastings. This was, therefore, selected as the GCR site. Comparable, although less diverse, floras have been reported in the past from higher horizons (Wadhurst and Tunbridge Wells formations) but most of these inland workings are no longer exposed.

There are numerous other sites in the Ashdown Formation and in the Wessex Formation of the Wessex Sub-Basin that have yielded plant macrofossils. These yield floras that vary considerably in both content and range of diversity. Some are dominated by a single species, such as the '*Pseudofrenelopsis* bed' (Wessex Formation) (Alvin *et al.*, 1981) and the '*Weichselia* bed' (Vectis Formation) (Alvin, 1974), both near Hanover Point on the Isle of Wight. *Lycopodites hannahensis* Harris in the Lower Tunbridge Wells Sand Formation (Ardingly Sandstone Member) at Philpots Quarry, West Hoathly, Sussex (Harris, 1976) and the *Equisetites lyellii* Mantell soil beds in the Wealden of Sussex (Watson and Batten, 1990) are also single-species assemblages but they are examples of rare in-situ preservation. Notable among these predominantly single species is the 'pine raft' of Hanover Point, which has been selected as a GCR site.

The marine Lower Greensand contains generally poorer macrofloras mostly consisting of drifted wood remains, although these can be

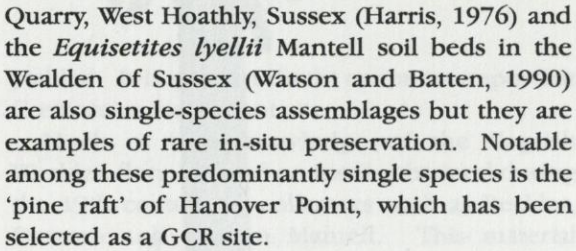

Figure 6.4 Reconstruction of the early possible angiosperm *Bevhalstia*, described by Hill (1996) from the English Wealden. (Redrawn from an original by Annette Townsend.)

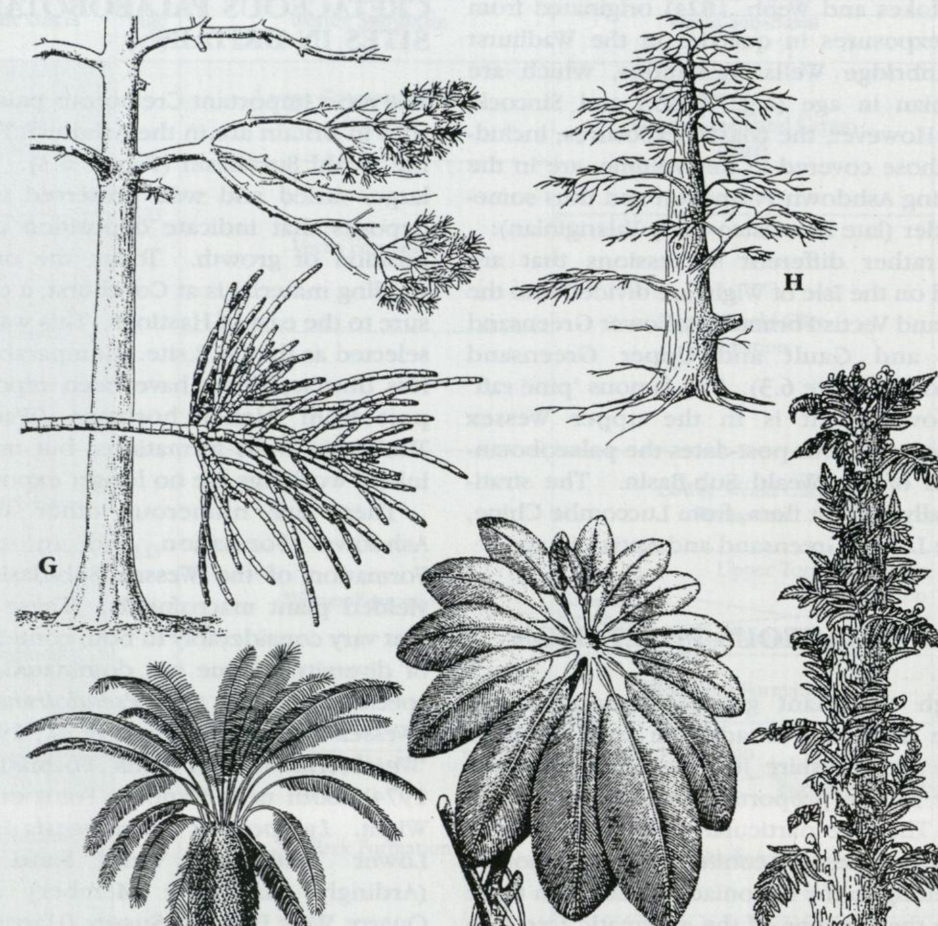

Figure 6.5 Reconstructions of typical plants found in the Wealden floras of southern England. (A) *Equisetum burchardtii*, *c.* × 0.1, (B) *Equisetites lyellii*, *c.* × 0.1, (C) *Tempskya*, *c.* 6 m tall, (D) *Weichselia reticultata*, *c.* × 0.08, (E) *Monanthesia*, *c.* 2 m tall, (F) *Cycadeoidea*, *c.* × 0.05, (G) *Pseudofrenelopsis parceramosa*, a tall forest tree (H) *Cupressinocladus valdensis*, also a tall forest tree. (From Watson and Alvin, 1996.)

