

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 9

*Late middle Eocene–early Oligocene
(Bartonian–Rupelian) and
Miocene palaeobotany of Great
Britain*

M.E. Collinson and C.J. Cleal

INTRODUCTION

This final chapter deals with the British sites yielding plant macrofossils of mainly late Eocene and younger age (i.e. post-Lutetian). It was a time of marked change in British vegetation as the climate cooled from the thermal maximum of early Eocene times. In southern Britain, where the bulk of the macrofossil record occurs, there was also a change from the mangrove and forests that dominated the Ypresian and Lutetian, to marshland. The excellent exposures of the middle and late Palaeogene deposits in southern Britain provide one of the most complete records of changing vegetation during this crucial time and make it an area of international importance for palaeobotanical studies.

Nearly all of the sites described here are Palaeogene in age and, together with the southern British sites dealt with in the previous chapter, form a coherent network. Included in this chapter, however, is a description of the sole GCR representative of the palaeobotany of the Brassington Formation, Bees Nest, in Derbyshire. It is the only known British locality for Neogene plant macrofossils. The conifer-dominated vegetation preserved at this last site seems to indicate far cooler conditions than seen at the Palaeogene sites and represents an intermediate between the more typical paratropical vegetation of early Palaeogene times and the vegetation of today.

HISTORY OF RESEARCH

There has not been the long history of research on these floras that there has been on the early and middle Eocene floras dealt with in the previous chapter, especially those from the London Clay. The earliest reports of plant macrofossils from the later Eocene and Oligocene deposits of southern Britain date from the middle to late 19th century. Two sites attracted most interest during these early years; the exposures of lower Headon Hill Formation at Hordle Cliffs, and the exposures of Bembridge Marls at Thorness and Gurnard Bay. They were first investigated in detail by Starkie Gardner, who included descriptions of some of the fossils in his monographs on Palaeogene ferns and conifers (Gardner and von Ettingshausen, 1879–1882; Gardner 1883–1886a). However, Gardner did not complete or publish his work on the angiosperm fruits and

seeds, which form the bulk of these floras.

Also working on the Bembridge Marls sites was a local amateur geologist, James A'Court Smith, who accumulated a large assemblage of both plant and animal (especially insect) fossils from these strata during the mid-19th century. These eventually found their way to the British Museum (Natural History) in London, where they were published in the first comprehensive review of the flora as a catalogue of the collection (Chandler, 1925–1926). During the early 20th century, the Hordle flora was investigated by Clement Reid. He was a geologist with the British Geological Survey, who had spent much time mapping the Tertiary deposits of southern England, and in the process had accumulated a large collection of plant fossils. However, his premature death in 1916 meant that he published little of the results of this work, other than a study on the charophytes (Reid and Groves, 1921). Describing the bulk of his collection fell to his wife Eleanor, who published a monograph with her student Marjorie Chandler (Reid and Chandler, 1926).

Interest in these later Eocene and Oligocene floras then went into decline, as the far more diverse London Clay flora drew the attention of British Tertiary palaeobotanists, especially Chandler (see previous chapter). Nevertheless, Chandler continued to collect and study these younger floras, both at the two well-known sites and at other sites along the coast of southern England. The fossils mostly went to the British Museum (Natural History) and it was through that institution that Chandler published a series of definitive monographs that dealt largely with the post-Lutetian floras (Chandler, 1961a, 1962, 1963b, 1964; a fourth supplement was published posthumously – Chandler, 1978). There were also numerous shorter papers in the *Bulletin of the British Museum (Natural History)*, dealing with particular taxa and some of the smaller floras (Chandler, 1955, 1960, 1961b, 1961c, 1963a).

Subsequent work on these floras has been mainly by Margaret Collinson. Following the completion of a doctorate thesis (Collinson, 1978a), a number of papers were published dealing with the taxonomy of some of the plant fossils found here, especially of the aquatic plants that dominate the stratigraphically higher floras (Collinson, 1978b, 1980a,b, 1982a, 1983a; see also Fowler, 1975). The palaeoecology of these floras was studied by a detailed examina-

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tion of the relationship between the provenance of the fossils and the sedimentology (Collinson, 1983a, 1996b; Collinson *et al.*, 1993a; Hooker *et al.*, 1995). From this work came a model of vegetation change occurring in southern Britain during middle and late Palaeogene times (Collinson *et al.*, 1981; Collinson and Hooker, 1987; Collinson, 1990b).

In addition to the sites covered in this chapter, a notable post-Lutetian flora has been reported from the Oligocene Bovey Tracey lignites in Devon (Heer, 1862; Chandler, 1957). This material was obtained from ball-clay workings that are no longer active. There have been other temporary workings in this area that have yielded sometimes well-preserved floras and it is always worth monitoring such sites for evidence of this important flora. There are also numerous post-Lutetian palynological sites in the Britain, many reviewed by Boulter (in Curry *et al.*, 1978) but these lie outside of the scope of this volume.

Knowledge of the Neogene vegetation of Britain has only really come to light in recent years. The only notable macrofossils of this age,

from Derbyshire, were discovered following work by the British Geological Survey (Chaloner, 1961) and have been the subject of detailed description by Boulter (1969, 1970, 1971a,b, 1974) and Boulter and Chaloner (1970). The only other Neogene macrofloras were reported by Reid (1920b) from possible Pliocene fissure deposits from County Durham, although West (1968) considers them to be Pleistocene in age.

PALAEOGEOGRAPHICAL SETTING

The geography of the post-Lutetian world did not differ significantly from that of early Eocene times. However, there was no longer a land bridge linking North America with Europe, and the vegetation of the two continents thus became further differentiated.

The palaeogeography of post-Lutetian Britain is summarized by Murray (1992) (Figure 9.1). Britain was joined to the rest of Europe at intervals during the Tertiary via the Weald–Artois

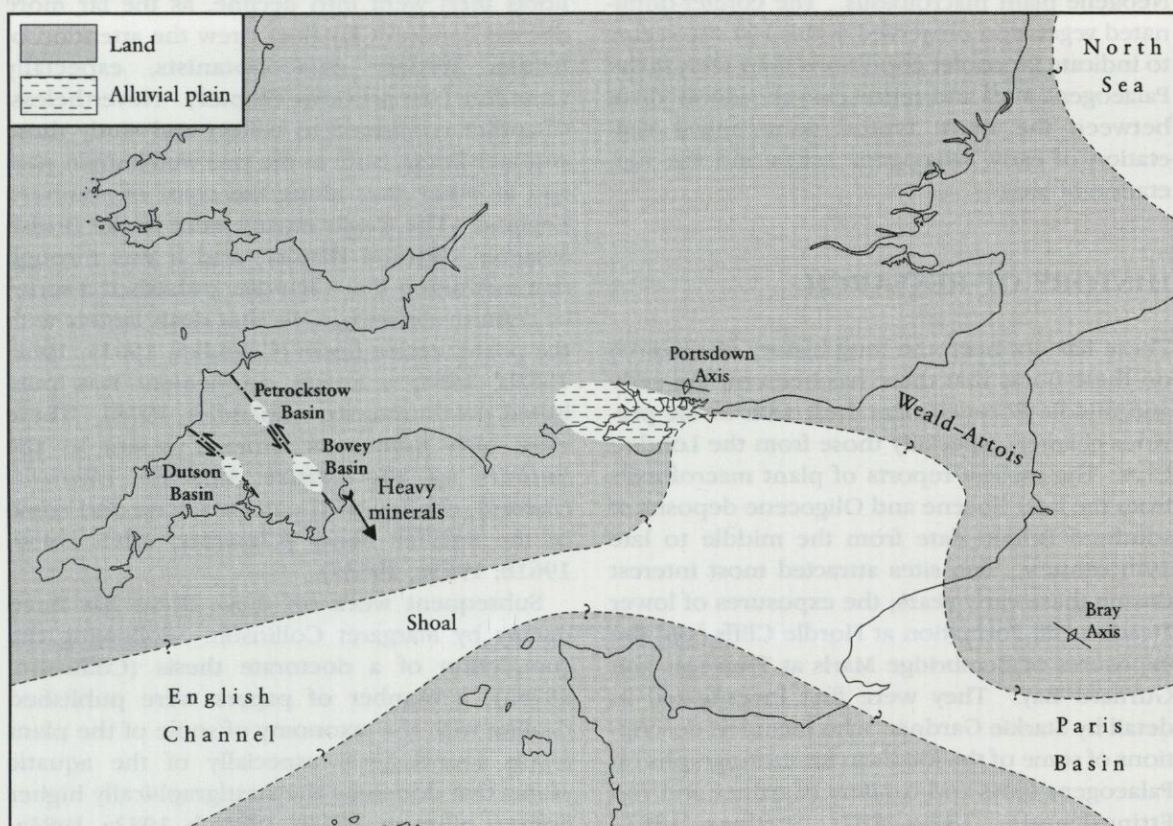


Figure 9.1 Palaeogeography of southern England during late Eocene times. (After Murray, 1992.)

High, which extended from Kent to Belgium. There was nevertheless a broad inlet from the Atlantic extending approximately along the present-day English Channel, up to the Weald–Artois High. However, this palaeo-English Channel progressively shallowed and narrowed through middle Eocene to Oligocene times, and by the latest part of this interval there was no sedimentation taking place in areas currently occupied by land and therefore there are no land outcrops of strata of this age along the south coast of Britain.

British post-Lutetian plant-bearing deposits occur mainly in the Hampshire Basin, which was an embayment on the southern coast of England. In the London Basin, the London Clay is overlain by marine Virginia Water Formation ('Bagshot Sands'), which have yielded practically no plant macrofossils. During middle Eocene times, the Hampshire Basin was under a shallow sea, but as the palaeo-English Channel shallowed, it became filled by fluvio-deltaic sediments. The post-Lutetian geological history of the Hampshire Basin was thus one of a change from shallow-marine, to marsh, to fully terrestrial conditions.

Our knowledge of conditions in inland Britain is very limited. However, recent work on various examples of so-called 'pocket deposits' (e.g. the Brassington Formation at the Bees Nest GCR site) suggests that there was a fairly flat topography over much of England and Wales, varying in altitude by only a few tens of metres (M.C. Boulter, pers. comm.).

STRATIGRAPHICAL BACKGROUND

The post-Lutetian deposits of the Hampshire Basin is characterized by marked lateral variation in facies, which has resulted in much confusion over the lithostratigraphical nomenclature. Since lithostratigraphy is not the main concern of this volume, we have merely attempted to remain consistent with the nomenclature used in the Tertiary stratigraphy GCR volume (Daley in Daley and Balson, 1999). In this scheme, the post-Lutetian deposits are divided into a shallow to marginal-marine Barton Group and a brackish to non-marine Solent Group. These groups are subdivided into a number of formations and in some cases members, which are summarized in Figure 9.2.

The Barton Group is middle Eocene in age,

Rupelian	Solent Group	Bouldnor Formation	Cranmore Member
			Hamstead Member
			Bembridge Marls Member
Priabonian	Solent Group	Headon Hill Formation	Bembridge Limestone Formation
			Seagrove Bay Member
			Osborne Member
			Fishbourne Member
			Lacey's Farm Limestone Member
			Cliff End Member
			Hatherwood Limestone Member
			Linstone Chine Member
			Colwell Bay Member
			Totland Bay Member
Bartonian	Barton Group		Becton Sand Formation
			Barton Clay Formation
			Boscombe Sand Formation
Lutetian			

Figure 9.2 Lithostratigraphical scheme for the middle and upper Palaeogene strata (mostly post-Lutetian) in the Hampshire Basin.

while the Solent Group is late Eocene to early Oligocene in age. The recognition of the Eocene–Oligocene boundary has been the subject of much dispute (e.g. see review by Curry *et al.*, 1978, and Daley in Daley and Balson, 1999). This has been compounded by the problems of trying to identify the boundary (defined on the extinction of hantkeninid foraminifera) in the Hampshire Basin, which by that time had become non-marine. The hantkeninid extinction, and therefore the boundary, occurs within nannoplankton zone NP21. There is a record of NP19/20 in the Colwell Bay Member of the Headon Hill Formation, in Hampshire, implying that the boundary must be significantly higher (Collinson, 1992; Hooker, 1992). The Grimmertingen Sand (with NP21) is often correlated (as a transgression) with the Bembridge

Oyster Bed on the Isle of Wight (base Bembridge Marls Member, Bouldnor Formation) (Hooker, 1992). The *Nematura* Band (low in the overlying Hamstead Member of the Bouldnor Formation at Hamstead, Isle of Wight) has been correlated with the *Argile Verte de Romainville* in the Paris Basin (with zone NP22) by means of dinoflagellates by Liengjaren *et al.* (1980) (see Collinson, 1992; Hooker, 1992). Zone MP21, post-*Grande Coupure* Oligocene mammals occur above the *Nematura* Band on the Isle of Wight (Hooker, 1992). A fluctuation in pollen floras, interpreted as indicative of cooling, occurs in the Paris Basin in strata that correlate with the upper Bembridge Marls and lower Hamstead Member; climatic cooling is documented in the marine realm above the hantkeninid extinction (Collinson, 1992, p. 441). Taken together, this information suggests that the boundary is low in the Bouldnor Formation in the English sequence (Collinson, 1992; Hooker, 1992). This means that the Bembridge Marls Member and the Hamstead Member below the *Nematura* Band should be treated as Eocene–Oligocene transitional strata until correlations can be refined. It is possible that the boundary could be lower in the sequence but this is judged highly improbable (Collinson, 1992; Hooker, 1992) and the Bembridge Limestone Formation is here treated as Eocene in age, as in Collinson *et al.* (1993a), Hooker *et al.* (1995) and Collinson and Hooker (2000).

The Neogene 'pocket deposits' of central and northern England are all assigned to the Brassington Formation, although they do not now form a continuous sedimentary unit and thus are arguably not a mappable lithostratigraphical unit in the strict sense.

POST-LUTETIAN VEGETATION

The same major phytochoria recognized in the early Eocene strata (see previous chapter) are also present in the late Eocene and early Oligocene successions: the Holarctic, Tropical, Notal and Australian Palaeokingdoms (Akhmetiev, 1987). Southern England is in the Tethyan Palaeoarea of the Holarctic Palaeokingdom, which can be recognized over southern North America, central and southern Europe, Central Asia and Kazakhstan. However, unlike early Eocene times, there was no longer a land bridge between North America and the rest of the Tethyan Palaeoarea and consequently its

fossil floras are assigned to their own palaeoprovince.

During late Eocene times, marked changes appear in both the plant macrofossil and palynological record (Collinson *et al.*, 1981; Collinson and Hooker, 1987; Collinson, 1990b, 1992, 1996b). The *Nypa* palm and associated mangrove elements disappear, as does '*Scirpus*' *lakensis* (Collinson, 1996b, 2000a) and there is a progressive decline in the proportion of species indicating paratropical rain forest conditions. Instead, the plant fossil record consists mainly of the remains of aquatic and marginal aquatic vegetation such as bullrushes, leather ferns, pondweeds, water lilies, water ferns and water soldiers with rarer taxodiaceous conifers. This floral change is independent of facies change, as brackish facies (including oyster beds) and fluviolacustrine facies are present throughout the Palaeogene Period in southern England (Collinson, 1990b, 1996b, 2000a).

Concentrating on the aquatic plants, Collinson *et al.* (1981) were able to recognize clear vegetational changes during the second half of the Eocene Epoch, in response to climatic cooling, further supported by later work on all floral elements and mammalian faunas (Collinson and Hooker, 1987; Collinson, 1990b, 1992, 1996b, 2000a). In some parts of the British late Eocene succession there is evidence of vegetation reminiscent of the cypress swamps of North America, such as in the Headon Hill Formation at Hordle Cliffs. The dominant floral associations of the Bembridge Limestone and the Bembridge Marls (Collinson, 1983a, 1990b; Collinson and Hooker, 1987; Collinson *et al.*, 1993a), including the bulrush-leather ferns, are also typical of the south-eastern USA today. This indicates cooler conditions than in early Eocene times, i.e. subtropical rather than tropical.

Undoubted Oligocene floras are poorly represented in Britain. Elsewhere in Europe, a change in the vegetation from evergreen subtropical to mixed evergreen and deciduous has been identified between the late Eocene and early Oligocene strata (Collinson, 1992) but the wetland vegetation in southern England was apparently little affected across the boundary (Collinson and Hooker, 1987; Collinson, 1990b, 1992). A palynological study by Machin (1971) suggested a change to vegetation favouring more temperate conditions, but Collinson (1992) concluded that the changes in Britain merely represented the culmination of those

commencing in early Late Eocene times.

The limited available macrofossil evidence of British Neogene vegetation suggests it was a mixture of mainly ericaceous heaths and forests dominated by conifers, such as *Cryptomeria*. However, the palynology suggests that many angiosperms were also present in these forests and that nearly one-third belong to genera that are today restricted to tropical or subtropical environments (Boulter, 1971a,c). Thus, even towards the end of the Neogene Period, conditions were significantly warmer than they are today.

POST-LUTETIAN PALAEOBOTANICAL SITES IN BRITAIN

Post-Lutetian palaeobotanical sites in Britain fall into two categories, one of which consists of the sole Neogene palaeobotanical locality in Britain: Bees Nest. As it is the only site to yield Neogene plant macrofossils of any quantity in this country, it was almost self-selecting for the GCR.

All the other sites covered in this chapter form a network within the Hampshire Basin that demonstrate the evolving vegetation from the middle of the Eocene Epoch to the early part of the Oligocene Epoch. The best sites for individual floras are in the mainly non-marine Solent group, and include the classic localities at Hordle-Beacon Cliffs (lower Headon Hill Formation) and Thorness Bay (Bembridge Limestone and lower Bouldnor Formations). These have been studied for over a century and are of international significance. They are complemented by the less well-known sites of Paddy's Gap, Hamstead Ledge and Bouldnor Cliff, which provide different insights into these same floras, the latter including the only confirmed Oligocene strata in Britain.

Many of the other sites described here have been selected to fill in the gaps between these better-known floras. Although they may not have yielded such diverse assemblages, they are nevertheless important for establishing the spatial and temporal context to give the remarkably complete history of vegetational change that can be documented in the Hampshire Basin. They include Highcliffe and Barton for the Barton Group floras; Colwell Bay and Chapel Corner for the middle and upper Headon Hill Formation floras; and Headon Hill and Totland, which provide extensive exposures of some of

these plant beds, allowing them to be studied in their sedimentological context.