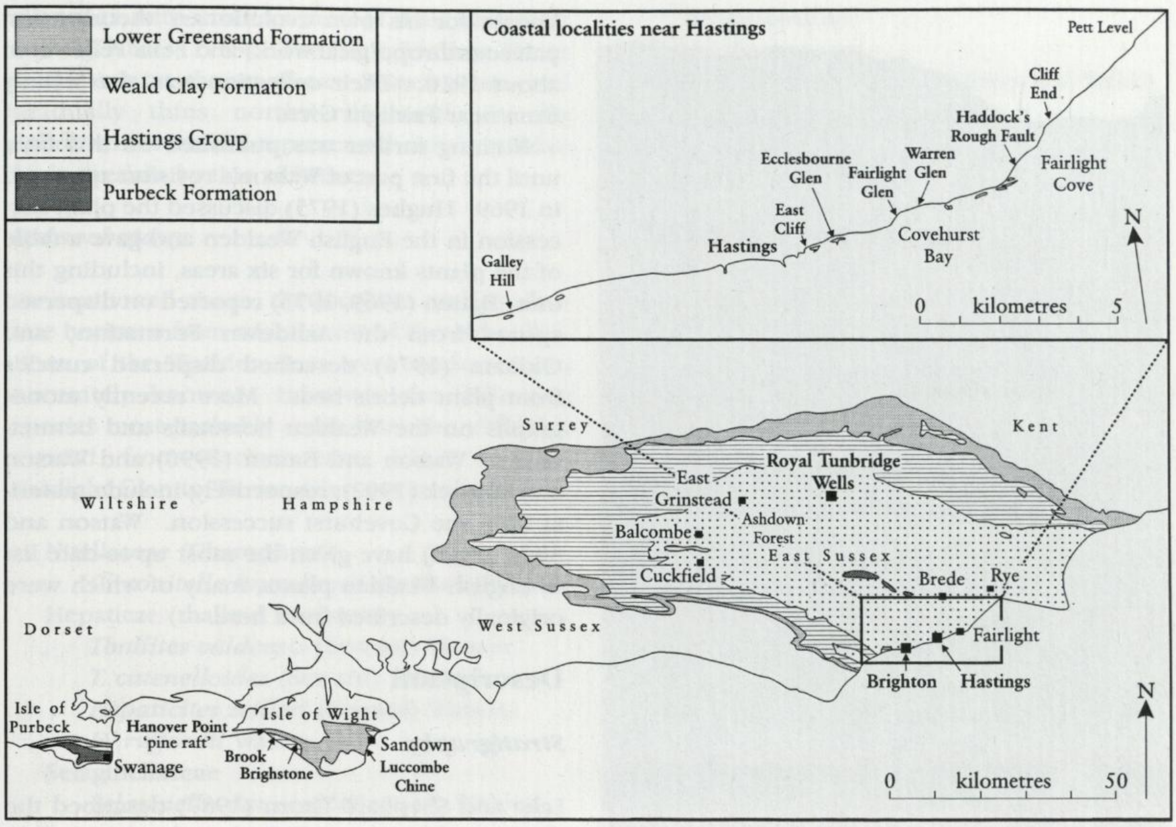

Figure 6.6 The coast of south-east England, showing main localities for plant fossils in the Lower Cretaceous Series. (After Watson and Sincock, 1992.)

anatomically well preserved. The remains found at Luccombe Chine on the Isle of Wight in particular stand out as being important and justify this part of the coastal exposure being selected for the GCR.

COVEHURST (TQ 846 101–TQ 867 110)

Introduction

This is the best-known and most productive site for the lower Wealden flora, and is the most important of all the palaeobotanical sites in the English Wealden strata. It contains a range of algae and mosses, and more common and varied pteridophytes and gymnosperms. The fossils are well preserved and include more or less whole cycad and bennettite fronds. Cuticles are often present and their study has proved vital in species distinctions. In Britain, it is unique for the abundance and diversity of the plants it has yielded. It is without doubt our most important Cretaceous fossil plant site.

Much of our knowledge of the English Wealden flora is based on fossils obtained during the 19th century by collectors such as Beckles, Dawson and Gideon Mantell. This material mainly came from inland exposures, especially in the Tilgate Forest, which are no longer accessible. Philip Rufford collected most of the fossils referred to by Seward (1894), in his classic account of the flora. He gave little in the way of locality details other than to indicate that they were from coastal exposures of 'Fairlight Clays' near Hastings, an argillaceous facies of the Ashdown Formation. According to Watson and Sincock (1992) and others before them (e.g. Batten, 1975; Hughes 1975; Allen, 1976), however, they probably mainly originated from rocks in the vicinity of Ecclesbourne and Fairlight glens, the latter falling within the boundaries of the present site. In 1913, Seward described another collection made by two Jesuit priests, P. Teilhard de Chardin (who later became well

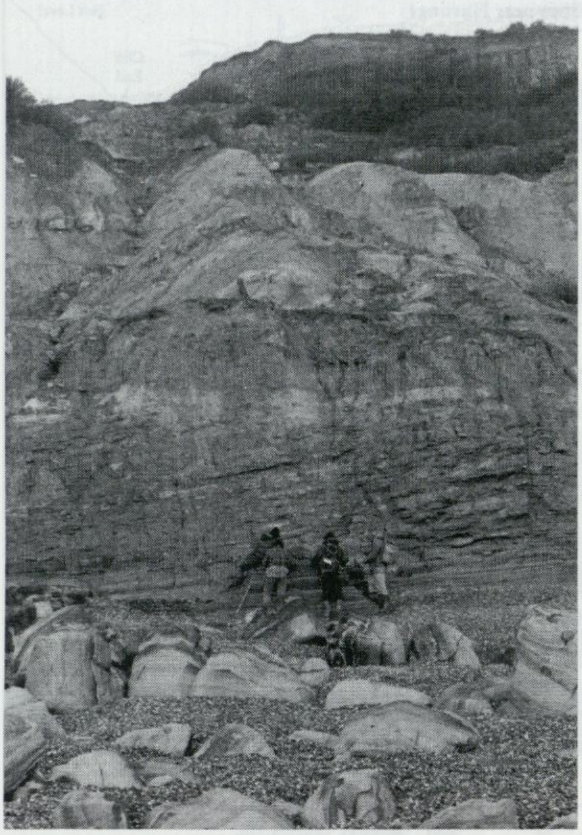

Figure 6.7 The Ashdown Formation, here at Covehurst Bay, is generally accepted to be the horizon from where such people as Rufford, Teilhard de Chardin and others collected fossils that are so characteristic of the lower Wealden flora. (Photo: D.J. Batten.)

known for his own evolutionary theories and palaeoanthropolgical work) and Felix Pelletier in about 1910. Their collection was also mainly from near Fairlight Glen.