HIGHCLIFFE (SZ 195 927-SZ 199 928)

Introduction

Highcliffe (also sometimes known as 'Friars Cliff, Mudeford') is the type section for the Boscombe Sand Formation, which is an arenaceous deposit immediately below the Barton Clay. This is the only site known to yield abundant plant macrofossils from the Eocene Boscombe Sand Formation. Over 50 species have been reported and it is the type locality for 14 of them. For 11 species and 3 genera, this is the only known British locality. The flora includes a mixture of wetland and paratropical rain forest plants, and represents a transitional phase in the history of European Palaeogene vegetation.

Plant fossils here were noted first by Prestwich (1849), but for many years they remained unstudied, at least partly due to the difficulties of collecting significant quantities of fresh material. During the 1930s, however, the direction of outflow of the River Run changed, causing the cliff to be eroded at its base (Burton, 1931). For two years, the resulting cliff-falls allowed considerable quantities of material to be collected, but in 1935 another change in the river flow caused this to cease and since then collecting has been difficult. Most of what we know about this site comes from Chandler's (1963b) descriptions of the fossils collected then.

Description

Stratigraphy

Daley (in Daley and Balson, 1999) discusses details of the geology of this site. The exposed sequence consists of about 14 m mainly of sands, which have been interpreted as being prograding mouth-bars at the seaward end of a tidal channel (Plint, 1988). Dinoflagellate biostratigraphy (Costa *et al.*, 1976) suggests that the Boscombe Sands are the same age as the upper Selsey Formation further east, and are thus late Lutetian in age (see also Collinson, 1996b).

Palaeobotany

Chandler (1963b) gives details of the plant

fossils that were found here. These include ferns, principally *Lygodium kaulfussii* Heer (Schizaeaceae), and the conifers *Pinus* sp., *Sequoia couttsiae* Heer (see footnote to Table 8.2) and *Cupressistrobus gardneri* Chandler. There are also conifer shoots originally described as '*Araucarites sternbergii* Göppert' but which may belong to *Sequoiadendron fordii* Chandler, 1978 (Chandler, 1978, p.36–40; see comments on '*Araucarites*' in the Bracklesham GCR site report). However, the angiosperms were by far the most diverse components; those included are listed in Table 9.1. The plant remains are mostly preserved as delicate compression fossils. Compared with some of the other Tertiary fruit and seed sites in southern England, the fossils here are sparse.

Interpretation

The Boscombe Sand flora belongs to the 'Late Middle Eocene floras' of Collinson and Hooker (1987), which they state to be poorly known. Highcliffe is the only known locality to have yielded abundant plant remains from these deposits. Lignites in the Boscombe Sands at Bournemouth have yielded some plant remains but they are poorly preserved (Chandler, 1963b). The flora is probably coeval with the basal Hengistbury Head assemblage (Chandler, 1960) and the upper Selsey Formation exposed at Bracklesham Bay (Collinson, 1996b), but these have not yielded anywhere near as diverse assemblages as Highcliffe.

Although not abundant, the plant fossils from Highcliffe are of considerable interest as they throw some light on the vegetational changes taking place in Europe during middle Palaeogene times. They represent the stratigraphically highest occurrence of several taxa of angiosperm, including *Rutaspermum rugosum*, *Toddaliospermum ornatum*, *Oncoba rugosa*, *Thymelaeaspermum bournense* and *Nysoidea eocenica*. On the other hand, it yields the oldest known remains of *Cladiocarya foveolata*, *?Gordonia truncata*, *Microdiptera parva* and *Epacridicarpum mudense*. Ten species have not been reported from other localities in the British Tertiary: *Sclerocarya tribracteata*, *Toddalia excavata*, *Grewia minima*, *Eurya mudense*, *Clethra bantonense*, *Sambucus mudensis*, *Cucurbitospermum mudense* and three species of *Carpolithus*.

Two genera are unique as fossils to Highcliffe. *Sclerocarya* was established for fruits similar to those of the living razor-sedge (*Scleria*), but which differed in details of shape and surface from any living species. The record of *Grewia* was based on a single endocarp that is very similar to those of the fruits of the mainly tropical living genus of that name. Highcliffe is also the only British site to yield fossils of *Clethra*, although it has been recorded from Polish amber (Conwentz, 1886) and Danish Miocene deposits (Friis, 1985). Friis (1985) considered the inclusion of the Highcliffe species in *Clethra* as uncertain.

Chandler (1963b) regarded the assemblage as having more in common with the Ypresian, paratropical rain forest vegetation than of the later Eocene and Oligocene floras. Some of the families found at Highcliffe (e.g. dogwood, flacourtia, moonseed and tea families) indeed suggest the surrounding vegetation had a tropical aspect. However, neither the mangrove palm *Nyssa*, which forms such a characteristic element of the Ypresian fossil floras, nor '*Scirpus lakensis*' occur at Highcliffe (Collinson, 2000a). Also absent are many of the characteristic families of the Ypresian paratropical forests, such as the sumac, custard apple, dogbane, frankincense, icacina, laurel and soapberry families. The presence of some sedges, pondweeds, water lilies and frog's bits indicates that freshwater wetlands were already starting to become a dominant habitat in southern England. It would seem that the Highcliffe flora represents a transition between the Ypresian paratropical mangroves and rain forests, and the late Eocene wetlands, but with, on the whole, more in common with the latter.

Conclusions

Highcliffe is the only site known to yield a significant number of fossil fruits and seeds from the Boscombe Sand Formation, about 42 Ma old. The flora includes 11 species and 3 genera that are unique in the British Tertiary deposits. It reflects the transition between the paratropical rain forests of early Eocene times and the wetlands of late Eocene times, and is thus important for understanding the vegetational and climatic changes that were occurring in Britain during that time.

Table 9.1. Composition of the angiosperm flora from the Boscombe Sand Formation, Highcliffe. Species are described in Chandler (1963b) unless otherwise referenced. Some are also discussed by Mai and Walther (1978, 1985) and Mai (2000). The family classification listed here is summarized in Chapter 1 of the present volume.

Family	Species
Actinidiaceae	<i>Actinidia eocenica</i> Chandler
	<i>Saurauia crassisperma</i> (Chandler) Mai ¹
Arecaceae	<i>Calamus daemonorops</i> (Unger) Chandler
Betulaceae	<i>Carpinus boveyanus</i> (Heer) Chandler
Boraginaceae	Genus? (?Ehretioideae)
Caprifoliaceae	<i>Sambucus mudensis</i> Chandler
Caryophyllaceae	<i>Hantsia pulcra</i> (Chandler) Chandler
Clethraceae	<i>Clethra bantonensis</i> Chandler
Cornaceae (including Mastixiaceae)	<i>Dunstania glandulosa</i> (Chandler) Chandler, 1961c (see also Chandler, 1963b) ²
	<i>Eomastixia rugosa</i> (Zenker) Chandler
	<i>Mastixia? glandulosa</i> Chandler
	<i>Mastixicarpum crassum</i> Chandler
Cucurbitaceae	<i>Cucurbitospermum mudense</i> Chandler
Cyperaceae	<i>Caricoidea obscura</i> Chandler
	<i>Scleriocarya tribrachteata</i> Chandler
	<i>Cladiocarya foveolata</i> Reid and Chandler
Cyrillaceae ³	<i>Epacridicarpum beadonense</i> Chandler
	<i>E. mudense</i> Chandler
Epacridaceae	? <i>Leucopogon</i> sp.
Flacourtiaceae	<i>Oncoba rugosa</i> Chandler
Hydrocharitaceae	<i>Stratiotes bantonensis</i> Chandler
Lythraceae	<i>Microdiptera parva</i> Chandler
	<i>Palaeolythrum bournense</i> Chandler
Menispermaceae	<i>Palaeosinomenium</i> spp.
Nymphaeaceae	<i>Sabrenia chandlerae</i> Collinson
Nyssaceae	<i>Nyssoidea eocenica</i> Chandler
Potamogetonaceae	<i>Potamogeton pygmaeus</i> Chandler (see Collinson, 1983a)
	<i>Limnocarpus forbesii</i> (Heer) Chandler <i>emend.</i> Collinson 1982a
Rosaceae	<i>Rubus acutiformis</i> Chandler
Rutaceae	<i>Rutaspermum rugosum</i> Chandler
	<i>Toddalia excavata</i> (Chandler) Gregor ⁴
	<i>Toddaliospermum ornatum</i> Chandler
Solanaceae	<i>Solanispermum reniforme</i> Chandler
Symplocaceae?	Genus?
Theaceae	? <i>Cleyera</i> sp.
	<i>Eurya dubia</i> (Chandler) Mai ⁵
	<i>Eurya stigmosa</i> (Ludwig) Mai ⁶
	<i>Eurya mudensis</i> Chandler
	? <i>Gordonia truncata</i> Chandler ⁷
Thymelaeaceae	<i>Thymelaeaspermum bournense</i> Chandler
Tiliaceae	<i>Grewia minima</i> Chandler
Vitaceae	<i>Vitis</i> sp.
<i>Incertae sedis</i>	<i>Carpolithus ecbinatus</i> Chandler
	<i>C. ornatus</i> Chandler
	<i>C. mudense</i> Chandler
	<i>Dicotylophyllum pinnatifidum</i> Reid and Chandler
	<i>Rhamnospermum bilobatum</i> Chandler
	<i>Wessexia fibrosa</i> (Chandler) Chandler

¹ Formerly *Hordwellia crassisperma* (Chandler) Chandler (see Mai and Walther, 1985).

² See Footnote 4 to Table 8.1.

³ See comment on *Epacridicarpum* in the Barton GCR site report.

⁴ Formerly *Toddaliospermum excavatum* Chandler (see Mai and Walther, 1978).

⁵ Formerly *Cleyera? lentiformis* Chandler (see Mai and Walther, 1985).

⁶ Formerly *Cleyera? stigmosa* (Ludwig) Chandler (see Mai and Walther, 1978, 1985).

⁷ *Gordonia truncata* = *Polyspora truncata* (Chandler) Gregor (see Mai and Walther, 1985).

Gordonia and *Polyspora* are both modern genera, which are considered synonyms by some authors.

BARTON (SZ 207 931–SZ 227 931)

Introduction

This is the best site for yielding fossil plants from the Barton Clay Formation, of late middle Eocene age. It has yielded 28 species, for five of which this is the type locality. It shows clear evidence of a mixed forest and wetland vegetation, which shows evidence of the initial Eocene climatic cooling.

The Barton Clay Formation has generally yielded only very poor fossil floras. This is unfortunate, as it represents a crucial time, when a marked cooling of the climate was taking place. Gardner (1884, 1887b) described conifer cones and twigs from Barton Cliff, but unfortunately the specimens have been lost, presumably through degradation. A number of fragments were discovered by Burton (1933) and examined by Reid and Chandler. However, a more significant set of plant fossils was collected from the same locality in 1952 by D. Curry, and was the basis of the palaeobotanical study by Chandler (1960). One additional specimen of *Pinus dixonii* cone was documented by Chandler (1964, p. 129), and a second was found in 1980 (Figure 9.3). Chandler (1978) later added a single species to those known from here.

Description

Stratigraphy

The classic paper on the stratigraphy of this site was by Burton (1933), whose classification of the beds is still widely used. More recently, the stratigraphy has been revised by Hooker (1986) (see also Daley in Daley and Balson, 1999). Within the boundary of this GCR site are exposed about 40 m of the Barton Group, including all of the Barton Clay and Becton Sand Formations (Beds A–K of Burton, 1933) (Figure 9.4). They represent upward-coarsening cycles interpreted by Hooker (1986) as representing marine transgressions in a littoral environment.

Palaeobotany

The bulk of the specimens reported by Burton (1933) and Chandler (1960) came from Burton's unit A3 in the Barton Clay, at the top of the first coarsening-upwards cycle. The bed is some-

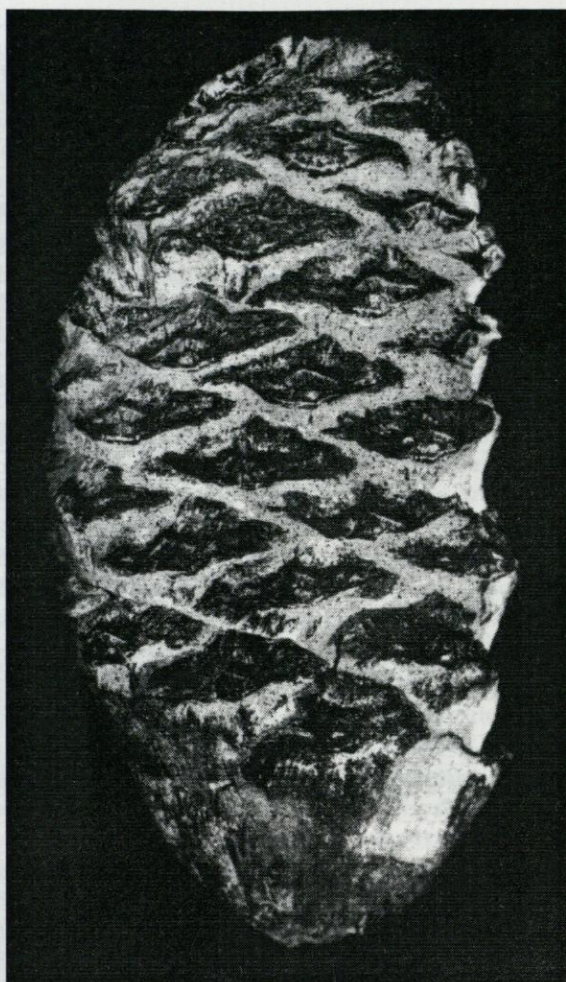


Figure 9.3 Cone of *Pinus dixonii*, a remarkable and rare fossil from Barton found in 1980, $\times 0.9$ (specimen number BMNH V.60468). (Photo: Natural History Museum, London.)

times referred to as the 'Highcliff Sands', but it should not be confused with the plant bed in the Highcliffe GCR site discussed previously. Plant fossils have also been recovered from Burton's beds A1, C, D and E (Chandler, 1960; Collinson, pers. obs.). Those described by Chandler from A3 were reported to have come from a pocket of sediment, also containing fossil shells that had been trapped on the lee side of a log of wood. Dominant are fruits and seeds of aquatic or sub-aquatic plants, including water soldiers (*Stratiotes bantonensis* Chandler), sedges (*Caricoidea obscura* Chandler), water lilies (*Sabrenia chandlerae* Collinson 1980a) and lythraceans (*Decodon gibbosus* (Reid) Reid, *Microdiptera minor* (Chandler) Mai, *Palaeolythrum bournense* Chandler), together

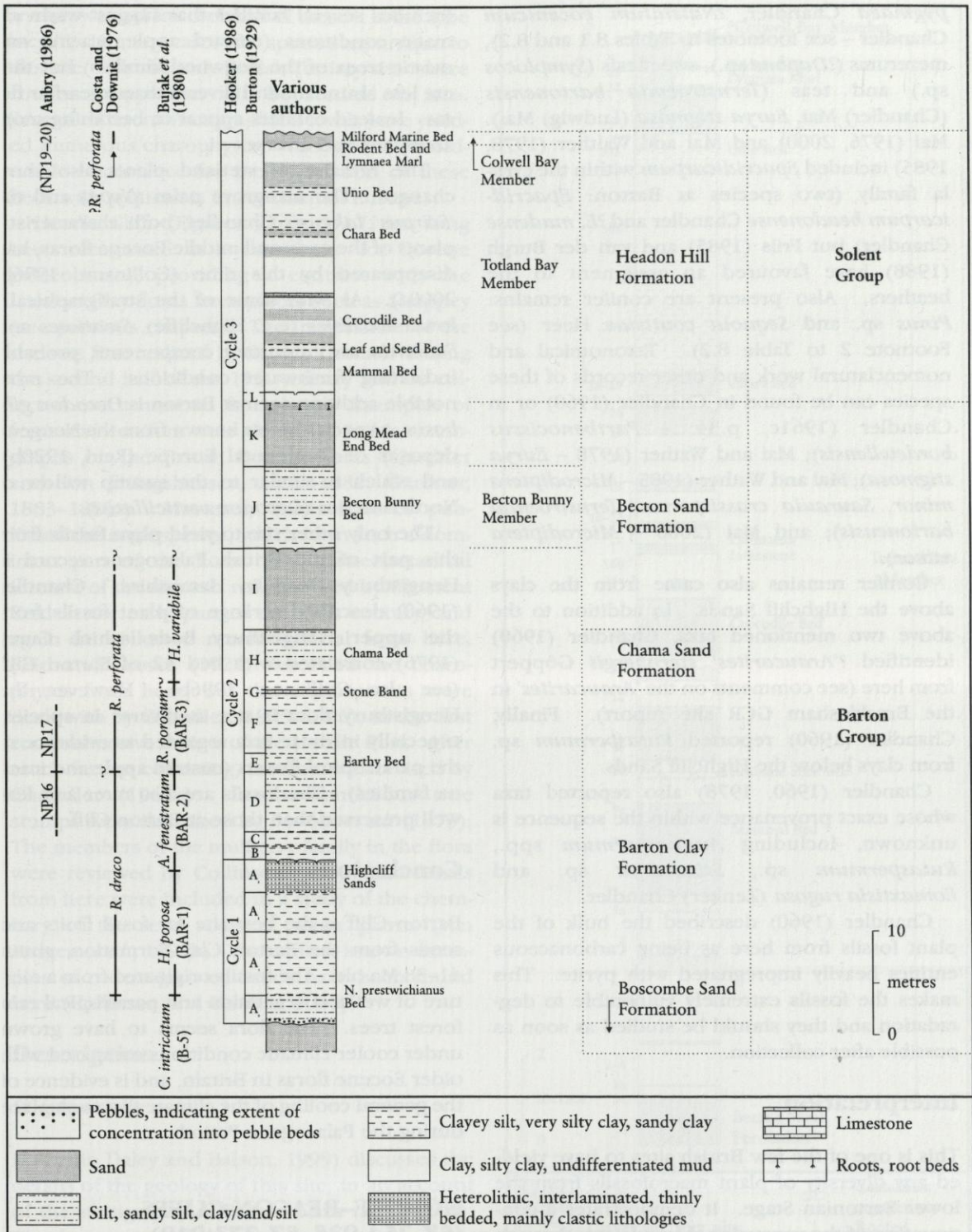


Figure 9.4 Stratigraphical succession at Barton Cliffs. (After Daley and Balson, 1999, fig. 6.14.)

with the enigmatic *Rhamnospermum bilobatum* Chandler. However, there are also fully terrestrial plants, including members of the families of

Chinese gooseberries (*Saurauia crassisperma* (Chandler) Mai), grape vines (*Parthenocissus bordewllensis* Chandler), icacinas (*icacinicarya*

pygmaea Chandler, ?*Natsiatum eocenicum* Chandler – see footnotes to Tables 8.1 and 8.2), mezerums (?*Daphne* sp.), sweetleaves (*Symplocos* sp.) and teas (*Ternstroemia bartonensis* (Chandler) Mai, *Eurya stigmosa* (Ludwig) Mai). Mai (1976, 2000) and Mai and Walther (1978, 1985) included *Epacridicarpum* within the cyrilla family (two species at Barton: *Epacridicarpum beadonense* Chandler and ?*E. mudense* Chandler) but Friis (1985) and van der Burgh (1988) have favoured an assignment to the heathers. Also present are conifer remains: *Pinus* sp. and *Sequoia couttsiae* Heer (see Footnote 2 to Table 8.2). Taxonomical and nomenclatural work and other records of these species can be found in Chandler (1960) or in Chandler (1961c, p.34 – *Parthenocissus bordewillensis*); Mai and Wather (1978 – *Eurya stigmosa*); Mai and Wather (1985 – *Microdiptera minor*, *Saurauia crassisperma*, *Ternstroemia bartonensis*); and Mai (2000 – *Microdiptera minor*).