Nothing further was published on this flora until the first part of Watson's revision appeared in 1969. Hughes (1975) discussed the plant succession in the English Wealden and gave a table of the plants known for six areas, including this one. Batten (1969, 1973) reported on dispersed spores from the Ashdown Formation, and Oldham (1976) described dispersed cuticles from plant debris beds. More recently monographs on the Wealden horsetails and bennettites by Watson and Batten (1990) and Watson and Sincock (1992), respectively, include material from the Covehurst succession. Watson and Alvin (1996) have given the most up-to-date list of English Wealden plants, many of which were originally described from here.

Description

Stratigraphy

Lake and Shephard-Thorn (1987) described the geology of this area. The plant fossils occur in lenses of sandstone and ironstone within locally red-mottled clays of the Fairlight Clays facies (lower Ashdown Formation) (Figures 6.7–6.9). The Ashdown Formation, which rests conformably on the underlying Purbeck Beds, consists mainly of fine-grained, silty sandstones and

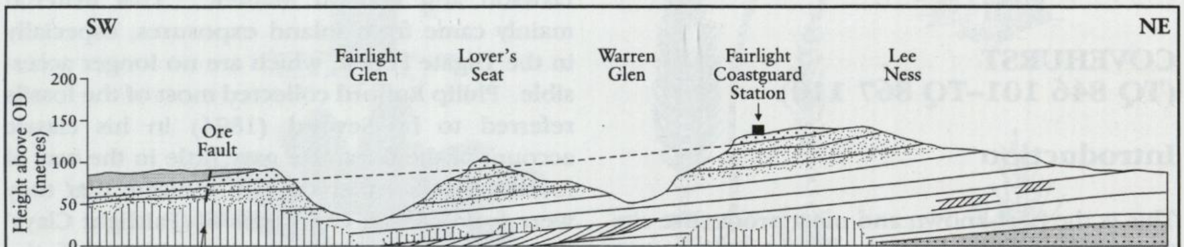

Figure 6.8 Cliff section at Covehurst Bay showing the outcrop of the plant-bearing Ashdown Formation. (After Lake and Shephard-Thorn, 1987.)

siltstones, with small amounts of shale and mudstone (Gallois, 1965). The Fairlight Clays Facies is thickest on the south-east Sussex coast, and gradually thins northwards until, in the Ashdown Forest, it is represented only by pebble beds overlain by thin siltstones.

Palaeobotany

As mentioned above, the localities and productive horizons from which most of the old collections of the Wealden flora were made are not accurately known. However, the following species most probably come from the cliffs that extend from Ecclesbourne Glen through Fairlight Glen to Warren Glen in Covehurst Bay.

Nitellaceae (Charophyta)
- *Circonitella knowltonii* (Seward) Watson

Hepaticae (thalloid liverworts)
- *Thallites valdensis* (Seward) Watson
- *T. catenelloides* (Seward) Watson
- *Hepaticites zeilleri* (Seward) Watson
- *H. ruffordii* Watson

Selaginellaceae
- *Selaginella dawsonii* (Seward) Dijkstra

Isoetaceae
- *Isoetes* sp.

Equisetaceae
- *Equisetum burchardtii* Dunker
- *Equisetites yokoyamae* Seward

?Osmundaceae
- *Cladophlebis albertsii* (Dunker) Seward
- *C. browniana* (Dunker) Seward
- *C. dunkeri* (Schimper) Seward
- *C. longipennis* Seward

Schizaeaceae
- *Ruffordia goeppertii* (Dunker) Seward
- *Pelletixia valdensis* (Seward) Watson and Hill

Gleicheniaceae
- *Gleichenites nordenskioldii* (Heer) Seward

Matoniaceae
- *Matonidium goeppertii* (Ettingshausen) Schenk
- *Phlebopteris dunkeri* Schenk

Dipteridaceae
- *Hausmannia dichotoma* Dunker

Dicksoniaceae
- *Onychiopsis psilotoides* (Stokes and Webb) Ward
- ?*Coniopteris* sp.

Cyatheaceae
- *Protopteris* sp.

Weichseliaceae
- *Weichselia reticulata* (Stokes and Webb) Ward

Tempskyaceae
- *Tempskya schimperi* Corda

Polypodiaceae
- *Aspidistes sewardii* Watson

Caytoniaceae
- *Sagenopteris mantellii* (Dunker) Schenk

Corystospermaceae
- *Pachypteris lanceolata* Brongniart

Cycadales
- *Becklesia anomala* Seward
- *B. sulcata* Watson
- *Nilssonia schaumburgensis* (Dunker) Schenk
- *Paracycas* sp.
- ?*Ctenis* sp.
- ?*Pseudoctenis* sp.
- ?*Almargemia* sp.

Bennettitales [leaves]
- *Otozamites titaniae* Watson and Sincock
- *Pseudocycas lesleyae* Watson and Sincock
- *P. roemeri* (Schenk) Holden
- *P. saportae* (Seward) Holden
- *Pterophyllum brongniartii* (Mantell) Morris
- *P. fontarianum* Watson and Sincock
- *P. lyellianum* Dunker
- *Ptilophyllum ashleyi* Watson and Sincock
- *P. marksilveri* Watson and Sincock
- *P. sibleyae* Watson and Sincock
- *P. sirfredii* Watson and Sincock
- *P. sirkennethii* Watson and Sincock
- *Zamites carruthersii* Seward
- *Z. corderi* Watson and Sincock
- *Z. dowellii* Watson and Sincock
- *Z. manoniae* Watson and Sincock
- *Z. nicolae* Watson and Sincock
- *Z. notokenensis* Watson and Sincock
- *Z. tatianae* Watson and Sincock
- *Z. wendyellisae* Watson and Sincock