Conifer remains also came from the clays above the Highcliff Sands. In addition to the above two mentioned taxa, Chandler (1960) identified ?*Araucarites sternbergii* Göppert from here (see comments on the 'Araucarites' in the Bracklesham GCR site report). Finally, Chandler (1960) reported *Rutaspermum* sp. from clays below the Highcliff Sands.

Chandler (1960, 1978) also reported taxa whose exact provenance within the sequence is unknown, including *Anonaspermum* spp., *Rutaspermum* sp., *Stizocarya* sp. and *Eomaxtisia rugosa* (Zenker) Chandler.

Chandler (1960) described the bulk of the plant fossils from here as being carbonaceous entities heavily impregnated with pyrite. This makes the fossils extremely vulnerable to degradation and they should be studied as soon as possible after collection.

Interpretation

This is one of the few British sites to have yielded any diversity of plant macrofossils from the lower Bartonian Stage. It demonstrates a continuation of the vegetational trend seen through the British Palaeogene deposits, which is generally interpreted as being due to climatic cooling. As with other sites in the upper middle and lower upper Eocene, such as Highcliffe, the flora consists of a mixture of the remains of wetland and forest vegetation. The forest vegetation

includes several families that suggest warm climatic conditions (custard apple, icacina and mastic trees of the dogwood families) but they are less abundant and diverse than in earlier floras. Instead conifers appear to becoming more abundant and diverse.

The remains of wetland plants also show changes. The mangrove palm (*Nypa*) and the 'Scirpus' *lakensis* Chandler, both characteristic plants of the early and middle Eocene floras, had disappeared by this time (Collinson, 1996b, 2000a). As with some of the stratigraphically lower localities (e.g. Highcliffe), *Stratiotes* and *Sabrenia* are important components, probably indicating freshwater conditions. The most notable addition seen at Barton is *Decodon gibbosus*, a species better known from the Neogene deposits of continental Europe (Reid, 1920b), and which is similar to the swamp willow of North America (*Decodon verticillatus*).

The only other site to yield plant fossils from this part of the British Palaeogene record is Hengistbury Head in Hampshire. Chandler (1960) described a range of plant fossils from the upper Hengistbury Beds, which Curry (1976) correlated with bed A2 of Barton Cliff (see also Collinson, 1996b). However, the Hengistbury flora is not as diverse in species, especially in those taxa regarded as evidence of the paratropical forests (custard apple and icacina families). The fossils are also rarer and less well preserved than those at Barton Cliff.

Conclusions

Barton Cliff is the best site for fossil fruits and seeds from the Barton Clay Formation, about 41–38 Ma old. The fossils originated from a mixture of wetland vegetation and paratropical rain forest trees. The flora seems to have grown under cooler climatic conditions compared with older Eocene floras in Britain, and is evidence of the general cooling of the climate that took place during the Palaeogene Period.

HORDLE–BEACON CLIFFS (SZ 254 925–SZ 273 919)

Introduction

This is one of the classic Tertiary palaeobotanical sites in Britain, having yielded the best-studied late Eocene fruit and seed flora. Over 80 species

Hordle-Beacon Cliffs

are known and for over half of these it is the type locality. In many cases, the species are unique to this site. It is the only British Tertiary site where conifer stumps can still be studied *in situ*. Several different stratigraphical levels have yielded numerous charophytes, which are of considerable importance for the correlation of these beds with sequences in continental Europe.

Hordle Cliffs (Figures 9.6 and 9.7) has long been recognized as a classic site for Eocene palaeobotany, providing a contrast with the London Clay floras from places such as Sheppey (see previous chapter). The importance of the site was first realized by Starkie Gardner during the second half of the 19th century and he collected much material from here. Examples of ferns and conifers were described in his monographs on the British Eocene floras (Gardner and von Ettingshausen, 1879–1882; Gardner, 1883–1886a). However, Gardner never published the angiosperms, which form such a dominant part of the flora. The palaeobotanical interest of the site was rediscovered by Clement Reid in the early part of the 20th century, and again he collected much material from here. Reid and Groves (1921) described the charophytes from here, but the angiosperms were dealt with by Chandler (1925–1926), in the first comprehensive review of the Hordle flora. After much further collecting, the flora was revised by Chandler (1961c). In-situ coniferous tree stumps were described by Fowler *et al.* (1973). The members of the mulberry family in the flora were reviewed by Collinson (1989) and fossils from here were included in a study of the chemistry of the seed coats of water plants (van Bergen *et al.*, 1994b). The earliest known examples of rodent-gnawed seeds have been found here (Collinson and Hooker, 2000).

Description

Stratigraphy

Daley (in Daley and Balson, 1999) discusses the details of the geology of this site, in an account of the stratigraphy of Barton Cliffs (Figure 9.5). The lower part of the exposed sequence here

Figure 9.5 A composite succession for the Totland Bay Member (Headon Hill Formation) at the eastern end of 'Barton Cliffs' (Hordle Cliff) (after Edwards and Daley, 1997). The bed numbers are those of Tawney and Keeping (1883).

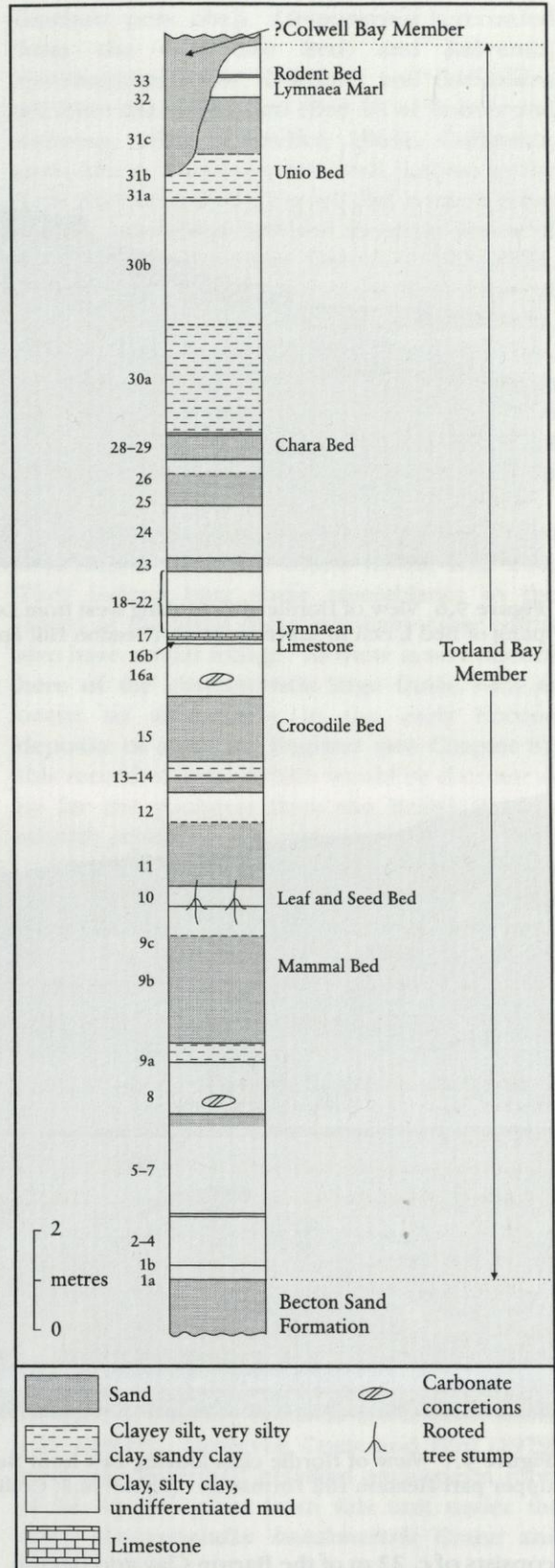




Figure 9.6 View of Hordle cliffs looking west from Long Mead End towards Becton Bunny, and showing sampling of Bed L rich in *Sabrenia* seeds (Headon Hill Formation). (Photo: M.E. Collinson.)



Figure 9.7 View of Hordle cliffs looking east from Becton Bunny. Lower part is Becton Sand Formation, the upper part Headon Hill Formation. (Photo: M.E. Collinson.)

consists of c. 22 m of the Barton Clay and Becton Sand Formations (with Bed K (Burton, 1933) yielding plant fossils – Chandler 1960). These

are overlain by c. 24 m of the Totland Bay Member (lower Headon Hill Formation), described in detail by Edwards and Daley

(1997). The main palaeobotanical interest at the site is in the Totland Bay Member, which is a unit of mainly freshwater to brackish deposits formed as the Barton marine basin became progressively silted-up (Curry, 1965).

The plant remains occur in lenses and laterally more persistent deposits occur at various levels through the sequence, including Bed I of Burton (1933) and Beds 9, 10, 13 and 28 of Tawney and Keeping (1883; Figures 9.4 and 9.5). They mostly represent deposits formed in marsh and lagoonal settings, and one layer (known as the 'Leaf and Seed Bed', Bed 10 of Tawney and Keeping, 1883), includes a lignite layer and in-situ tree stumps.

Palaeobotany

The bulk of the plant fossils found here are carbonaceous fruits and seeds. They are often in a soft condition, but uncrushed (Figure 9.8), and can therefore be dissected with care, to reveal details of the anatomy. Most of the accumulations of fruits and seeds are from aquatic angiosperms. For instance, the Mammal Bed has yielded *Stratiotes*, *Caricoidea* and *Sabrenia*, while the Rodent Bed has *Stratiotes*, *Limnocarpus* and *Aldrovanda* (Collinson and R.

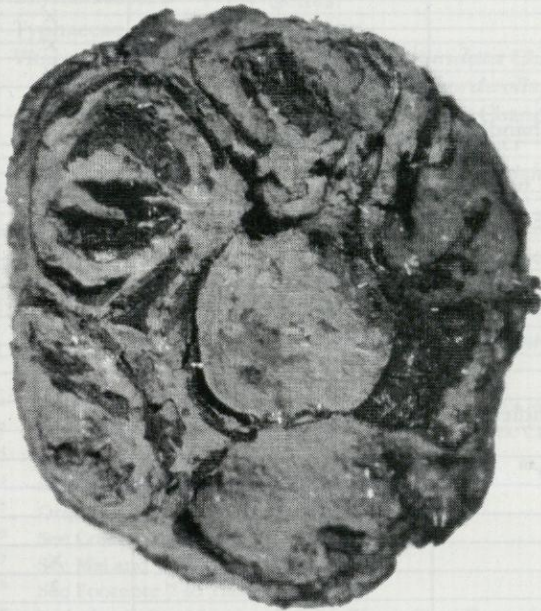


Figure 9.8 Compound fruiting head of *Steinbauera subglobosum* with bilocular fruits, in carbonaceous preservation, from the Hordle GCR site, $\times 6$ (see footnotes to Table 9.2). (Photo: M.E. Collinson.)

Gardner, pers. obs.). *Limnocarpus* is recorded from the Crocodile Bed, and *Sabrenia*, *Spirematospermum*, *Stratiotes* and *Caricoidea* are from the *Chara* Bed (Bed 28 of Tawney and Keeping, 1883; Chandler, 1961c; Collinson, pers. obs.). However, one level, known as the 'Leaf and Seed Bed', has yielded a much more diverse assemblage and was the main source of the material studied by Chandler (1925-1926, 1961c, 1962). In addition to the above types of aquatic plant, there is also a range of forest taxa, including members of the icacina, mulberry, rue, sweetleaf, tea and grape families, and mastic trees of the dogwood family. The full list of 76 species of angiosperm fruits and seeds (both of aquatic and forest plants) found at Hordle is given in Table 9.2.

Chandler (1925-1926) recorded *Nypa* from here based on leaves found in the Leaf Bed. They indeed bear some resemblance to the leaves of the living *Nypa* but many other palms also have similar foliage. As there is no evidence here of the characteristic large fruits, such as occur so abundantly in the early Eocene deposits of southern England (see Chapter 8), this record of *Nypa* (which would be aberrant as by far the youngest from the British Tertiary record) should be rejected.

Hordle has also yielded the ferns *Acrostichum lanzaeanum* (Visiani) Chandler, *Salvinia mildeana* Göppert foliage and *Azolla prisca* Reid and Chandler megaspores (Collinson, 1980b). Conifers are mainly represented by remains of the probable taxodiaceous conifer *Sequoia couttsiae* Heer (see Footnote 2 to Table 8.2, this volume), including twigs, cones, cone-scales and seeds (Chandler, 1922, 1925, 1961c, 1962). The Leaf and Seed Bed here has yielded in-situ coniferous stumps with taxodiaceous wood (*Glyptostroboxylon*), which on the basis of association have been suggested to have been produced by the same plant that yielded *S. couttsiae* foliage, cones and seeds (Fowler *et al.*, 1973).

The Mammal Bed (Bed 9 of Tawney and Keeping, 1883), at the base of the Totland Bay Member at Hordle, yields far fewer plant fossils (see earlier). However, Crane and Plint (1979) have also described petrified angiosperm roots of an aquatic plant from this unit under the name *Lacunoradix beadonensis* Crane and Plint.

Stonewort remains are scattered throughout the succession here, but better assemblages

Bartonian–Rupelian and Miocene palaeobotany

Table 9.2. Angiosperm floras from the Headon Hill Formation. Species descriptions or reference to them may be found in Chandler (1961c, 1963a), unless otherwise referenced. Discussion and other records for some of these species may be found in Mai and Walther (1978, 1985, 1991) and Mai (2000). The family classification used here is summarized in Chapter 1 of the present volume.

Family	Species	Hordle Cliffs	Colwell Bay (Totland Bay Member)	Colwell Bay (Linstone Chine Member)
Acanthaceae	? <i>Acanthus</i> sp.	×		
Actinidiaceae	<i>Actinidia</i> sp.	×		
	<i>Saurauia crassisperma</i> (Chandler) Mai ¹	×		×
Anacardiaceae	Genus (Spondieae) ?	×		
Araceae	Genus ?	×		
Arecaceae	Leaves	×		
Betulaceae	<i>Carpinus boveyanus</i> (Heer) Chandler	×		
Boraginaceae	<i>Ompbalodes platycarpa</i> Chandler	×		
Burseraceae	<i>Palaeobursera lakensis</i> Chandler	×		
Caprifoliaceae	<i>Sambucus parvulus</i> Chandler ²	×		×
Carophyllaceae	<i>Hantsia pulchra</i> (Chandler) Chandler	×		
	<i>H. glabra</i> Chandler	×		
Cercidiphyllaceae	<i>Nyssidium arcticum</i> (Heer) Iljinskaja ³	×		
Cornaceae (including Mastixiaceae)	<i>Dunstania glandulosa</i> (Chandler) Chandler ⁴	×		
	<i>Eomastixia rugosa</i> (Zenker) Chandler	×		
	<i>Swida quadrilocularis</i> (Chandler) Mai, 1999 ⁵	×		
	Genus ?	×		
Cucurbitaceae	<i>Cucurbitospermum reidii</i> Chandler	×		
Cyperaceae	<i>Caricoidea angulata</i> Chandler ⁶			×
	<i>C. nitens</i> (Heer) Chandler			×
	<i>C. obscura</i> Chandler	×		
	<i>Cladiocarya minima</i> (Chandler) Mai ⁷	×		
	<i>C. colwellensis</i> (Chandler) Mai ⁷			×
	<i>Carex colwellensis</i> Chandler			×
	<i>C. spp.</i>			×
	? <i>Scirpus</i> sp.			×
Cyrillaceae ⁸	<i>Epacridicarpum beadonense</i> Chandler	×		×
	<i>E. colwellense</i> Chandler			×
Droseraceae	<i>Aldrovanda ovata</i> (Chandler) Chandler	×	×	×
Ebenaceae	<i>Diospyros beadonensis</i> Chandler	×		
Ericaceae	2 Genera ?	×		
Hamamelidaceae	<i>Steinbauera subglobosa</i> Presl ⁹	×		
Hydrocharitaceae	<i>Stratiotes beadonensis</i> Chandler	×	×	×
	<i>S. bantonensis</i> Chandler	×		
Icacinaceae	? <i>Iodes</i> sp. (or ? <i>Natsiatum</i>)	×		
	? <i>Iodes</i> ? <i>bordwellensis</i> Chandler	×		
	<i>Icacinicarya transversalis</i> Chandler	×		
	<i>I. becktonensis</i> Chandler	×		
	<i>Natsiatum eocenicum</i> Chandler ¹⁰	×		
Lauraceae	Genus ?	×		
'Legumes'	2 Genera ?	×		
Lythraceae	<i>Decodon vectensis</i> Chandler			×
	<i>Microdiptera parva</i> Chandler	×		?
	Genus ?	×		
Menispermaceae	<i>Palaeosinomenium obliquatum</i> (Chandler) Chandler	×		
Moraceae ¹¹	<i>Cblorophora bicarinata</i> Chandler	×		
	<i>Broussonetia rugosa</i> Chandler	×		
	<i>Moroidea boveyana</i> Chandler ¹²	×		
	<i>Becktonia bantonensis</i> Chandler	×		
	<i>Ficus lucidus</i> Chandler			×

Hordle-Beacon Cliffs

Family	Species	Hordle Cliffs	Colwell Bay (Totland Bay Member)	Colwell Bay (Linstone Chine Mbr)
Myricaceae	<i>Myrica boveyana</i> (Heer) Chandler	×		×
	<i>M. colwellensis</i> Chandler			×
Nymphaeaceae	<i>Sabrenia chandlerae</i> Collinson 1980a	×	×	×
	<i>Brasenia spinosa</i> Chandler	×		×
	<i>B. oblonga</i> Chandler	×		
	<i>Nymphaea</i> sp.			×
Oleaceae	<i>Olea beadonensis</i> Chandler	×		
Potamogetonaceae	<i>Potamogeton pygmaeus</i> Chandler (see Collinson, 1983a)	×	×	×
	<i>P.</i> sp.	×		×
	<i>Limnocarpus forbesii</i> (Heer) Chandler ¹³	×	×	×
Rhamnaceae	<i>Frangula bordwellensis</i> Chandler	×		
Rosaceae	<i>Rubus acutiformis</i> Chandler	×		
	? <i>R. microspermus</i> Reid and Reid			×
Rutaceae	<i>Pbelloidendron costatum</i> Chandler	×		
	<i>Acronychia ornata</i> (Chandler) Mai, 1976 ¹⁴	×		
	<i>Zanthoxylum bordwellense</i> Chandler	×		×
	<i>Z. compressum</i> Chandler	×		
Sabiaceae	<i>Meliosma</i> sp.	×		
Styracaceae	<i>Styrax elegans</i> Chandler	×		
Symplocaceae	<i>Symplocos beadonensis</i> Chandler	×		
	<i>S.</i> sp.	×		
Theaceae	<i>Anneslea?</i> <i>costata</i> Chandler	×		
	<i>Visnea bordwellensis</i> (Chandler) Mai ¹⁵	×		
	<i>Eurya becktonensis</i> Chandler	×		
	<i>E. stigmosa</i> (Ludwig) Mai ¹⁶	×		
	<i>Gordonia minima</i> Chandler	×		
	<i>Polyspora truncata</i> (Chandler) Gregor ⁸	×		
Thymelaeaceae	Genus?	×		
Typhaceae	<i>Typha</i> sp.			×
Vitaceae	<i>Ampelopsis rotundata</i> Chandler	×		
	<i>Parthenocissus bordwellensis</i> Chandler	×		
	<i>Tetrastigma lobata</i> Chandler	×		
	<i>Vitis uncinata</i> Chandler	×		
Zingiberaceae/ Musaceae	<i>Spirematospermum wetzleri</i> (Heer) Chandler ¹⁷	×		
<i>Incertae sedis</i>	<i>Carpolithus fibrosus</i> Chandler	×		
	<i>C. apocyniformis</i> Chandler	×		
	<i>C. colwellensis</i> Chandler			×
	<i>C.</i> spp.	×		×
	<i>Rhamnospermum bilobatum</i> Chandler	×		×

¹ Formerly *Hordwellia crassisperma* (Chandler) then included within the Theaceae (see Mai and Walther, 1985).

² This includes *Sambucus colwellensis* Chandler (see Collinson, 1983a).

³ See Crane (1984).

⁴ See Footnote 4 to Table 8.1.

⁵ Originally *Cornus quadrilocularis* Chandler.

⁶ See Collinson (1983a).

⁷ See Mai and Walther (1978).

⁸ See Footnote 7 to Table 9.1.

⁹ Includes *Eoliquidambar bordwellensis* Chandler and *Protaltingia bantonensis* Chandler (see Mai and Walther, 1985).

¹⁰ See footnotes to Tables 8.1 and 8.2.

¹¹ See Collinson (1989).

¹² Includes *Moroidea bordwellensis* Chandler (see Mai and Walther, 1978).

¹³ Emended by Collinson (1982a).

¹⁴ Formerly *Rutaspermum ornatum* (Chandler) (see Mai, 1976; Collinson and Gregor, 1988).

¹⁵ Formerly *Campylospermum bordwellensis* Chandler (see Mai and Walther, 1991).

¹⁶ Formerly *Cleyera?* *stigmosa* (Ludwig).

¹⁷ See text under Hordle site for discussion of *Spirematospermum*.

occur at a number of restricted horizons, including Beds 9, 10, 14, 15, 17, 28 and 30 of Tawney and Keeping (1883) (Reid and Groves, 1921; Groves, 1926; Collinson, pers. obs.). The most productive level is of limestone (Bed 17 of Tawney and Keeping, 1883), but good assemblages were also found in the Mammal Bed and Rodent Bed. The charophytes include both isolated gyrogonites and vegetative remains, although only the former are named. The following list is based on the work of Reid and Groves (1921) and Groves in Reid and Chandler (1926) as emended in part by Feist-Castel (1977). *Gyrogona wrightii* (Salter) Pia, *G. caelata* (Reid and Groves) Pia, *Grovesichara distorta* (Reid and Groves) Horn af Rantzien, *Stephanochara edwardsii* Grambast, *Psilochara polita* (Reid and Groves) Grambast, *P. bitruncata* (Reid and Groves) Feist-Castel, *Sphaerochara headonensis* (Reid and Groves) Horn af Rantzien, *S. parvula* (Reid and Groves) Horn af Rantzien, *Harrisichara vasiformis* (Reid and Groves) Grambast and *Chara subcylindrica* Reid and Groves.

Interpretation

This is the best locality for the study of the late Eocene floras of the lower Headon Hill Formation. Of the 76 species of angiosperm fruits and seeds found here (Table 9.2), for 17 species this is the only British locality: *Broussonetia rugosa*, *Chlorophora bicarinata*, *Hantsia glabra*, *Palaeosinomenium obliquatum*, *Acronychia ornata*, *Zanthoxylum compressum*, *Iodes? bordwellensis*, *Icacinicarya transversalis*, *Ampelopsis rotundata*, *Vitis uncinata*, *?Anneslea costata*, *Visnea bordwellensis*, *Eurya becktonensis*, *Gordonia minima*, *Omphalodes platycarpa*, *Cucurbitospermum reidii* and *Scleria bordwellensis*. The Hordle flora also contains the earliest records of several species that range up into Miocene or Pliocene deposits of continental Europe (e.g. *Amoelopsis rotundata*, *Tetrastigma lobata* (Mai, 2000)). It is also the type locality for another 26 angiosperm species, reflecting the long history of palaeobotanical research that there has been on this flora. No other palaeobotanical site in the late Eocene deposits of Britain can match this for diversity and history of research.

The Totland Bay Member marks the return of brackish to non-marine conditions in southern England and thus provides a more abundant and

diverse plant fossil record than the immediately underlying beds, such as seen at Barton. It is markedly different from the earlier Barton Clay floras, especially among the aquatic component. The aquatic flora at Hordle has a different composition (both of genera and species), higher diversity and more widespread occurrence than the earlier floras. Among the aquatic plants, true *Brasenia* appears. This genus had been previously recorded from lower horizons (e.g. Crane, 1977) but this was based on records of *Brasenia ovula*, which are now assigned to *Sabrenia chandlerae* Collinson, 1980a. Also in the Totland Bay Member, we see the first appearance of *Stratiotes headonensis*, which starts to take over from the earlier occurring *S. bantonensis* (Collinson *et al.*, 1981), and of the *Azolla*. Earlier occurring species that do not occur in the Totland Bay Member include '*Scirpus*' *lakensis*, *Decodon gibbosus* and *Microdiptera minor*. *Nypa burtinii* has also disappeared by this level, if one discounts the indeterminate foliar remains.

Like the aquatic plants, the forest species at Hordle show clear signs of the climatic change that was taking place during late Eocene times. The palms had all but disappeared, being only represented by some indeterminate foliage. Many of the families found in earlier Eocene floras and thought to reflect warm conditions have either disappeared or have their last rare and low-diversity occurrences here: moonseed, custard apple, sumac, icacina, dillenia, flacourtia, mezerum, ebony, styrax, olive and squash families. The tea family occurs rarely above the Totland Bay Member, but has undergone a significant decline by this level.

Sequoia couttsiae (see Footnote 2 to Table 8.2, this volume) is the most widespread of the taxodiaceous conifers found in the upper Eocene and lower Oligocene deposits of southern England. The presence of these conifers invites comparison between southern England at this time and the taxodiaceous swamps of today in southern Florida (e.g. Fowler *et al.*, 1973). Hordle is the best single locality for the study of this plant, having yielded cones, conescales, seeds, twigs and probable roots and stumps. Furthermore, the specimens from here have generally suffered less pyritization than those from other localities and thus tend to yield better-preserved cuticles. Consequently, Hordle has proved central to the development of our ideas about this important extinct conifer.

Among the angiosperms found at Hordle, the presence of *Nyssidium arcticum* is of particular interest. This member of the katsura-tree family is best known from the Palaeogene–Eocene transition interval (see Chapter 7) and until the mid-1980s was unknown above the London Clay. However, Crane (1984) found that specimens from the London Clay that Chandler (1961a) had referred to as *Carpolithus gardneri* were probably the same as his better-preserved material from the Reading Formation. Chandler (1961c) had also tentatively identified *C. gardneri* from Hordle and Crane included this material within *N. arcticum*.

Hordle has yielded four species of the mulberry family, which is more than any other British site. They have been reviewed by Collinson (1989). Some have the same level of organization as the fruits of living forms, such as *Chlorophora* and *Broussonetia*, while *Moroidea* seems to show features of more than one living genus. The taxonomic position of *Becktonia* is uncertain.

Small roots are generally rare and poorly preserved in the British Tertiary deposits. A notable exception is the anatomically preserved *Lacunoradix beadonensis* Crane and Plint, 1979, which is to date known only from Hordle. These show a small stele and well-developed system of air spaces, features normally found in roots of aquatic plants. However, because of their generalized character, it has proved impossible to link them to any of the known aquatic plants from Hordle.

Hordle is the best site in Europe for late Eocene stoneworts and is the basis of the Verzenay Biozone (Grambast, 1972). Hordle is the type locality for seven of the most widespread species of that zone. Both vegetative and fertile remains can be found here, thus providing considerable potential for work on the palaeobiology of these plants.

Hordle has yielded bulk samples of seeds (e.g. of *Sabrenia* from Bed I) and specific taxa that have been important for the application of new organic geochemical studies. These studies have revealed chemosystematic affinities and taphonomic histories of ancient plants (reviewed in van Bergen *et al.*, 1995, 2000). For instance, *Spirematospermum* seeds from here were shown to carry a chemosystematic affinity of the Musaceae (van Bergen and Collinson, 1999), supporting an affinity proposed by Manchester and Kress (1993) on morphological grounds.

Because this work has not been fully published, we have not formally altered the family affinity in this volume.

Hordle has also yielded the earliest examples of trace fossils (from Bed 28 of Tawney-Keeping (1883), named *Gliretremmorpha*, Collinson and Hooker, 2000) representing gnawing by glirid rodents in *Stratiotes* seeds. This shows that the gnawing mechanism used by the ancient rodents was similar to that used by modern wood mice.

Conclusions

Hordle has been the subject of a longer history of palaeobotanical study than any other Upper Eocene site in this country and has yielded the types of over 40 species. It yields a mixture of aquatic and forest plants and thus provides a broad insight into the vegetation growing in southern Britain at that time. It was a time of climatic cooling in Britain and the Hordle flora reflects changes taking place in both the aquatic and forest vegetation. For instance, many of the families characteristic of the earlier floras (Barton and Bracklesham Groups and below) and thought to represent tropical to subtropical conditions, have disappeared by this time. Hordle is particularly important because several levels in the succession yield material in sufficient abundance to enable organic geochemical studies to be undertaken that are throwing a new light on the affinities and preservation of these fossils. These abundant fossil floras also enable the recovery of very rare items such as rodent-gnawed seeds. Hordle is the best site for the remains of taxodiaceous conifers, including their stumps, which invites comparison with the taxodiaceous swamps of south-eastern USA. Hordle is also the best site in Europe for stoneworts (charophytes) of the Verzenay Biozone, including both vegetative and reproductive structures. The site is clearly of international importance for the study of late Eocene floras (c. 37 Ma old).

PADDY'S GAP (SZ 282 915)

Introduction

The site (Figure 9.9) is a short distance to the east of the Hordle Cliffs site discussed earlier in this chapter, and it exposes strata of only slightly younger age. Paddy's Gap is the best site for

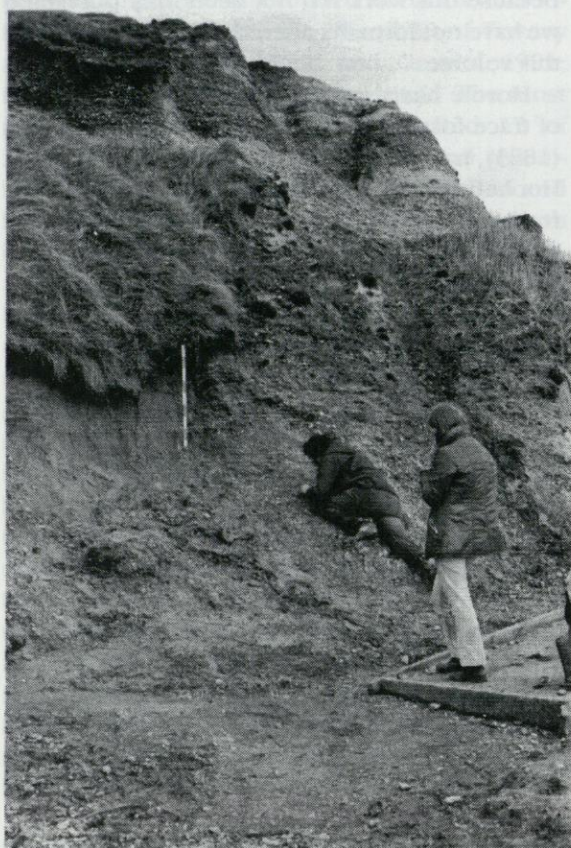


Figure 9.9 Low cliff at Paddy's Gap with exposure of *Limnocarpus* band in the *Unio* Bed, Headon Hill Formation. The photograph was taken in the mid 1970s. The section is now largely obscured by new sea defences. (Photo: M.E. Collinson.)

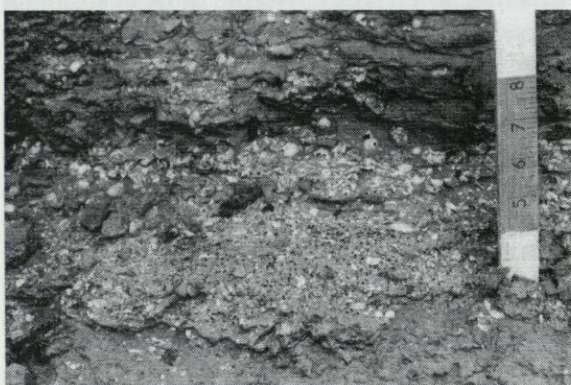


Figure 9.10 Detail of the exposure of the *Limnocarpus* band at Paddy's Gap, showing numerous small, black *Limnocarpus* fruits *in situ*. (Photo: M.E. Collinson.)

the late Eocene *Limnocarpus* band, which yields abundant fruits and seeds of the aquatic plant *L. forbesii* (Figure 9.10). The specimens described by Reid (1898) probably originated from here. The site is also included in the monograph on the flora of the Totland Bay Member (lower Headon Beds of earlier authors) by Chandler (1961c).

Description

Stratigraphy

The cliffs below Paddy's Gap expose the upper strata in the Totland Bay Member, often referred to as the '*Unio* Bed' or '*Limnocarpus* Band' (Bed 31 of Tawney and Keeping, 1883). They are mainly laminated clays in the lower part, grading up into coarse sands.

Palaeobotany

The plant fossils at Paddy's Gap consist almost exclusively of carbonaceous fruits of the aquatic plants, including *Limnocarpus forbesii* (Heer) Chandler *emend.* Collinson 1982a, *Stratiotes beadonensis* Chandler, *Aldrovanda ovata* (Chandler) Chandler and *Sabrenia chandlerae* Collinson (Chandler, 1961c; Collinson, 1978a, 1980a, pers. obs.). Collinson (1980b, pl. 24, fig. 11) also documented from here *Azolla prisca* Reid and Chandler *emend.* Fowler. *L. forbesii* is especially abundant here.

Interpretation

The abundant remains of the aquatic plant *Limnocarpus forbesii* have attracted considerable attention from palaeobotanists over the years. Tawney and Keeping (1883) noted the presence of 'little black seeds' in what they termed the '*Unio* Bed', and Reid (1898) described them as *Limnocarpus beadonensis*. Chandler (1961b) demonstrated that they should more correctly be referred to as *L. forbesii*. Most recently, the species has been reviewed and emended by Collinson (1982a), who included it in a cladistic analysis of extant and fossil potamogetonean fruits. She suggested that it was probably a primitive member of this tribe of pondweeds, being distinguished from the other members by the fruits being bicarpellate rather



Figure 9.11 Fruits of the extinct pondweed *Limnocarpus*, viewed under Scanning Electron Microscope (see Collinson 1982a). On the left is a single fruit, in which the bicarpellate condition is indicated by the straight margin opposite the germination valve, $\times 37$. On the right is a bicarpellate fruit, $\times 30$. Only sites such as Paddy's Gap, where large numbers of specimens can be studied, have ever yielded the bicarpellate fossils themselves. (Photo: M.E. Collinson.)

than individual (Figure 9.11). The fossils from Paddy's Gap have been crucial in demonstrating this phylogenetically important feature (first documented by Reid and Chandler, 1926, p. 69); only five specimens preserved in the original bicarpellate condition were recovered from a sample of 8000 (Collinson, 1982a, p. 87). The concentrated remains of *Limnocarpus* are significant in understanding the growth site of the plant, which is thought to have tolerated both fresh and slightly brackish water (Collinson, 1996b). Furthermore, the abundance of specimens is valuable for new, organic geochemical or isotopic approaches, which involve destructive analyses. Van Bergen *et al.* (2000) have shown that *Limnocarpus* carries a chemosystematic signature confirming an affinity with the pondweeds, as originally proposed on morphological grounds (Collinson, 1982a).