Williamsoniaceae [female flowers]
- *Bennetticarpus anatoinetteae* Watson and Sincock
- *B. madamae* Watson and Sincock
- *B. nataliae* Watson and Sincock
- *Williamsonia bryonyae* Watson and Sincock
- *W. carruthersii* Seward
- *W. cynthiae* Watson and Sincock
- *W. margotiana* Watson and Sincock

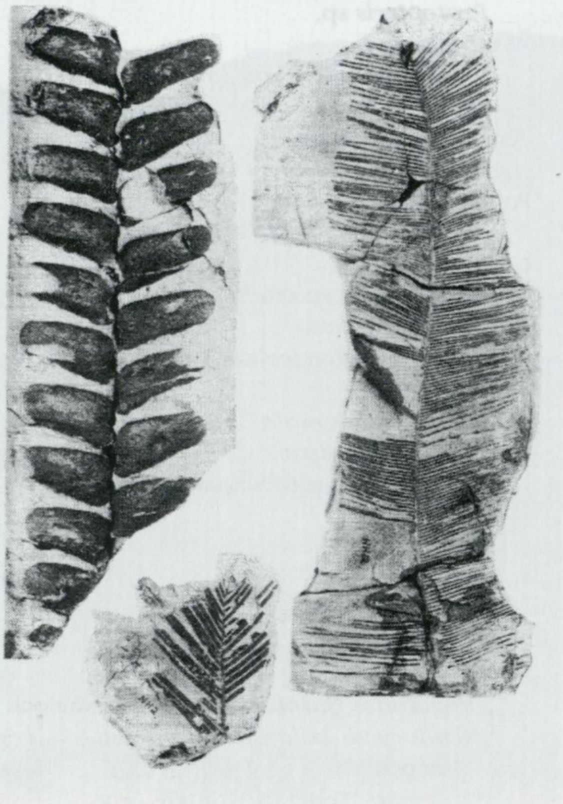

Figure 6.9 Plant fossil specimens collected from the Fairlight Clay of Covehurst Bay in the middle of the 20th century and figured by Hughes (1975); the names he used are in brackets where they have been subsequently changed. (A) *Zamites carruthersii* Seward emend. Watson and Sincock 1992 [*Otozamites klipsteinii* (Dunker) var. *angustifolia* Heer] ×0.25; (B) *Pseudocycas saportae* (Seward) Holden, × 0.25; (C) *Zamites dowelli* Watson and Sincock 1992 [*Zamites buchianus* (Ettingshausen) Seward] × 0.17.

Williamsoniaceae [male flowers]
Bennettistemon valdensis (Edwards) Watson and Sincock
Williamsoniaceae [scale leaves]
Cycadolepis cedricii Watson and Sincock
C. crawleyana Watson and Sincock
C. cromwellensis Watson and Sincock
C. markii Watson and Sincock
C. shuteana Watson and Sincock
Williamsoniaceae [shoots]
Bucklandia anomala (Stokes and Webb) Presl
B. florovia Watson and Sincock
Bennettitaceae
Cycadeoidea saxbyana (Brown) Morris
Czekanowskiaceae
Phoenicopsis sp.
Ginkgoales
?*Baiera* sp.
?*Ginkgoites* sp.
Ginkgoales/Coniferales ***incertae sedis*** [?araucariaceous affinity]
Pseudotorellia linkii (Romer) Watson and Harrison
Pseudotorellia sp.
Sciadopityoides sp.
Cheirolepidiaceae
Hirmeriella sp. [female cone]
Pseudofrenelopsis parceramosa (Fontaine) Watson
Araucariaceae
Conites elegans (Carruthers) Seward
Taxodiceae
Elatides sp.
Sciadopitytes sp.
Sphenolepis kurriana (Dunker) Schenk
Pinaceae
Pityites solmsii (Seward) Seward
Taxaceae
Torreya sp.
Conifers ***incertae sedis***
Brachyphyllum obesum Heer
B. punctatum Seward
B. spinosum Seward
Conites berryi Seward [probable female cone of *B. punctatum*]
Pagiophyllum spp.
?Chloranthaceae
Bevhalstia pebja Hill
Incertae sedis
Withamia saportae Seward

Interpretation

This is the most studied floral assemblage in the English Wealden strata and is represented by a wide range of plant groups. No other site has yielded anything like the diversity of plant remains. About 90 species have been identified, and for most of these it is the type and only known locality. The site therefore offers a unique opportunity to study the Early Cretaceous vegetation in Britain.

The flora is particularly important for studies on the Bennettitales. Some of the best examples of Early Cretaceous bennettitalean fronds with cuticles have been found here, providing an important insight into the group at the height of its diversity. Many of the bennettite flowers described by Watson and Sincock (1992) apparently came from Ecclesbourne Glen, a little to the west of the present site. However, the sedimentary facies there are similar to those seen in Fairlight and Warren glens; hence, similar fossils can be expected at the latter localities.

Comparable 'Wealden'-type floras are also known from elsewhere in Europe, notably in north-west Germany (Dunker, 1846; Daber, 1960, 1968), Belgium (Seward, 1900b; Alvin, 1968, 1971; van Amerom *et al.*, 1976), and northern France (Carpentier, 1927). However, much of the material from continental Europe came from temporary exposures and boreholes, which can no longer be accessed. Furthermore, with the possible exception of one or two of the German sections, none of the sites has yielded the diversity of plant remains found in the English Wealden. The comparison also tends to be weak at the rank of species. For instance, Watson and Sincock (1992) have shown that among the bennettites, only 11 of the 46 species in the British Wealden floras also occur in Germany. This combination of good exposure and high floristic diversity makes Covehurst in effect the standard locality for the pre-Aptian Europe Palaeoprovince of Vakhrameev (1991).