Conclusions

Paddy's Gap is the best site in Britain for the fruits of the primitive pondweed *Limnocarpus forbesii*, one of the most characteristic plants of

the British late Eocene floras (c. 36 Ma old).

HEADON HILL AND TOTLAND BAY (SZ 305 857–SZ 323 875)

Introduction

Plant fossils have been found at various stratigraphical levels through this classic section of the late Eocene succession on the Isle of Wight, from the upper Barton Clay Formation to the Bembridge Limestone Formation. They provide information on the vegetation and their habitats for this crucial part of the late Eocene, when climatic change was having a significant impact on this part of Britain.

Reid and Strahan (1889) and Chandler (1963a, 1964) have recorded plant fossils from here, but no single horizon has so far yielded a significant flora. However, the extensive exposures and the associated mammalian faunas allow the palaeoecology to be investigated (Hooker *et al.*, 1995). Specimens from here were used in a study of the chemistry of water-plant seed coats (van Bergen *et al.*, 1994a).

Bartonian–Rupelian and Miocene palaeobotany

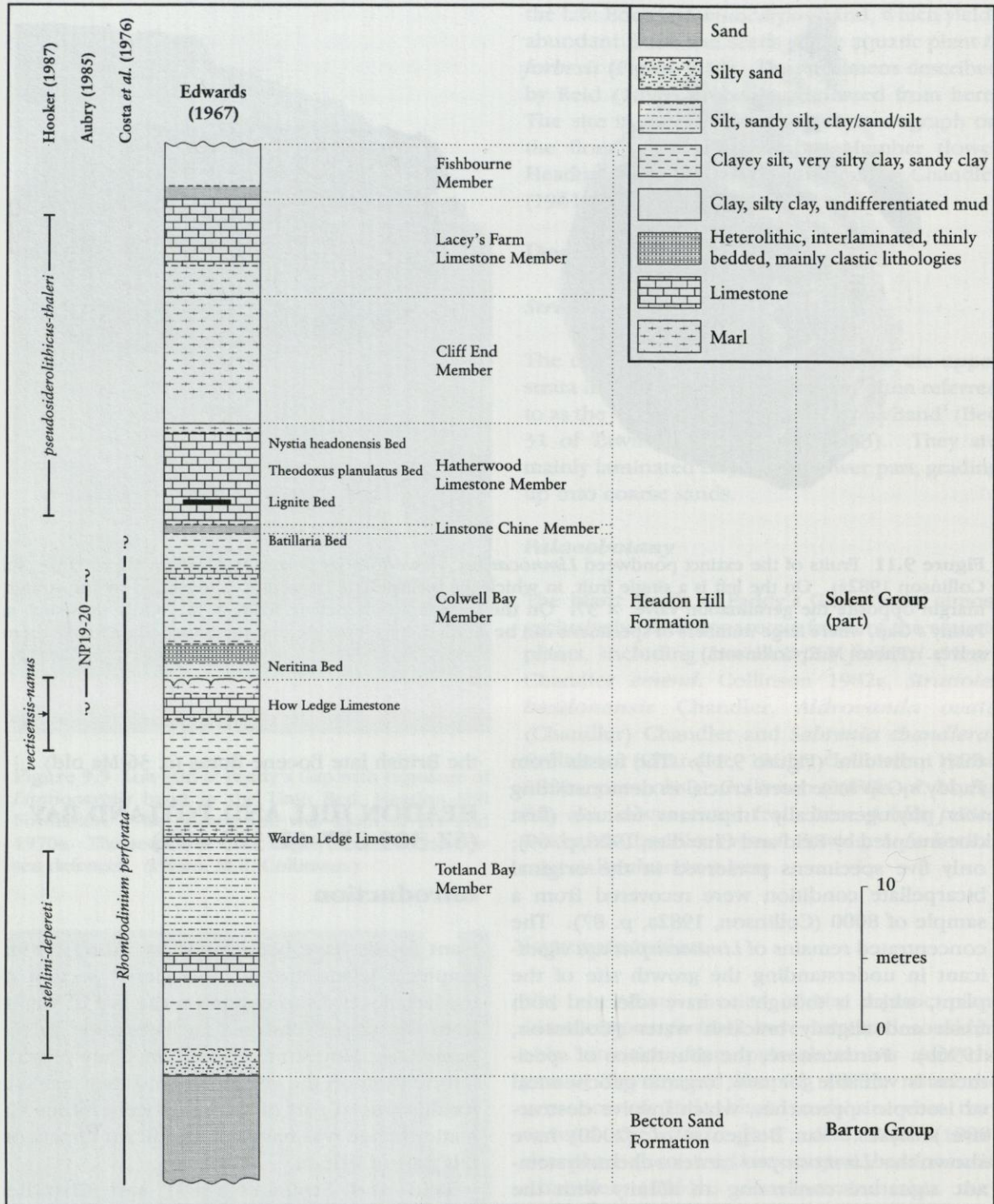


Figure 9.12 Stratigraphical succession at Alum Bay, Isle of Wight, which includes the plant beds at Headon Hill and Totland Bay. (After Daley and Balson, 1999, fig. 5.28.)

Description

Stratigraphy

Exposed along this part of the Isle of Wight coast

is an almost unbroken succession of late Eocene strata, including the Barton Clay, Headon Hill and Bembridge Limestone Formations (Figures 9.12, 9.13 and 9.17). Of particular interest are the lignite bands that occur at several levels

Headon Hill and Totland Bay



Figure 9.13 View of Alum Bay and Headon Hill, Hatherwood Point, as seen from the Needles Headland. (Photo: M.E. Collinson.)



Figure 9.14 Headon Hill Formation exposed at Headon Hill, including plant fossiliferous Totland Bay Member at lower left. (Photo: M.E. Collinson.)

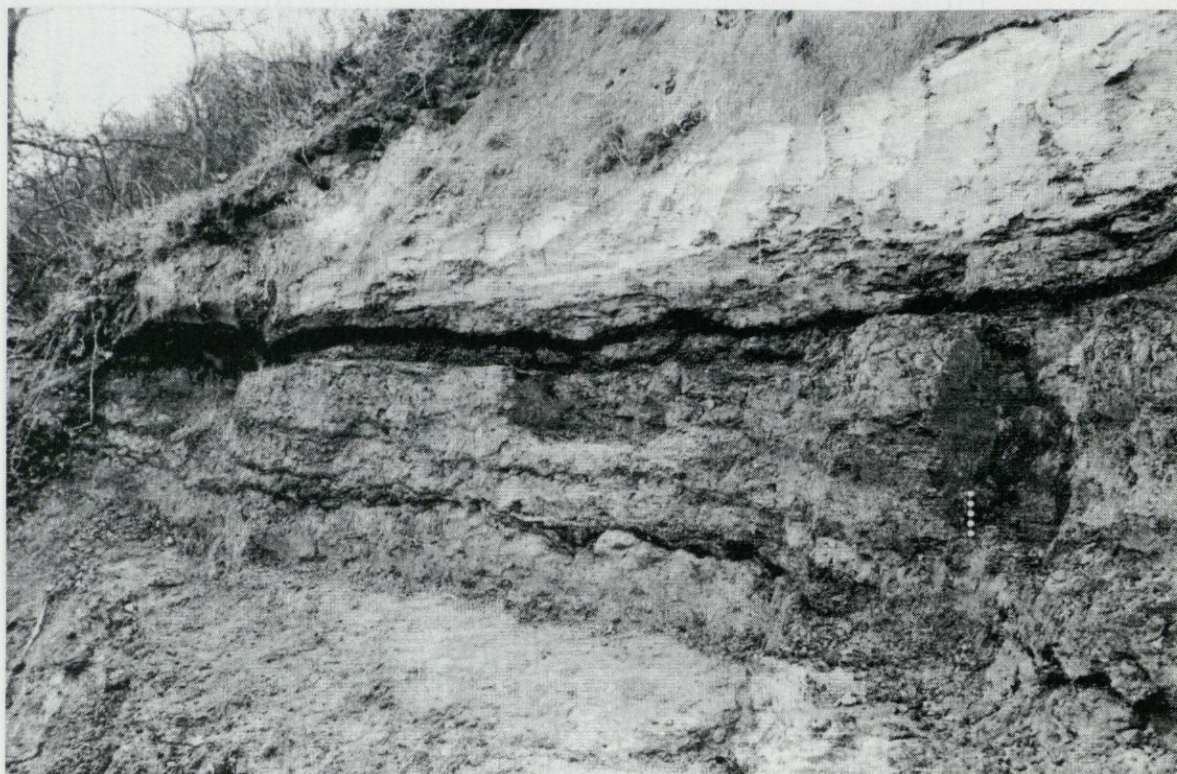


Figure 9.15 Section of Bembridge Limestone Formation on the north-east face of Headon Hill, where the multidisciplinary study of Hooker *et al.* (1995) was undertaken. (Photo: M.E. Collinson.)



Figure 9.16 The Lignite Bed in the Hatherwood Limestone Member and overlying beds exposed at Hatherwood Point, Headon Hill. (Photo: M.E. Collinson.)

Headon Hill and Totland Bay



Figure 9.17 View of Totland Bay looking north, showing exposures of Totland Bay Member (Headon Hill Formation) in the distance. (Photo: M.E. Collinson.)



Figure 9.18 Close up of exposures of the Totland Bay Member (Headon Hill Formation) at the north end of Totland Bay. (Photo: M.E. Collinson.)

through the succession, the thickest being the Hatherwood lignite (Figure 9.16), some 8 m above the *Chara* Bed. Keeping and Tawney (1881) and Insole and Daley (1985) document the stratigraphy of this site. Daley (in Daley and Balson, 1999) deals with its broader significance.

Palaeobotany

Plant fossils occur here in the Totland Bay Member (lower Headon Hill Formation; Figures 9.14 and 9.18). Fruits and seeds have never been described in the literature, but come from the same level (*Limnocarpus* band) as those described by Chandler (1961c) from nearby Colwell Bay and Hordle (see Table 8.2). The flora is exclusively aquatic, including pondweeds (*Limnocarpus*), water lilies (*Sabrenia*) and water soldiers (*Stratiotes*) (Collinson, pers. obs.).

Coniferous tree stumps from here with *Glyptostroboxylon* wood, together with those at Hordle, are the only in-situ tree stumps in the Tertiary deposits of the Isle of Wight (Fowler *et al.*, 1973).

Reid and Strahan (1889) reported the presence here of a Leaf Bed from the Fishbourne Member (upper Headon Hill Formation). No fossils have ever been described from the Leaf Bed at this locality but the flora is likely to be similar to that found at Chapel Corner on the east side of the island (see GCR site report).

Chandler (1963a) reported calcite casts of *Celtis edwardsii* Chandler from the lower part of the Bembridge Limestone Formation. It was the only species found at this level at this locality and has not been found since. Hooker *et al.* (1995) reported other, mainly aquatic, plant remains including charophytes, and fruits of *Stratiotes* (Figure 9.19) and *Caricoidea*. Other significant fossils include leech cocoons and pellets of wood-feeding termites (Hooker *et al.*, 1995).

Charophytes were described by Feist-Castel (1977) from several horizons through the Headon Hill Formation along this stretch of coast. The sequence demonstrated the difference between what Feist-Castel referred to as the Verzenay and Bembridge Charophyte Zones. The former (lower Headon Hill Formation) included characteristic forms such as *Stephanochara edwardsii* Grambast, *Psilochara polita* (Reid and Groves) Grambast, *P. bitrunca-ta* (Reid and Groves) Feist-Castel and the early

form of *Harrisichara vasiformis* (Reid and Groves) Grambast. These taxa were missing from the higher horizons, and instead *Chara attenuata* Grambast, *Grambasticbara tornata* (Reid and Groves) Horn aff. Rantzien and the transitional forms of *Harrisichara vasi-formis*–*H. tuberculata* were found.

Interpretation

There have been few detailed palaeobotanical studies along this stretch of coast on the Isle of Wight and its full potential has therefore still to be established. However, nowhere else in Britain are there such good exposures of plant-bearing strata through the upper Eocene, and the site holds considerable potential for further collecting, as well for palaeoecological study.

Significant work here has been on the palaeoecology of the Bembridge Limestone Formation (Figure 9.15) by Hooker *et al.* (1995), where the macropalaeobotany was integrated with palynological, mammal, invertebrate, organic geochemistry and stable isotope evidence. This revealed apparently conflicting results. The mammal evidence strongly indicated that the freshwater lake in which these deposits were formed was surrounded by a forest or closed woodland, with no more than a narrow belt of open habitat around the shore. However, the other lines of evidence all indicate that there was an extensive zone of marshland around the margins of the lake. The only evidence of trees was the calcified endocarps of *Celtis*, and bisaccate pollen, both of which were capable of being transported over considerable distances. There is clearly much potential here for similar work, which may help reconcile these apparently conflicting lines of evidence.

The exposures near Totland and on Headon Hill are important for their aquatic angiosperm flora, found in the Totland Bay Member. The deposits here are more freshwater-dominated than those seen at the Hordle Cliffs site, which has yielded the classic flora from the lower Headon Hill Formation. If they sample only local vegetation this may explain the absence of fruits and seeds of forest plants. Paddy's Gap may represent a similar situation.

Headon Hill is the best section in Britain for the study of late Eocene charophyte biostratigraphy. Nowhere else in this country has it been possible to document the succession of charophytes through the rocks of this age, and it is the

Headon Hill and Totland Bay

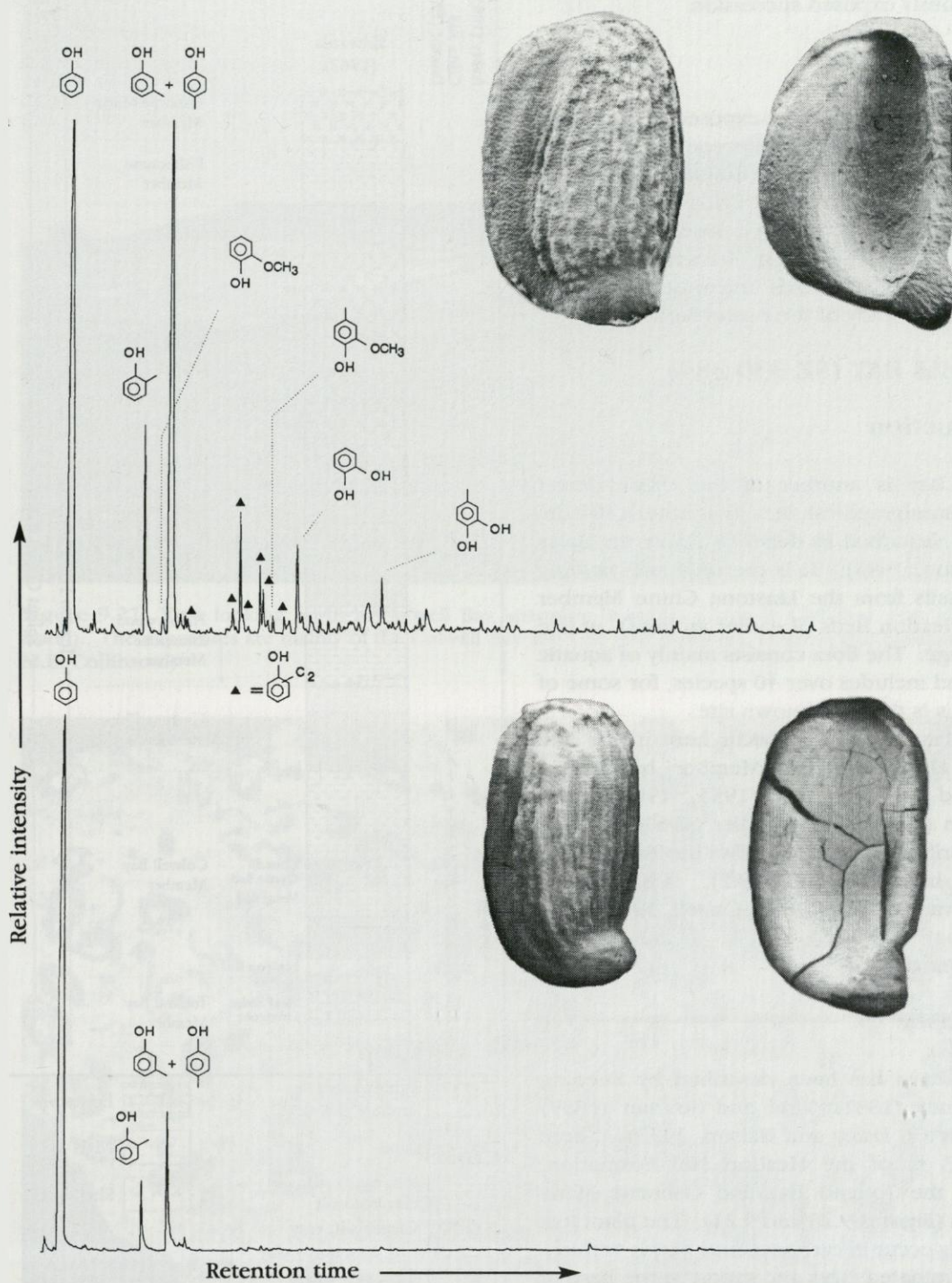


Figure 9.19 The seeds of the water plant *Stratiotes* from the Bembridge Limestone Formation of Headon Hill show severe degradation both in morphology and chemistry (bottom), compared to their equivalents at Gurnard, Thorness Bay (top). This suggests oxidative decomposition prior to or following fossilization. The Scanning Electron Microscope images of the seeds show outer (left) and inner (right) views, $\times 7.5$. See Hooker *et al.*, 1995. (Photos: M.E. Collinson.)

only site in Europe where they can be seen in a continuously exposed succession.

Conclusions

Headon Hill has the best-exposed sequence of plant-bearing rocks of late Eocene age in Britain. It provides excellent opportunities for studying the vegetational habitats of Britain as they were 35–37 Ma ago. The section is especially valuable because of the association of fossil plants with the remains of mammals and other tetrapods, enabling the study of their co-evolution.

COLWELL BAY (SZ 330 884)

Introduction

Colwell Bay is another of the classic lower Tertiary stratigraphical sites in southern Britain, and it is described in detail by Daley (in Daley and Balson, 1999). It is the only site yielding plant fossils from the Linstone Chine Member (upper Headon Beds of earlier authors), of late Eocene age. The flora consists mainly of aquatic plants and includes over 40 species, for some of which this is the only known site.

The plant fossils that occur here in the late Eocene Linstone Chine Member have been described by Chandler (1955, 1963a) and Collinson (1980a,b). Chandler (1961c, p. 101) also described a small flora from the Totland Bay Member here (see Table 9.2). Charophytes occur at various levels (Feist-Castell, 1977).

Description

Stratigraphy

The sequence has been described by Keeping and Tawney (1881), Reid and Strahan (1889) and Daley (in Daley and Balson, 1999). There are c. 33 m of the Headon Hill Formation, between the Totland Bay and Osborne Marls Members (Figures 9.20 and 9.21). The plant fossils mostly occur in carbonaceous bands within a unit of laminated clays and sands, at the base of the Linstone Chine Member. This unit contains abundant fossils of the bivalve *Potamomya*, indicating brackish conditions.

Palaeobotany

The plant fossils found here are mainly carbona-

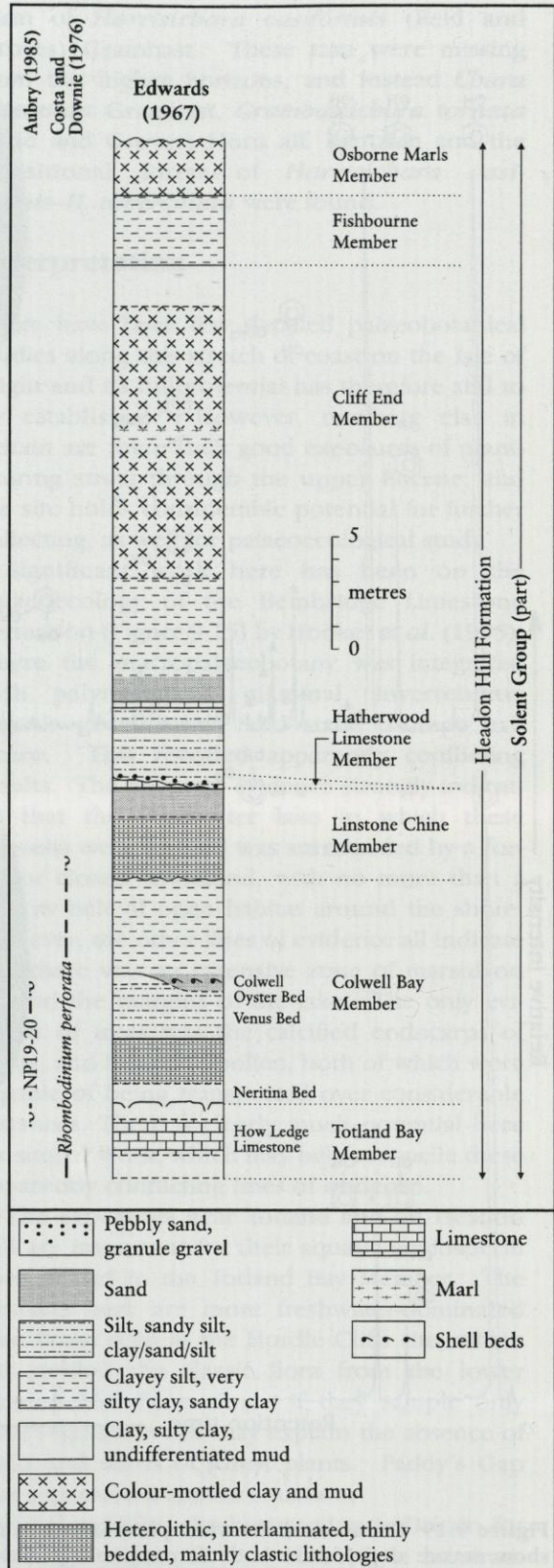


Figure 9.20 Stratigraphical succession at Colwell Bay, Isle of Wight. (After Daley and Balson, 1999, fig. 5.33.)

Colwell Bay



Figure 9.21 View looking north in Colwell Bay, spanning Brambles Chine to Cliff End, Fort Albert (now a hotel). The exposures are mainly of the Colwell Bay and Cliff End members, Headon Hill Formation. (Photo: M.E. Collinson.)



Figure 9.22 Bedding surface in the Headon Hill Formation covered in fruits of the pondweed *Potamogeton*, $\times 8$, from Colwell Bay. (Photo: M.E. Collinson.)

ceous fruits and seeds, often with replacement by amorphous pyrite. Chandler (1963a) states that there are some 38 taxa known from here, 27 of which were named to species. Angiosperms are by far the commonest, and over half of these are aquatic or marsh plants, including rushes, water soldiers, water lilies and pondweeds (Figure 9.22; a full list of the angiosperm fruits and seeds found here is given in Table 9.2). The remains of plants that grew in drier conditions are much scarcer, although fragments of twigs, seeds and cone-scales of the taxodiaceous conifer *Sequoia couttsiae* Heer (see Footnote 2 to Table 8.2, this volume) are locally common. In addition, there are rare fruits of elder (*Sambucus*), fig (*Ficus* – see comments by Collinson, 1989), bog-myrtle (*Myrica*) and silkwood (*Zanthoxylon*).

Ferns are uncommon here, but Chandler (1955) described a single fertile pinnule of the schizaeacean *Anemia colwellensis* Chandler. Barthel (1976) regarded this species as a synonym of *Ruffordia subcretacea* (Saporta) Barthel. *Ruffordia* clearly belongs in a clade including *Anemia* and is very similar to *Anemia* (Collinson, 1996a, in press a). Collinson (1980b) described the megaspore of the water fern *Azolla colwellensis* Collinson, which is

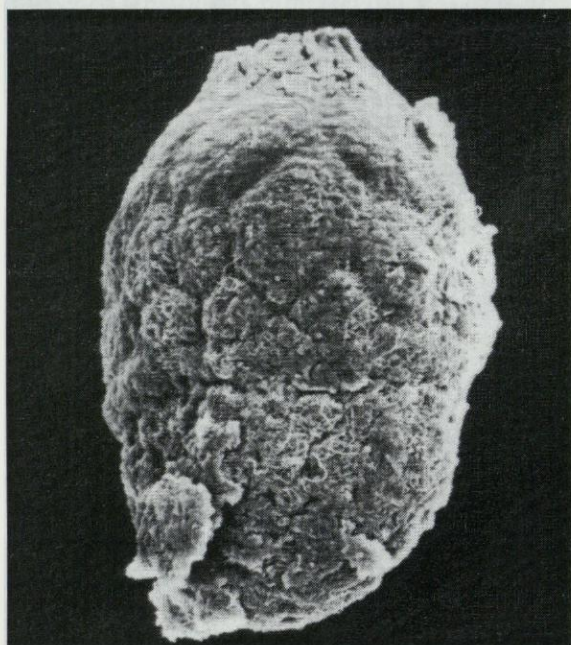


Figure 9.23 Megaspore of the water fern *Azolla colwellensis* from Colwell Bay, with attached microspore massula, viewed under Scanning Electron Microscope, $\times 195$ (see Collinson, 1980b). (Photo: M.E. Collinson.)

unique to this site, and is the youngest record of the primitive form with many ‘floats’ in the megaspore (Figure 9.23).

Interpretation

Chandler (1963a) was of the view that the Colwell Bay flora ‘is not a very remarkable or informative one’. It is indeed similar in many ways to that from the lower part of the Headon Hill Formation (Totland Bay Member), such as seen at Hordle, consisting predominantly of aquatic and marsh plants. However, there are many features that make the Colwell Bay flora distinctive and important, not least the fact that it is the type locality for nine species: *Azolla colwellensis*, *Anemia colwellensis*, *Carex colwellensis*, *Cladiocarya colwellensis*, *Myrica colwellensis*, *Decodon vectensis*, *Sambucus colwellensis* (synonymized with *S. parvula* Chandler by Collinson, 1983a), *Epacridicarpum colwellense* and *Carpolithus colwellensis*. The *Anemia* has been tentatively identified from another locality (Chandler, 1964) and is more widespread if included in *Ruffordia subcretacea* (Barthel, 1976). *Decodon vectensis* ranges up into the early Miocene deposits in Europe; the record from Colwell Bay is the oldest (Mai, 2000).

Colwell Bay is the only site to yield plant fossils from the late Eocene Linstone Chine Member (Headon Hill Formation), and as such is important for establishing the pattern of vegetational and climatic change in southern England during the Palaeogene Period. This is most clearly seen in the aquatic part of the flora. It shows the extinction of *Stratiotes bantonensis*, which becomes replaced by the larger *S. beadonensis*, and the youngest possible occurrences of ?*Caricoidea angulata* and ?*C. obscura*. Collinson (1983a) considered these specimens of ?*C. obscura* to be similar to some from the Bembridge Marls but probably distinct from those in older strata. Also here is the first appearance of *Nymphaea* in the British fossil record.

The forest component provides less evidence of the environmental changes occurring at this time, but this is probably merely a function of the scarcity of the fossils of this part of the flora. It is nevertheless of note that these beds include the youngest occurrences of *Ficus lucidus*, *Hordwellia crassisperma* and *Epacridicarpum beadonense*. Bulk sampling has the potential

Chapel Corner

for yielding plant fossils from other levels in this section and it is worth noting that *Stratiotes* has been recovered from the *Venus* Beds (Collinson, pers. obs.). Charophytes, of value in palaeoenvironmental analysis and biostratigraphy, occur throughout the site (Feist-Castell, 1977).

Conclusions

Colwell Bay is the only British site to have yielded plant fossils from the Linstone Chine Member (Headon Hill Formation), of late Eocene age (c. 36 Ma old). It is thus crucial for understanding variations in the geographical and temporal distribution of these floras. The fossils are mainly the fruits and seeds of aquatic and marsh plants, and they help demonstrate the progressive cooling of the climate that was taking part in southern Britain at this time. Although the flora is not as diverse as at some other Lower Tertiary sites in Britain, it has yielded seven species that are unique to this site.

CHAPEL CORNER (SZ 553 936)

Introduction

Chapel Corner is the only site now known to yield fossil plant remains from the late Eocene

Fishbourne Member of the upper Headon Hill Formation. Although in an essentially non-marine facies, the Fishbourne Member (the 'Osborne Beds' of earlier authors) has yielded very little in the way of palaeobotanical material. To date, rare plants have only been found at Colwell Bay (exposure not accessible) and on the coast near Osborne, both on the Isle of Wight (Chandler, 1963a). Colenutt (1888) recorded plant remains from Chapel Corner but the only detailed description of fossils from here is by Chandler (1963a).

Description

Stratigraphy

White (1921) has described the geology of this site. The plant remains occur in deposits that are now assigned to the Fishbourne Member in the upper part of the Headon Hill Formation. The exposures occur in the foreshore (Figure 9.24) and can only be studied at low tide.

Palaeobotany

Colenutt (1888) recorded plant remains from Chapel Corner, and there are specimens of *Limnocarpus* and *Sabrenia* housed in the Natural History Museum, London. However, the



Figure 9.24 Foreshore exposures of the Fishbourne Member at Chapel Corner, as seen in 1982. (Photo: M.E. Collinson.)

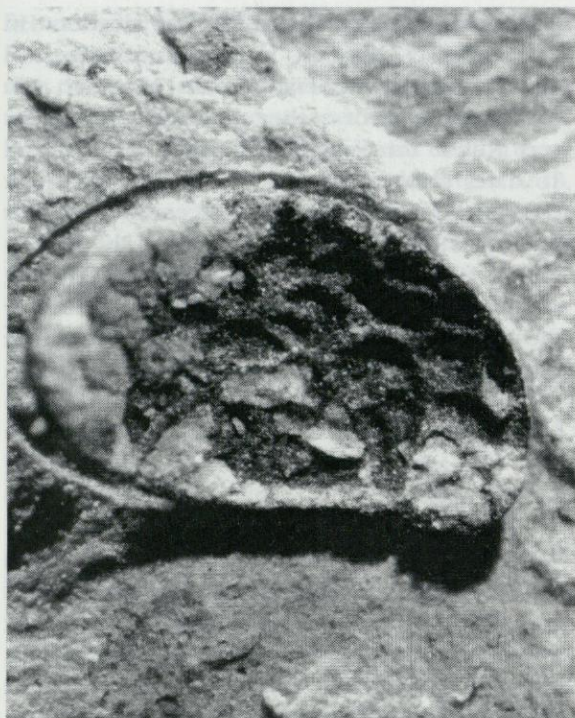


Figure 9.25 Endocarp of *Rubus* sp. in carbonaceous preservation, $\times 54$. Collected from Chapel Corner and donated by E. A. Jarzembowski. (Photo: M.E. Collinson.)

only published description of plant remains from here are of poorly preserved, immature seeds that were tentatively assigned by Chandler (1963a) to *Stratiotes neglectus* Chandler. From former exposures of the Fishbourne Member in Colwell Bay (at Cliff End) on the Isle of Wight, Chandler also described fragments of the nymphaeacean rhizome *Nelumbium buchii* Ettingshausen, fragments of the fern *Acrostichum lanzaeanum* (Visiani) Chandler, and the enigmatic leaf *Dicotylophyllum pinnatifidum* Reid and Chandler. Pallot (1961) also recovered pollen and spores from here indicating the presence of *Rbus?* and the floating fern *Azolla*.

The potential of the Chapel Corner site is shown by rare specimens of *Rubus* (collected by E.A. Jarzembowski; Figure 9.25), undetermined conifer leafy shoots (collected by J. Quayle) and specimens of *Stratiotes*, *Sabrenia*, *Sambucus*, *Typha* and *Carpolithes hamsteadensis* Collinson 1983a (recorded by Collinson from various beds in the foreshore exposures over the last 20 years).

Interpretation

The Fishbourne Member represents a lacuna in the sequence of floras through the Palaeogene deposits of southern Britain – very little is known about the flora during this part of the Eocene Epoch. The only site where some fossil plant material can still be obtained from this member is at Chapel Corner, near Osborne.

Conclusions

Chapel Corner is the only site known to yield plant fossils from the Osborne Marls, about 35 Ma old.

THORNESS BAY (SZ 436 926–SZ 463 948)

Introduction

This is the classic site (Figure 9.26) for yielding plant remains from the Bembridge Marls, from the Eocene–Oligocene transitional interval (see ‘Stratigraphical Background’ in the introductory part of this chapter). Over 100 species of mainly angiosperms have been found here, and many are unique to this site. The preservation in some levels is particularly fine, allowing delicate structures such as seed wings and plumes to be studied. It provides important evidence of the vegetational and climatic changes occurring in Europe during the Eocene–Oligocene transition, and is thus of international importance for both palaeobotanical and palaeoclimatic studies. Uniquely in Britain, the Insect Limestone preserves plants and insects in association, allowing evidence from both to be compared in a palaeoenvironmental study. The Bembridge Limestone from here also yields an important flora.

The Insect Limestone in the Bembridge Marls (Figure 9.27) is exposed along a stretch of the Isle of Wight coast in Thorness and Gurnard Bay. It has been known as a rich source of palaeobotanical remains for over a century, with early records by Gardner (1883–1886a, 1886c, 1888). However, much of our knowledge of this flora arose from the collecting activities of an amateur geologist, James A’Court Smith, who spent some 30 years amassing a large collection of fossils from these beds. This collection eventually found its way to the British Museum (Natural

Thorness Bay



Figure 9.26 General view of the cliffs of Bembridge Marls, with Bembridge Limestone at the base, at Gurnard, Isle of Wight. The foreshore outcrop of Bembridge Limestone forms the Gurnard Ledge in the foreground. (Photo: M.E. Collinson.)



Figure 9.27 The lowest part of the cliffs at Gurnard, showing, at the base, the Bembridge Limestone muds rich in fruits and seeds. The overlying Bembridge Marls include patches of plant-rich Insect Limestone (the 10 cm scale is on the Insect Limestone). (Photo: M.E. Collinson.)

History) and was the subject of the first extensive study of the flora, by Reid and Chandler (1926), who also give the historical background to A'Court Smith's work. The flora was reviewed again by Chandler (1963a), who renamed some of the species from here. Fowler (1975) described whole, fertile plants of *Azolla* from here, one of the few examples in the world and the only one from England (Collinson, 1991, 1996a, in press a). Collinson (1999) emphasized the importance of plumed seeds from here as the best-published example of Palaeogene seeds with a pappus (hair tuft) facilitating dispersal by wind.

Chandler (1963a) also reported a small flora from the Bembridge Limestone that underlies the Bembridge Marls. Collinson (1980b) included specimens from here in her revision of the Tertiary Nymphaeaceae. Fossils from both the Bembridge Marls and the underlying Bembridge Limestone were figured and named by Collinson (1978a) and Collinson *et al.* (1993a). Collinson (1983a) recorded the monocot fruit *Alismaticarpum* from Gurnard Bay, while van Bergen *et al.* (1994a,b) used specimens from here in studies on the chemistry of seed coats of fossil water plants (see also reviews in van Bergen *et al.*, 1995, 2000). Collinson and Hooker (2000) recorded rodent-gnawed seeds from here (Figure 9.28). Jones *et al.* (1996) used charophytes from here in an isotopic study showing that such fossils can potentially eluci-

date the geochemistry of ancient water bodies.