Allen (1976) interpreted the environment of deposition in which the plant remains occur as a mudplain with lagoons and sandy watercourses sometimes with coalescent alluvial fans. He suggested that large expanses of the plains probably supported rich growths of ferns. Watson and Alvin (1996), however, interpreted the situation rather differently. Accepting that the lowland vegetation was complex in structure, they suggested that many gymnosperms (Bennettitales, Cycadales and perhaps some conifers) were also constituents of the vegetation. This view was based on the fact that ferns are seldom preserved alone in the Hastings Beds. On the basis of his palynological studies, Batten (1973, 1975, 1982) also came to the conclusion that the lowlands were inhabited by a mixed flora of pteridophytes and gymnosperms.

Conclusion

This is the most important locality for Early Cretaceous plants in Europe. It has yielded about 90 species, many of which are known only from here. The flora, which is dominated by horsetails, bennettites and conifers, gives a unique insight into the plant life living in this region about 140 Ma ago.

HANOVER POINT (SZ 385 837–SZ 371 848)

Introduction

Hanover Point is the best site in Britain for the study of Early Cretaceous conifers, especially of the extinct family Cheirolepidiaceae. The fossils, which occur in several different beds in the sequence, include shoots with well-preserved cuticles, and petrified cones, shoots and trunks. The trunks include the famous Hanover Point 'Pine Raft' (Figure 6.10, and see Figure 6.13). Also found here are petrified bennettite and cycad cones.

Wealden (Early Cretaceous) fossil floras occur at various points along the coast between Brook Chine and Shippards Chine. They are represented mainly by fragmentary plant debris, in which cuticles showing epidermal structures are preserved. However, there are also rather larger petrifactions to be found, showing fine details of the plant anatomy. The fossils have been described by Oldham (1976), Watson (1977),

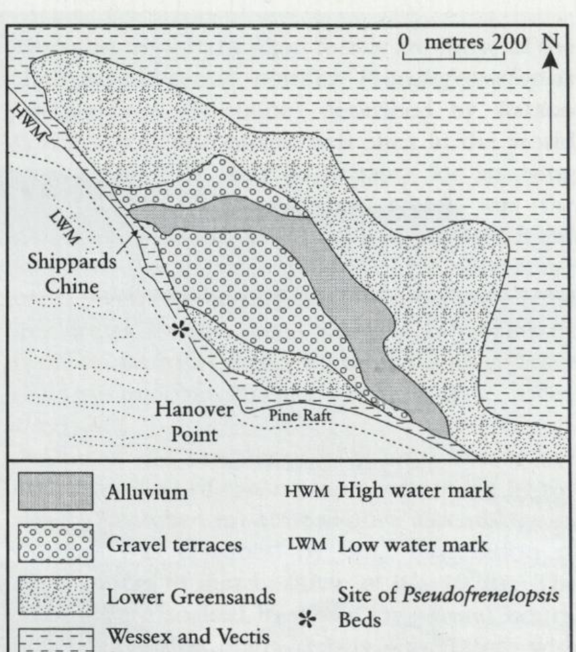

Figure 6.10 Geology of the coast near Hanover Point, showing the location of the main plant beds. (After Alvin *et al.*, 1981.)

Harris (1981), Alvin (1974, 1983) and Alvin *et al.* (1978, 1981, 1994).

Description

Stratigraphy

The fossiliferous beds at this locality are in the Wessex Formation (formerly known as the 'Wealden Marls') and are all Barremian in age. They are exposed at the foot of the cliff and in the foreshore (Figures 6.10–6.12). Three major plant beds have been identified:

(1) Upper Plant Bed: 0.4 m thick, exposed in the cliff about half-way between Shippards (sometimes called 'Compton') Chine and Hanover Point.
(2) Lower Plant Bed: 0.3 m thick, exposed in the cliff and on the shore at low tide about 20 m to the west.
(3) The 'Pine Raft': at Hanover Point itself.

Immediately above the upper bed is a thin brown, organic-rich layer without well-preserved plants, which has been suggested to be a podsol. Alvin *et al.* (1981) envisaged the whole deposit as representing a stream channel in which the flow rate was variable and which progressively silted up. The two beds were interpreted as deposits of forest-floor debris that may have been derived from bank erosion upstream. The Hanover Point 'Pine Raft' site is about 50 m lower down the section than the other two sites and is exposed only at low tide.

Palaeobotany

The plant remains consist almost entirely of gymnosperms, including cycads, bennettites, ginkgos and conifers. At certain points in the section, rather larger permineralizations can also be found, showing fine details of the plant anatomy. Particularly significant are the well-preserved specimens of the cheirolepidiacean conifer *Pseudofrenelopsis parceramosa* (Fontaine), showing details of the wood anatomy, and leaf and cone structure. Well-preserved bennettite and cycad cones have also been reported.

The 'Pine Raft' (illustrated in Figure 6.13) is composed of massive logs of *P. parceramosa*

Figure 6.11 Hanover Point from Roughland Cliff. The beds of the Wessex Formation are exposed in the cliffs of Brook Bay running south-eastwards from Hanover Point (left). The darker upper layer in the cliff consists of unconformable Quaternary deposits. (Photo: D.J. Batten.)

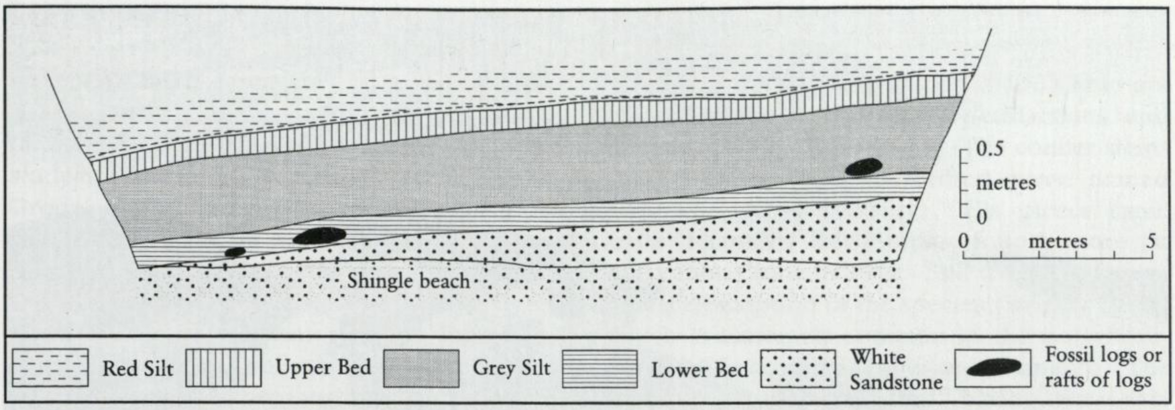

Figure 6.12 Diagrammatical representation of the two *Pseudofrenelopsis* Beds at Hanover Point. (After Alvin *et al.*, 1981.)

that are up to about 40 cm across and are a few metres long. They are mineralized in carbonate. Their anatomy has been described by Alvin *et al.* (1981). Logan and Thomas (1987) used material from these logs in their study of fossil lignin.

Alvin (1974) described fusainized fragments of the fern *Weichselia reticulata* (Stokes and Webb) Ward, which, although fragmentary, showed remarkably fine anatomical preservation. Other examples of fusainized fern fragments were mentioned by Harris (1981), including *Phlebopteris dunkeri* Schenk.

Oldham (1976) described cuticular fragments of a variety of gymnosperms from the plant debris beds including cycads, bennettites, ginkgos, representatives of the Cheirolepidaceae and Taxaceae, and other conifers, but he did not identify them to genera and species. In their study of English Wealden Bennettitales, Watson and Sincock (1992) subsequently identified some of Oldham's cuticles from this locality as follows:

Pseudocycas saportae (Seward) Holden (Oldham's 13 BENN, occasional)

P. roemeri (Schenk) Holden (Oldham's 14 BENN, occasional)

P. lesleyae Watson and Sincock (Oldham's 14 BENN *pro parte*, occasional)

Zamites carruthersii Seward (Oldham's 18 BENN, frequent)

Z. wendyellisae Watson and Sincock (Oldham's 16 BENN, frequent)

Ptilophyllum marksilveri Watson and Sincock (Oldham's 17 BENN, frequent)

Pterophyllum lyellianum Dunker (Oldham's 19 BENN, occasional or frequent)

Cycadolepis shuteana Watson and Sincock (Oldham's 23 BENN, frequent)

Watson (1977) has also identified Oldham's conifer (30 CHEIR, rare or occasional) as *Pseudofrenelopsis parceramosa* (Fontaine) Watson.

Interpretation

The most important plant fossils are those of the cheirolepidiaceous conifer *Pseudofrenelopsis parceramosa* (Fontaine) described by Watson (1977). It is one of the best sites in the world (and by far the best in Britain) for studying Cretaceous Cheirolepidiacea, which was the dominant family of conifers during much of the Mesozoic Era. Much of what we know about the later members of this important family (the frenelopsids) has arisen directly or indirectly from studies on specimens from Hanover Point (summarized by Watson, 1982, 1988; Alvin, 1983).

One of the most important advances in our understanding of these plants was made in the mid-1970s when an almost pure assemblage of conifers was obtained by bulk maceration of dried blocks of matrix (Alvin *et al.*, 1978). The blocks were soaked in water for several hours, sieved and the plant debris macerated with Schulze's solution. Abundant shoots and wood fragments were recovered, together with fragments of its male cone, which was given the name *Classostrobus comptonensis*. The cone fragments bore peltate sporophylls, each with

Figure 6.13 The Pine Raft at Hanover Point, Isle of Wight. These massive petrified logs, exposed at low tide, are mineralized in carbonate and lie in sandstone. They have tracheid pitting similar in character to the better-preserved cheirolepidiaceous woods of *Pseudofrenelopsis parceramosa* (Fontaine) Watson found at Shippards Chine but the arrangement of these is more araucarioid. They are better classified in the form-genus *Dadoxylon*. (Photo: B.A. Thomas.)

two or more pollen sacs containing pollen of the *Classopollis* type. The pollen did not completely agree with any species of *Classopollis*, but Alvin *et al*. (1978) thought it to be close to, although smaller than that of *Classolepis rishra* (Barnard). This pollen was also found in association with dispersed cuticles (Oldham, 1976) that were identified by Watson (1977) as *P. parceramosa*. Taylor and Alvin (1984) studied the ultrastructural wall development of *Classopollis* using pollen from these cones.

The cheirolepidiaceous conifers are the most important element of the plant fossils found at the Hanover Point site, although they are associated with rare examples of cycads and bennettites. In his palaeoecological interpretation of the English Wealden, Batten (1975) gave four alternative reconstructions for the flora and three alternatives for the *Classopollis*-producers. These were sandy bars and barrier islands along the 'coast', mangrove-like communities, and floodplain or upland slopes. Alvin *et al*. (1978) suggested that the Cheirolepidiaceae might have been sufficiently diverse to occupy and dominate a variety of different habitats.

Alvin *et al*. (1994) described another new species of conifer male cone from the same bed as *Masculostrobus vectensis*. The pollen was attributable to *Araucariacites* Cookson ex Couper by Batten. The parent tree is unknown, but Alvin *et al*. suggested the structure of the cone is closest to that found in the Taxodiaceae and Araucariaceae.

The studies by Alvin (1974) and Harris (1981) on fusain from here were among the first to use this type of preservation to study the anatomy of plant remains.

Conclusion

Hanover Point is an exceptional site for studying the morphology of trees of the Cheirolepidiaceae, the most important family of conifers growing in Britain about 130 Ma ago. Well-preserved remains of cycads, bennettites, ginkgos, and other conifer groups are also present. There is much research potential in the floras found in this section, which are of considerable palaeobotanical significance.