Description

Stratigraphy

Daley (in Daley and Balson, 1999) discuss the stratigraphy of this site and its significance. The exposed sequence is less than 30 m thick, and consists mainly of 6.7 m of Bembridge Limestone overlain by 21.5 m of Bembridge Marls (including, near the base, the Insect Limestone) the basal member of the Bouldnor Formation (Figure 9.29). The rocks represent brackish to freshwater deposits formed under relatively quiet conditions.

Palaeobotany

Despite the long history of research on the flora from the Insect Limestone, not all of it has been described and named. Chandler (1963a) records that at that time, 113 taxa had been discovered, but only 54 had been identified to species. Angiosperms dominate the flora and the 44 that have been identified to species are given in Table 9.3. In addition, Chandler (1963a) lists nine ferns (*Acrostichium lanzeanum* (Visiani) Chandler, *?Anemia* sp. (= *?Ruffordia subcretacea* (Saporta) Barthel – see Collinson, 1996a, in press a), *?Lygodium* sp., and *Azolla prisca* Reid and Chandler *emend.*



Figure 9.28 Fruits and seeds of aquatic plants typical for the Bembridge Limestone Formation viewed under the Scanning Electron Microscope. Left shows a seed of a free-floating aquatic plant *Stratoites*, showing rodent gnaw marks in the seed coat, $\times 20$ (see Collinson and Hooker, 2000). Upper right shows the fruit of the water lily *Brasenia*, $\times 20$. Bottom right shows the fruit of the bur reed *Sparganium*, $\times 8$. All from Thorness Bay. (Photos: M.E. Collinson.)

Thorness Bay

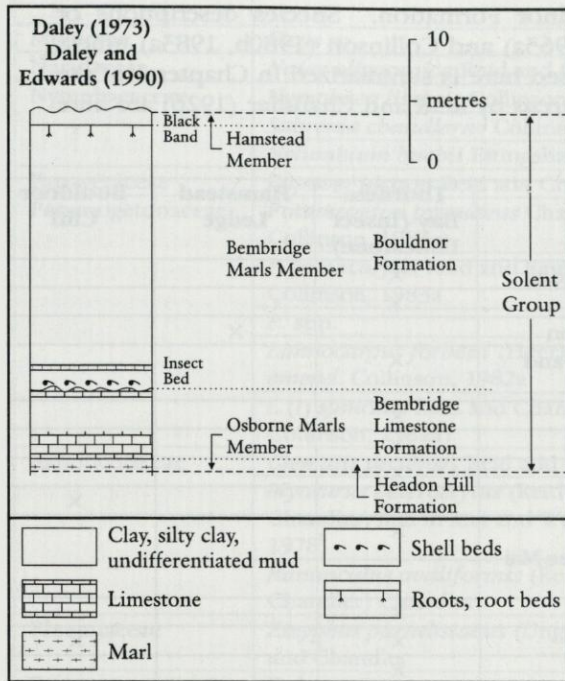


Figure 9.29 Stratigraphical succession at Thorness Bay, Isle of Wight. (After Daley and Balson, 1999, fig. 5.43.)

Fowler, 1975, plus five others), one horsetail (*Equisetum lombardianum* Saporta) and nine conifers (*Araucarites gurnardi* Florin, *Pinus dixonii* (Bowerbank) Gardner, *P. vectensis* Gardner, two other *Pinus* spp., *Pityospermum ambiguum* Reid and Chandler, *Sequoia couttsiae* Heer (see Footnote 2 to Table 8.2, this volume), *Cupressus* sp. and *?Libocedrus* sp.). The fruits and seeds are mainly preserved as moulds or are carbonaceous, while the leaves may be compressions with preserved cuticles. The preservation is often remarkable, showing very fine structures such as seed and fruit wings and plumes, and whole *Azolla* plants.

Other horizons within the Bembridge Marls have also yielded plant remains. These are mainly fruits and seeds of aquatic plants, and include *Rhamnospermum bilobatum*, *Stratiotes neglectus* and *Sabrenia chandlerae* (Collinson, 1983a).

The Bembridge Limestone in the lower part of the succession has yielded a small but expanding flora. Chandler (1963a) reported a small collection made by J.F. Jackson, whilst others were figured by Collinson *et al.* (1993a). The species list now includes *Azolla prisca*, *Sparganium multi-*

loculare, *Stratiotes neglectus*, *S. cf. beadonensis*, *Caricoidea cf. maxima*, *Sabrenia chandlerae*, *Brasenia spinosa*, *Potamogeton pygmaeus*, *P. tenuicarpus*, *Alrovanda intermedia*, *Sambucus parvula*, *?Pilea* sp., *?Juncus* sp., *Carpolithes* sp., *Rhamnospermum bilobatum*, *Dictyophyllum pinnatifidum*, undetermined genera of the Alismataceae and Sabiaceae, a possible taxodiaceous seed, and several other undetermined seeds. Collinson *et al.* (1993a) also reported palynomorphs from the upper part of the Bembridge Limestone.

Collinson and Hooker (2000) described a few specimens of *Stratiotes* seed from here (out of hundreds that were studied) which carried trace fossils of rodent gnaw marks (Figure 9.28). Thorness Bay is only the second site at which these have been found, and shows the persistence of this feeding behaviour in glirid rodents from the time of deposition of the Totland Bay Member (Hordle) to the Bembridge Limestone.

Charophyte remains occur in both the Bembridge Limestone and the Bembridge Marls on the Isle of Wight. Groves (1926) described several specimens in the A'Court Smith collection that came from Thorness Bay but did not specify the exact horizon (see also Feist-Castel, 1977). The species described are *Harrisichara tuberculata* (Lyell) Grambast, *Stephanochara vectensis* (Groves) Grambast and '*Chara*' *vespiformis* Groves. From the upper Bembridge Limestone, Collinson *et al.* (1993a) and Jones *et al.* (1996) also documented *Nitellopsis latispira* Feist-Castel, *H. tuberculata* (Lyell) Grambast, *H. vasiformis* (Reid and Groves) Grambast and *Grovesichara distorta* (Reid and Groves) Grambast.

Interpretation

This site has yielded by far the most diverse fossil floras from Bembridge Limestone and Bouldnor Formations in Britain, including the remains of aquatic plants, herbaceous plants, climbers and rare trees of the neighbouring forests, and charophytes. Among the vascular plants, only just over a half have been fully described and named. Nevertheless, for 39 of these species, Thorness Bay is the type locality. In addition to the 32 new angiosperm species described by Reid and Chandler (1926) (see Table 9.3), it is the type locality for *Stephanochara vectensis*, '*Chara*' *vespiformis*,

Bartonian–Rupelian and Miocene palaeobotany

Table 9.3 Angiosperm floras from the Bouldnor Formation. Species descriptions or references to them may be found in Chandler (1963a) and Collinson (1980b, 1983a) unless otherwise referenced. The family classification used here is summarized in Chapter 1 of the present volume. (Note: records of *Fagus* and *Quercus* by Reid and Chandler (1926) are here considered indeterminate.)

Family	Species	Thorness Bay (Insect Limestone)	Hamstead Ledge	Bouldnor Cliff
Acanthaceae	<i>Acanthus rugatus</i> Reid and Chandler	×		
Actinidiaceae	? <i>Actinidia</i> sp.	×		
Alismataceae	<i>Alismaticarpum alatum</i> Collinson		×	
Apocynaceae	<i>Apocynospermum striatum</i> Reid and Chandler ¹	×		
	<i>A. rostratum</i> Reid and Chandler ¹	×		
	<i>A. elegans</i> Reid and Chandler ¹	×		
	<i>A. dubium</i> Reid and Chandler ¹	×		
Aquifoliaceae	? <i>Ilex</i> sp.			×
Araceae	<i>Epipremmites ornata</i> (Reid and Chandler) Gregor and Bogner (see Mai and Walther, 1991) ²	×		
Arecaceae	<i>Palmophyllum</i> sp.	×		
	<i>Sabal major</i> (Unger) Heer ³	×		×
Asclepiadaceae	<i>Phyllanthera vectensis</i> Reid and Chandler	×		
	<i>Tylophora antiqua</i> Reid and Chandler	×		
Betulaceae	<i>Asterocarpinus</i> sp. ⁴	×		
Bignoniaceae	<i>Catalpa rugosa</i> Reid and Chandler	×		
	<i>Incarvillea pristina</i> Reid and Chandler	×		
	<i>Radermachera pulchra</i> Reid and Chandler	×		
Caprifoliaceae	<i>Dipelta europaea</i> Reid and Chandler	×		
	<i>Sambucus parvula</i> Chandler <i>emend.</i> Collinson, 1983a		×	
Cyperaceae	? <i>Caricoidea obscura</i> Chandler		×	
	<i>C. nitens</i> (Heer) Chandler ⁵		×	
	<i>Carex gurnardii</i> Reid and Chandler	×		
	? <i>Caricoidea minima</i> (Chandler) Chandler			×
	<i>C.</i> sp.	×	×	×
	<i>Cladiocarya foveolata</i> Reid and Chandler	×		
	Genus indet. (Collinson, 1983a)		×	
Droseraceae	<i>Aldrovanda intermedia</i> Reid and Chandler	×		×
Hydrocharitaceae	<i>Ottelia britannica</i> Reid and Chandler	×		
	<i>Stratiotes neglectus</i> Chandler	×	×	?
	<i>S. websteri</i> (Brongniart) Chandler			×
	<i>S. acuticostatus</i> Chandler			×
	<i>S.</i> sp. (leaf margin teeth – see Collinson, 1983a)		×	
Juglandaceae	<i>Palaeocarya macroptera</i> (Brongniart) Jähnichen, Friedrich and Takáč (see Manchester, 1987) ⁶	×		
	<i>Engelhardtia</i> sp.	×		
	<i>Hooleya bermis</i> (Heer) Reid and Chandler	×		
Juncaceae	<i>Juncus vectensis</i> Collinson		×	
Lamiaceae	<i>Melissa parva</i> Reid and Chandler	×		
	<i>Ajuginucula smithii</i> Reid and Chandler	×		
Lauraceae	<i>Daphnogene lanceolatum</i> Unger ⁷	×		
	<i>Neolitsea</i> sp.	×		

Family	Species	Thorness Bay (Insect Limestone)	Hamstead Ledge	Bouldnor Cliff
Moraceae	<i>Ficus</i> sp.	×		
Najadaceae	<i>Naias oligocenica</i> Reid and Chandler	×		
Nymphaeaceae	<i>Nymphaea liminis</i> Collinson ⁸		×	
	<i>Sabrenia chandlerae</i> Collinson	×	×	×
	<i>Nelumbium buchii</i> Ettingshausen			×
Papaveraceae	<i>Papaver pictum</i> Reid and Chandler	×		
Potamogetonaceae	<i>Potamogeton pygmaeus</i> Chandler (see Collinson, 1983a)	×		
	<i>P. tenuicarpus</i> Reid and Reid <i>emend.</i> Collinson, 1983a		×	×
	<i>P.</i> spp.	×	×	
	<i>Limnocarpus forbesii</i> (Heer) Chandler <i>emend.</i> Collinson, 1982a	×	×	×
	<i>L. (?) spinosus</i> Reid and Chandler (see Collinson, 1982a)	×		
Ranunculaceae	<i>Clematis vectensis</i> Reid and Chandler	×		
	<i>Myosurus heterostylus</i> (Reid and Chandler) Mai in Mai and Walther, 1978 ⁹	×		
	<i>Ranunculus ovaliformis</i> (Reid and Chandler) Chandler	×		
Rhamnaceae	<i>Zizyphus paradisiacus</i> (Unger) Reid and Chandler	×		
Rosaceae	<i>Rubus</i> sp.			×
Rutaceae	<i>Zanthoxylum (?) costatum</i> Reid and Chandler	×		
Sparganiaceae	<i>Sparganium multiloculare</i> Reid and Chandler	×		?
	<i>S.</i> sp.			×
Typhaceae	<i>Typha latissima</i> (Braun) Reid and Chandler (see Collinson, 1983a)	×	×	
	<i>T.</i> sp. (Collinson, 1983a)		×	×
Zingiberaceae/ Musaceae	? <i>Costus</i> sp.	×		
	<i>Spirematospermum wetzleri</i> (Heer) Chandler ¹⁰	×	×	
<i>Incertae sedis</i>	' <i>Abelia</i> ' <i>quadrialata</i> Reid and Chandler ¹¹	×		
	' <i>A.</i> ' <i>quinquealata</i> Reid and Chandler ¹¹	×		
	' <i>A.</i> ' <i>trialata</i> Reid and Chandler ¹¹	×		
	<i>Carpolithes collumus</i> Collinson		×	
	<i>C. bamsteadensis</i> Collinson		×	
	<i>C.</i> spp.	×		×
	<i>Dicotylophyllum pinnatifidum</i> Reid and Chandler	×	×	
	<i>Flabellricula anglica</i> Reid and Chandler	×		
	<i>Monocotylophyllum</i> sp.	×		
	<i>Rhamnosperrum bilobatum</i> Chandler	×	×	×

¹ See Footnote 5 for Table 8.2, this volume.

² Formerly *Epipremnum? ornata* Reid and Chandler.

³ This may not be a true *Sabal* (Collinson, pers. obs.).

⁴ Described by Reid and Chandler (1926) as *Carpinus* sp. and *Abelia* sp. 4, each from a single specimen. They were transferred to *Asterocarpinus* by Manchester and Donoghue (1995, p. 721).

⁵ Includes *C. cf. maxima* Chandler *emend.* Chandler *sensu* Collinson, 1983a (see Mai and Walther, 1978).

⁶ Formerly *Engelbardtia macroptera* (Brongniart) Reid and Chandler.

⁷ Reid and Chandler (1926) referred to this as *Cinnamomum lanceolatum* (Unger) Heer (see Mai and Walther, 1978, 1985).

⁸ The generic position of this species as a *Nymphaea* has been confirmed by new, more complete material (Collinson and van Bergen, work in progress).

⁹ Formerly *Ranunculus heterostylus* Reid and Chandler.

¹⁰ See text for the Hordle GCR site for discussion of *Spirematospermum*.

¹¹ These are regarded as *incertae sedis* by Manchester and Donoghue (1995).

Azolla prisca, 'Araucarites' *gurnardii*, *Pinus vectensis* and *Pityospermum ambiguum*. It is the only British Tertiary site to yield examples of *Equisetum*, *Pityospermum*, *Najas*, *Epipiremnites*, *Costus*, *Palaeocarya*, *Hooleya*, *Clematis*, *Myosurus*, *Ranunculus*, *Papaver*, *Zizyphus*, *Pbyllanthera*, *Tylophora*, *Catalpa*, *Incarvillea*, *Radermachera*, *Dipelta* and *Flabellricula*. It is also the only British site for fossils of the trumpet-creeper, milkweed, water nymph, poppy and buttercup families. With the exception of the walnut-tree family, and *Dipelta* (see below) and *Myosurus* (see Mai and Walther, 1978, 1991) these potentially exciting fossils have yet to be re-examined using modern approaches. The continued collecting opportunities at Thorness Bay will be vital to accomplish the full potential of this site.

The flora shows marked changes from the earlier floras of the British Tertiary record, in both the aquatic and forest components. The bulrush *Typba latissima* and the bur-reed *Sparganium multiloculare* become the most abundant of the aquatic species, replacing the cyperaceans as the common reed-like plants. The combination of *Typba* and the leather fern (*Acrostichum*) is a characteristic of these Eocene–Oligocene transition floras in southern Britain (Collinson, 1983a; Collinson and Hooker, 1987). *Potamogeton tenuicarpus* is progressively replacing *P. pygmaeus*, although some examples of the latter can still be found in the Bembridge Marls. *Stratiotes beadonensis* is replaced by *S. neglectus*. These are all part of the progressive change in the aquatic flora of southern Britain that occurred during the Palaeogene Period (Collinson *et al.*, 1981, 1993a; Collinson and Hooker, 1987; Collinson, 1990b, 1992).

Pappus hairs are very rare in the Palaeogene record and those from the Insect Limestone are among the best examples (Collinson, 1999). Seeds of *Apocynospermum* from here have a pappus up to 13 mm long. Similar, unpublished examples occur in the German Eocene succession (Collinson, in press b). Manchester (1999) mentions other examples, and draws attention to the fact that the name 'Echitonium' has priority for these seeds. The fine-grained limestone has also enabled the preservation of whole plants of the water fern *Azolla* – the only examples from England, and the only examples of this age in the world (Collinson, 1991, 1996a, in press a).

The forest component of the fossil flora also

appears markedly different and is very rare. Chandler (1964) interpreted this as being in part taphonomic, as the Insect Limestone preferentially preserved wind-transported fruits and seeds with wings or plumes. Many of the tropical–subtropical families found in the British Eocene fossil record are absent here, despite the depositional environment not being so different. Even the palms, although still present, are of low diversity and rare. Instead we see the remains of wing nuts (Juglandaceae), and of elder and birch families, all of which are also very rare. The decline in the tropical–subtropical elements in the Bembridge Marls flora, give the clear impression of cooling conditions.

The species of the walnut-tree family (Juglandaceae) from the Insect Limestone belong to *Palaeocarya* of the Engelhardiaceae (modern tropical trees of Asia and Central America) and *Hooleya* of the Platycaryae (modern trees in broad-leaved forests of eastern China and Japan). Both had wind-dispersed small winged nutlets, and were discussed in detail in a wide-ranging review of the fossil history of the family by Manchester (1987).

The record of *Dipelta* (Caprifoliaceae, a family of modern deciduous trees of central and south China) was critically re-appraised and accepted by Manchester and Donoghue (1995). However, the same authors rejected all records of *Abelia* from here, excluding all of them from the Caprifoliaceae.

Fossils of the Bignoniaceae (trumpet creeper family) are very rare and the seeds from the Insect Limestone are the earliest examples (Collinson *et al.*, 1993b). Meyer and Manchester (1997) described a similar seed of *Catalpa* (Indian Bean Tree) from the Oligocene deposits of Oregon. However, the Insect Limestone fossils are now in very poor condition and all three genera are each based on only a single specimen. New collections are needed to confirm the recognition of this family in the Eocene–Oligocene transitional strata.