LUCCOMBE CHINE (SZ 583 793)

Introduction

Luccombe Chine is the best available site for the study of plant fossils from the Lower Greensand Group (Early Cretaceous Epoch), which has yielded an important Aptian flora. The specimens are permineralized, showing well-preserved anatomical details. The assemblage is dominated by coniferalean remains, including a variety of woods of the type known as *Protocupressinoxylon*, and of cones of the *Pityostrobus*-type. There are also finely preserved cones of the now-extinct cycadeoids, including the famous *Bennettites gibsonianus*, which for a long time was taken as the 'standard' cone type for this group. In addition, there is the enigmatic wood type known as *Aptiana*, which some authors have suggested may belong to an early angiosperm. Many of the species reported from here are unknown elsewhere. Together with the quality of the preservation, this makes Luccombe Chine a site of considerable palaeobotanical significance.

The first record of coniferous wood from the Lower Greensand of the Isle of Wight was by Mantell (1847), although he did not specifically mention this site. Barber (1898) provided a more detailed description of some small conifer stems and pieces of larger ones from the succession, although again the locality information is vague. The earliest reference specifically to Luccombe Chine appears to have been made by Stopes (1912, 1915).

Description

Stratigraphy

On the Isle of Wight, the Lower Greensand Group is about 260 m thick. It is clayey in the lower part (Atherfield Clay Formation, lower Aptian) and sandy above (Ferruginous Sands, Sandrock and Carstone Formations, upper Aptian and lower Albian). The plant fossils found at Luccombe Chine are from the Sandrock Formation and are late Aptian in age. They occur in a layer of pyrito-phosphatic nodules in the upper of two clay bands that form ledges in Knock Cliff. Above the Sandrock here are bright yellow and white sands with laminae of clay and bands of green sand of the Carstone Member.

Palaeobotany

The plant fossils found at Luccombe Chine are all preserved as carbonate petrifactions and show good internal anatomy. The conifer stems that Barber (1898) described were named *Cupressinoxylon vectense*. His pieces came from Shanklin but Stopes found more at Luccombe Chine in 1912. She used all of them in her description of the species (Stopes, 1915), which is extremely common in the neighbourhood of Luccombe Chine and Shanklin. The wood is clearly coniferous, having secondary wood of small, regular tracheids up to just over 25 mm in diameter, with bordered pits. The medullary rays are mostly uniseriate but a few are partly biseriate. Annual rings are well marked although they are composite, with some having three or four irregular amalagamated zones in each. Similar wood, called *Cupressinoxylon luccombense* Stopes, was based on a woody branch that was probably not less than 5 cm in diameter when alive.

Stopes (1915) also described two species of *Podocarpoxylon* from Luccombe Chine: *P. gothanii* and *P. solmsii*. The material on which these are based was found by Solms-Laubach in 1889, Jones in 1898, as well as by Stopes herself in 1912. Capellini and Solms-Laubach (1892) mentioned finding the wood in their account of *Cycadeoidea gibsoniana*. Both species are clearly coniferalean with tracheid and uniseriate rays in their secondary wood. The radial walls of the medullary ray cells have single, very large, simple pits (occasionally with borders) or sometimes two or even more pits.

Stopes found another type of conifer wood in 1912 and gave it the new name *Vectia luccombensis* because she could not include it in any known genus. This was founded on massive, uniform secondary tissue that is entirely composed of regular, alternating, thick-walled elements (fibres) and thin-walled elements (probably sieve tubes) in tangential bands. It appears to be phloem from a large trunk.

Sequoia giganteoides Stopes was described from a single minute leafy twig that had drifted into a large decaying piece of *V. luccombensis*. The adpressed leaves are very similar to those of the extant *Sequoia gigantea* but smaller (0.5 mm in diameter) and with an axis that is 0.3 mm across.

Stopes (1912) first described three species of stem from the Lower Greensand as being of angiosperm origin. She later (1913, 1915) redescribed them, together with two more species, although only one, *Aptiana radiata* Stopes, came from Luccombe Chine. It was a single portion of stem, partly embedded in the characteristic glauconitic sandstone of the Lower Greensand. The exposed portion was only wood, but the embedded portion still had its phloem and part of the cortex preserved. Overall it is an exceptionally well-preserved specimen. The primary wood, surrounding the central pith, appears to be without bundles. The secondary wood, with its obvious growth rings, consists of bordered-pitted fibre-tracheids and single vessels with associated wood parenchyma. The medullary rays are numerous and either uniseriate or multiseriate. The phloem is composed of thickened elements and thin-walled cells in irregular alternating patches.

There is, however, a problem relating to the provenance of Stopes' woods. Harris (1956b) first expressed doubts about where they came from and Hughes (1961) suggested that confirmatory observations should be made before their provenance can be accepted. Hughes (1976) reiterated this problem and stated that, although gymnosperm wood is abundant at Luccombe Chine, no other specimen of *Aptiana* has yet been found. He stressed the urgent need to find at least one reliably located specimen, noting that Luccombe Chine appears to be the best locality for further searches.

The cycadeoid stems that have been collected from the Isle of Wight are of extreme taxonomic, nomenclatural and historical importance even though they are of doubtful provenance (Watson and Sincock, 1992). The problem is that some specimens have a water-worn appearance suggesting that they were found as beach pebbles rather than extracted from the cliff. Carruthers' original specimen of *Cycadeoidea gibsoniana* was one of these. It has exquisitely preserved flowers with a small domed receptacle (Watson and Sincock, 1992). From this specimen Carruthers (1870a) was able to recognize and illustrate the female flower structure of cycadeoids for the first time. Watson and Sincock (1992) have redescribed the specimen. They showed that, like many other cycadeoid stems, it has diamond-shaped indentations that mark the original positions of leaf petiole bases. The ridges between them consist of petrified scales from the basal portions of the petioles. Flowers, preserved in cavities, are sparse and difficult to detect except in cut surfaces. Carruthers completely overlooked them.

Reconstructions of cycadeoids, as illustrated in Figure 6.4, are based on petrified trunks belonging to either *Cycadeoidea* Buckland or *Monanthesia* Wieland ex Delevoryas. Both are known as short and tall trunks and are separated on the basis of the distribution of their flowers. *Monanthesia* shows a flower in the axil of almost every leaf while in *Cycadeoidea* they are scattered.

Interpretation

The Lower Greensand flora as a whole is rich in species, with Stopes (1915) listing one alga, two ferns, nine cycadophytes, 27 conifers and five angiosperms. Of these, a significant seven came from Luccombe Chine. Their excellent preservation as petrifactions permits detailed anatomical studies to be undertaken and accurate comparisons made with living taxa.

The Lower Greensand flora differs from that of the underlying Wealden in a number of respects, other than in mode of preservation. There are fewer pteridophytes and cycadophytes and more conifers. There are also angiosperms, which have yet to be unequivocally identified in macrofossil material from the Wealden. The Lower Greensand flora is of course largely composed of woods and the specimens were all transported some distance before being covered by marine sediments. There is, therefore, a distinct probability of sorting as wood, seeds and fruits can float a long way before sinking. In contrast, leaves become waterlogged much more quickly and sink or decay far from the more buoyant organs. The Tertiary locality of Sheppey (Chapter 7) is another marine deposit that contains only buoyant seeds, fern petioles and wood.

Conclusions

Luccombe Chine is an important site for beautifully preserved petrified gymnosperm and angiosperm stems and especially for bennettitalean trunks. At about 110 Ma old, they are the oldest macrofossil remains known in Britain that are unquestionably derived from flowering plants. All deserve further study, and collecting should yield additional specimens that would increase knowledge of this significant flora.

CLIFF END (TQ 887 127)

Introduction

The succession at Cliff End contains the only known examples of in-situ remains of a lycopsid, which has hitherto been informally identified as *Isoetites* (Jarzembowski *et al.*, 1996). The name implies that the plant has a sufficient number of morphological characteristics for it to be compared closely with the extant genus *Isoetes*. This may not prove to be correct once its anatomy has been fully described (at the time of writing, this work is in progress). However, for the sake of consistency it will continue to be referred to here as '*Isoetites*'.

There is no detailed published account of the plant fossils found at Cliff End, although Hughes (1976) and others have previously noted that water-worn pebbles and cobbles of portions of the silicified tree-fern trunk of *Tempskya schimperi* Corda can be found loose on the shore; indeed these may be found occasionally almost anywhere along the beach from Cliff End to Hastings. This is the only known location in Britain of representatives of the now extinct family Tempskyaceae.

The occurrence of *Tempskya* at outcrop was first recorded, as *Endogenites erosa* Stokes and Webb, in the thin basal shales of the Wadhurst Clay in the old sea cliffs behind White Rock Place (TQ 8132 0925; Fitton, 1836), just north-east of Hastings Castle at Ladies Parlour (TQ 821 095; Tylor, 1862), and in the East Hill succession to the east of the Old Town, Hastings (TQ 827 095: Fitton, 1836; Tylor, 1862). These deposits, which became known as the '*Endogenites*' Beds, crop out beneath a massive sandstone, both here and at Cliff End, from whence its name: the Cliff End Sandstone (Figure 6.14).

Description

Stratigraphy

The exposure at Cliff End comprises upper

Figure 6.14 Cliff End. The sea is washing beds of the upper Ashdown Formation within which the *Isoetites* plant fossils are found. The massive sandstones above belong to the Cliff End Sandstone within the Wadhurst Clay Formation. (Photo: D.J. Batten.)

Ashdown and lower Wadhurst Clay formations. The former is dominated by sandstones that display many sedimentary structures, among the most abundant of which are small-scale cross-lamination and mud-draped rippled surfaces. The overlying Wadhurst Clay is composed of sandstones with subordinate siltstone-mudstone beds. The latter occur at the base ('*Endogenites*' Beds) and the top of the cliff, with the prominent Cliff End Sandstone imbetween.

Palaeobotany

The grey silty beds of the Ashdown Formation have yielded many plant microfossils (small spores, megaspores and gymnosperm pollen grains). They are particularly abundant in channel-fill deposits in the coastal section (Batten, 1969; Hughes, 1976). The Wadhurst Clay contains *Equisetites* rootlets and rhizomes in position of growth, but not at Cliff End, although roots of unknown plants *in situ* occur in both this formation and the Ashdown Beds here and at other points along the coast towards Hastings.

The beds containing '*Isoetites*' are fine, well-sorted, uncemented sandstones that weather rapidly and contain almost no particulate organic matter. The in-situ remains are irregularly dispersed within the sediment; although some are close together, they are not tightly packed. Superficially they may have a root-like appearance, and indeed may have been mistaken for roots in the past. Alternatively, it is possible that their occurrence is very local and that erosion of the cliffs has led to their current exposure. It would be premature to comment further on this plant until it has been formally described.

No study has been made of the occurrence of *Tempskya* in the Hastings-Pett Level succession. This is no doubt at least partly because the basal Wadhurst Clay is accessible in only a few places in the cliffs. The silicified remains on the beach are presumed to reflect a local stand of the ferns at the time of deposition of the enclosing sediment.

The anatomy of *Tempskya* indicates that it had an unusual pattern of growth. The trunk, to which the name is applied, is false in that it consists of several intertwining stems and roots. All of the fronds were small and produced from the sides of the upper portions of the trunks. Other Mesozoic tree ferns grew from an apical crown, as do all extant species.

Interpretation

The Cliff End site, and the foreshore from this locality along the beach towards Hastings, have considerable potential for broadening our understanding of two important groups of Mesozoic plants: the lycopsids and ferns. More work is needed to determine why the particular species concerned should have been preserved in this part of the succession. They have not so far been found anywhere else in the Wessex–Weald Basin. The site exposes the basal Wadhurst beds that closer to Hastings are known to have yielded remains of *Tempskya*. It is possible that they may also be recorded from here in due course.

Conclusion

The only known occurrences of Wealden lycopsids *in situ*, and of the tree fern *Tempskya* that has clearly been preserved close to, or within, the site in which it grew, have considerable potential importance for improving current knowledge of the biology and palaeoecology of the two families they represent.