A single partial impression of a nut assigned tentatively to *Quercus* by Reid and Chandler (1926) was not considered by Kvaček and Walther (1989) in their revision of European Fagaceae fossils, or by Manchester (1994) who described the oldest fossil acorn. The Insect Limestone specimen is best considered indeterminate. The leaf tentatively referred to *Fagus* was also not discussed by Kvaček and Walther (1989) and, as no cuticle details are known, is

also probably indeterminate.

This was one of the main sites to yield material used in the study of the composition and diagenesis of the seed coats of fossil water plants by van Bergen *et al.* (1994a,b) (material was also obtained from Headon Hill and Bouldnor Cliff). This has helped considerably in our understanding of how these fossils are preserved and the degree to which they have become altered during fossilization. The analytical techniques used in this study are amongst a number of newly developing procedures (e.g. carbon isotope analysis for understanding palaeoatmospheric compositions) that require newly collected specimens. Without sites such as Thorness Bay, where fresh fossils can be collected *in situ*, work of this kind would be impossible.

Collinson *et al.* (1993a) analysed the differences between the floras found in the Bembridge Limestone and the Bembridge Marls, which they interpret as due to differing ecologies. The Bembridge Limestone was formed in calcareous-rich ponds or lakes in relatively dry surroundings, while the Bembridge Marls represent marshlands with more immediately adjacent woodlands. This is argued as possibly being a reflection of a fluctuation in temperatures during deposition.

Conclusions

Thorness Bay is the best site for studying the plant fossils from the Eocene–Oligocene transition beds, which are about 34–35 Ma years old. The flora consists of over 100 species and for many of them this is the only known locality. The flora consists mainly of aquatic plants, especially of bulrushes and leather ferns, but there are also rarer remains of plants from the surrounding forests, including wing nuts and elders. The flora is thus important for understanding the broader environmental history of Britain during the Palaeogene Period and its relationship to the global cooling of the climate that was then taking place. The association of plants and insects is valuable for environmental interpretation. Trace fossils on seeds have proved rodent gnawing and seed predation by glirid rodents. The high quality of preservation in the Insect Limestone at Thorness Bay provides one of the very few examples of Palaeogene seeds with a hairy pappus for wind dispersal, as well as the only known examples of whole *Azolla* (water fern) plants in the English Tertiary record.

HAMSTEAD LEDGE (SZ 402 918)

Introduction

Hamstead Ledge has extensive exposures of plant fossil beds in the Bembridge Marls and Hamstead Members (Bouldnor Formation), and is transitional in age between the Eocene and Oligocene epochs. It is the best site for the palaeoecological study of Tertiary floras in Britain and is of particular importance for understanding the evolution of the aquatic plant communities in this part of the world. It is also important because of its role in improving our understanding of the vegetation in Britain immediately after the global climatic cooling that took place near the end of the Eocene Epoch.

The classic site for plant fossils from the Bembridge Marls is near Thorness Bay (discussed above), but the cliffs there suffer from poor and intermittent exposure. In a search for sites better suited to palaeoecological studies, Collinson (1978a, 1983a) discovered floras from more extensive cliff and foreshore exposures of Bembridge Marls (and the lower Hamstead Member) further east along the Isle of Wight coast, at Hamstead Ledge. Although not yielding as diverse a flora as Thorness Bay, the foreshore exposures (Figure 9.30) at Hamstead Ledge, which are only available at low tide, allow the plant beds to be more easily sampled and their sedimentological context to be more easily investigated. Some of these fossils were also figured by Collinson (1978a,b; 1980b) and Collinson *et al.* (1993a). The floras formed a critical part of the studies by Collinson (1992) of vegetational change near the terminal Eocene event. Van Bergen *et al.* (1994a,b, 1995, 2000) included fossils from here in their studies of the chemistry of water-plant seed coats.

Description

Stratigraphy

Daley (in Daley and Balson, 1999) has described the stratigraphy of this section and its significance. The exposed sequence consists of about 21 m of mainly clays and mudstones of the Bembridge Marl and lower Hamstead Members (Bouldnor Formation). They are interpreted as mainly lagoonal or floodplain–lake deposits (Daley, 1973). Figure 9.31 is a summary stratigraphical log showing the plant bed levels.



Figure 9.30 Foreshore exposure (at low water spring tide) of the lower part of the Bembridge Marls at the eastern end of Hamstead Ledge. The Bembridge Limestone ledge is at the far right, out to sea. (Photo: M.E. Collinson.)

Palaeobotany

The only detailed published account of the plant fossils from this site is by Collinson (1983a), who studied both macrofossils and palynology. Almost uniquely, this includes details of the exact bed from which the fossils came, and the numbers of each species found within each bed. Twenty beds were sampled by Collinson, nine of which yielded plant fossils: eight in the Bembridge Marls and one in the lowest part of the Hamstead Member. A further two beds higher in the Hamstead Member were also sampled (Collinson, 1983a, pp. 195–7). Sixteen species of vascular plant were reported: 14 angiosperms (listed in Table 9.3) and the floating fern *Azolla prisca* Reid and Chandler *emend.* Fowler and the leather fern *Acrostichum anglicum* Collinson (Figure 9.32; see also Collinson, 1978b). They are nearly all aquatic plants, except for rare examples of *Sambucus*, the fruit and seeds of *Spirematospermum* (see also the account of the flora at the Hordle GCR site) and the leaves *Dicotylophyllum pinnatifidum*. Collinson (1978a) and Collinson *et al.* (1993a) described an undetermined Alismataceae fruit. In addition, there are examples of the stonewort

Harrisichara tuberculata (Lyell) Grambast.

When the clays are split along bedding planes, leaves of *Acrostichum* and *Dicotylophyllum* are often seen. However, the most instructive fossils are the very small fruits and seeds obtained by disaggregating the clays. Despite their small size, they are extremely well preserved and yield very fine details under the Scanning Electron Microscope. It was, for instance, possible for Collinson to show that some of the seeds had germinated while others had not, an important observation for understanding the palaeoecology of this site.

The higher floras in the Hamstead Member show little difference from those lower down in the section, although *Acrostichum angicum* has not been recorded above the basal-most Hamstead Member (Bed 9 in Collinson, 1983a). This may reflect a threshold level in cooling of the climate (Collinson, in press a).

Interpretation

This site has yielded only a fraction of the plant species that have been found at Thorness Bay. It is nevertheless the type and only known locality for several species: *Juncus vectensis*,

Hamstead Ledge

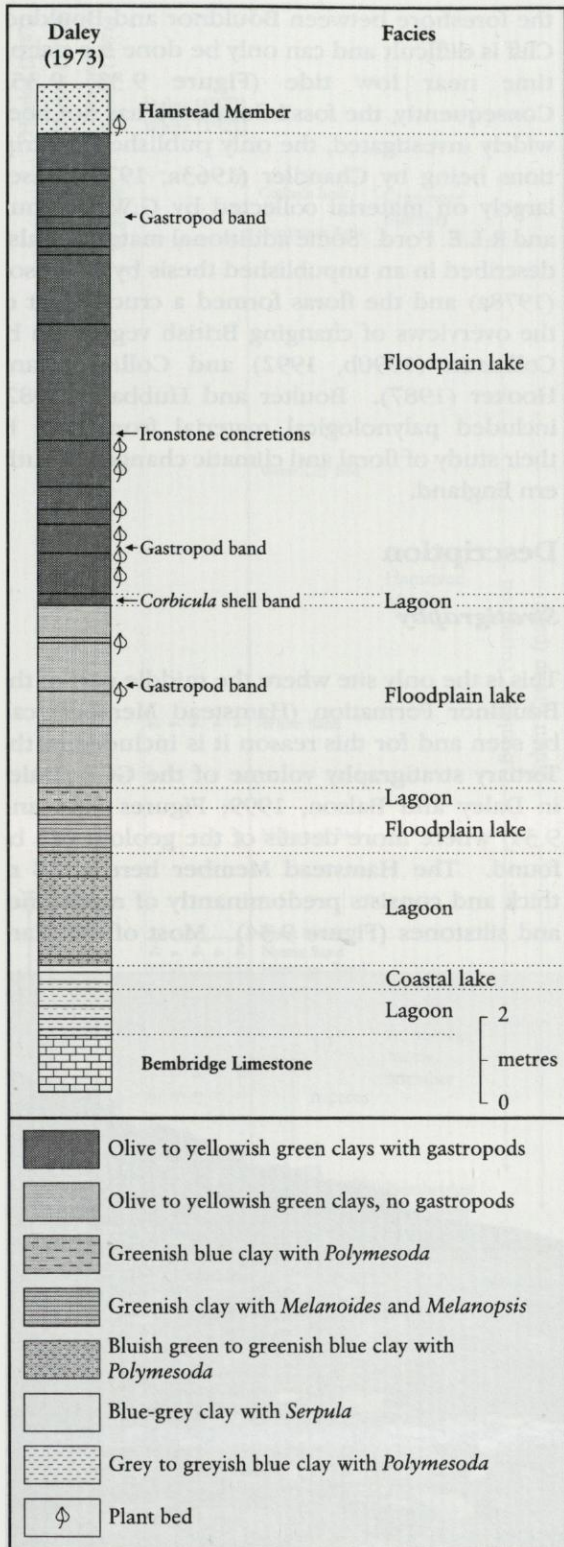


Figure 9.31 Stratigraphical section through the Bembridge Marls Member, Bouldnor Formation at Hamstead Ledge, showing position of main plant beds. (After Collinson, 1983a.)



Figure 9.32 Sporangium of the fern *Acrostichum anglicum*, containing a residual trilete spore, $\times 280$ (see Collinson, in press a). From the Hamstead Ledge GCR site. (Photo: M.E. Collinson.)

Alismaticarpum alatum, *Carpolithes bamsteadensis* and *C. collumus*. It is also the type locality for the fern *Acrostichum anglicum* Collinson, 1978b (Figure 9.32).

The main interest of these floras is the potential for palaeoecological study as demonstrated by Collinson (1983a). No other site has such an extensive exposure of plant-bearing deposits in the Eocene–Oligocene transition interval of Britain. It allows detailed sampling from different levels within the Bouldnor Formation, thus providing an insight into the subtle changes of vegetation taking place during this part of the Tertiary sub-Era. Most beds are dominated by the remains of the *Typba*–*Acrostichum* marshland flora that was common in Britain at this time. However, there are also occasional remains of trees such as elder (*Sambucus*), suggesting the existence of localized islands of raised ground within the marsh. The macrofloral evidence is complemented here by the palynology, fauna and sedimentology, which together make this an internationally important site for interpreting the terrestrial biotas and environment of north-western Europe during late Palaeogene times.

Conclusions

Hamstead Ledge is an extensive foreshore exposure of the Eocene–Oligocene transition Bembridge Marls and lower Hamstead Members, about 34 Ma old. These offer an unrivalled opportunity to study the marsh vegetation dominated by bulrush and leather ferns, which covered large parts of southern Britain at this time.

BOULDNOR CLIFF (SZ 375 901–SZ 398 917)

Introduction

Bouldnor Cliff is the only site known to yield plant fossils from the Hamstead Member (Bouldnor Formation). It is the youngest Palaeogene flora in Britain and provides a link with the younger floras found in continental Europe. It is also the type locality for *Sequoia couttsiae* Heer, one of the most widely occurring conifers in the Tertiary deposits of Europe.

The Bouldnor Formation is the youngest succession of Tertiary strata in southern Britain, as well as the youngest to yield plant macrofossils. It provides the final part of the story of the Palaeogene vegetational history of this part of the world, as summarized by the sites reviewed in this and the previous chapters. Collecting at

the foreshore between Bouldnor and Bouldnor Cliff is difficult and can only be done for a short time near low tide (Figure 9.33, 9.35). Consequently, the fossil flora here has not been widely investigated, the only published descriptions being by Chandler (1963a, 1978), based largely on material collected by G.W. Colenutt and R.L.E. Ford. Some additional material is also described in an unpublished thesis by Collinson (1978a) and the floras formed a crucial part of the overviews of changing British vegetation by Collinson (1990b, 1992) and Collinson and Hooker (1987). Boulter and Hubbard (1982) included palynological material from here in their study of floral and climatic change in southern England.

Description

Stratigraphy

This is the only site where the middle part of the Bouldnor Formation (Hamstead Member) can be seen and for this reason it is included in the Tertiary stratigraphy volume of the GCR (Daley in Daley and Balson, 1999; Figures 9.33 and 9.34) where more details of the geology can be found. The Hamstead Member here is 78 m thick and consists predominantly of mudstones and siltstones (Figure 9.34). Most of the plant

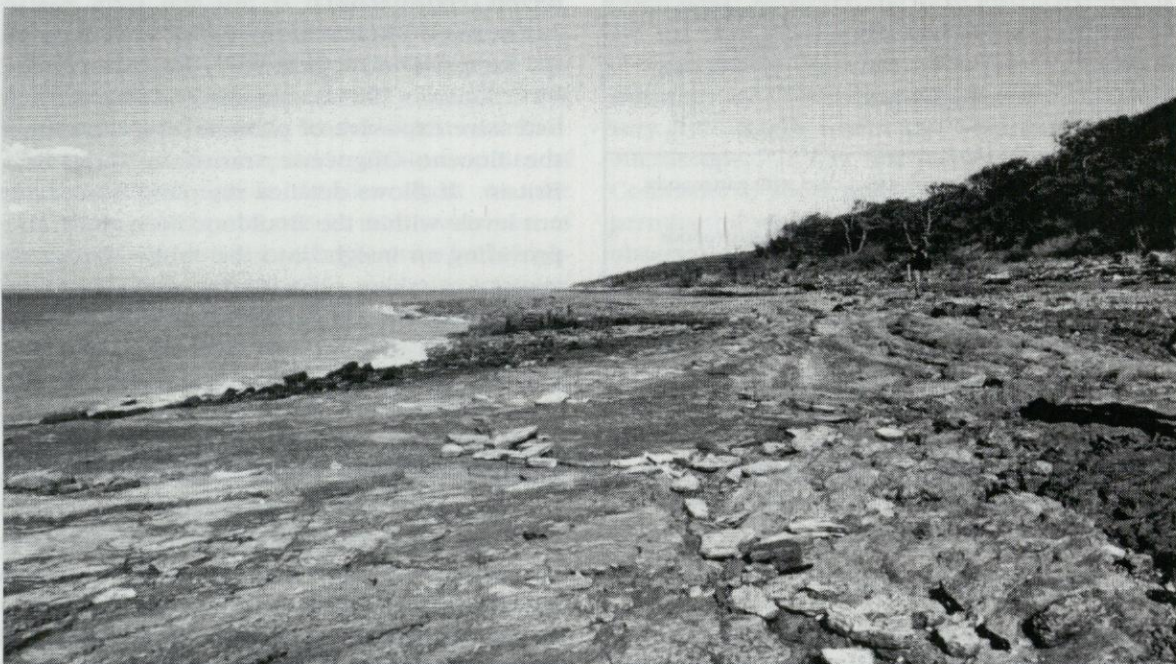


Figure 9.33 Hamstead Member exposed on the foreshore below, Bouldnor Cliffs. (Photo: M.E. Collinson.)

Bouldnor Cliff

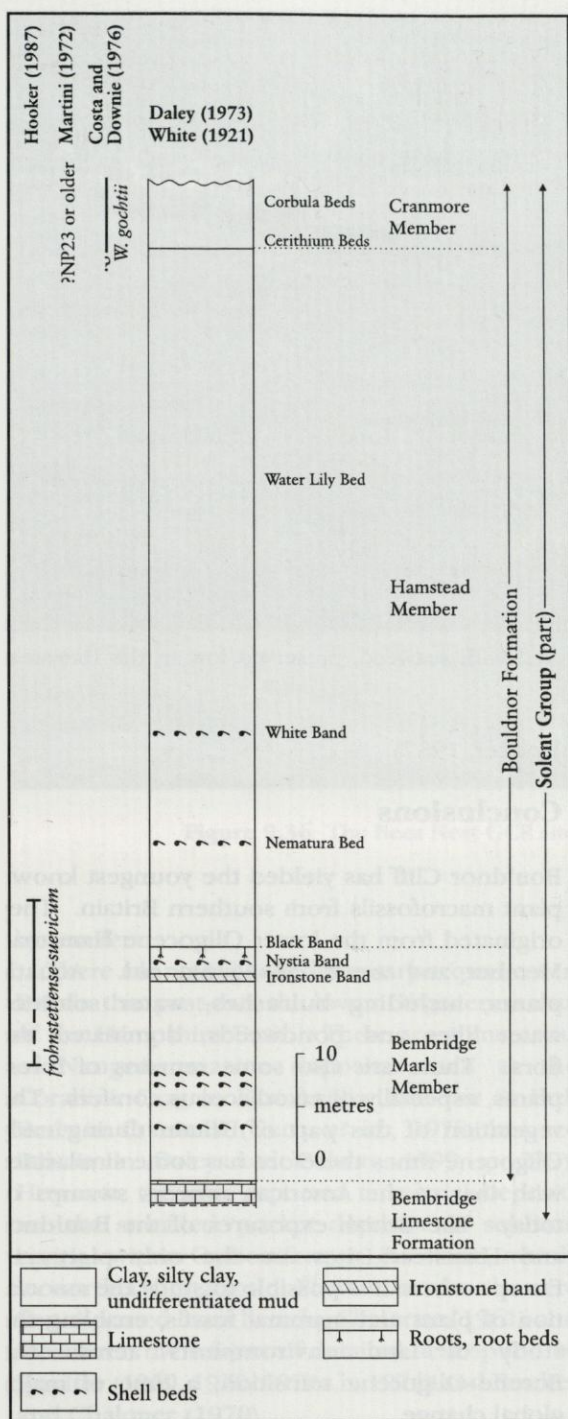


Figure 9.34 Stratigraphical succession at Bouldnor Cliff, Isle of Wight. (After Daley and Balson, 1999, fig. 5.39.)

fossils described by Chandler (1963a) came from two levels, one known as the 'White Band', and the other the 'Waterlily Bed'. These lie above the Grande Coupure mammal event and are there-

fore Oligocene in age (Collinson, 1992; Hooker, 1992). Other post-Grande Coupure levels also yield plant fossils (Collinson, 1992, pers. obs.).

Palaeobotany

The Bouldnor fossil flora consists predominantly of angiosperms, the 18 species being listed in Table 9.3. In addition, there are four species of conifer: *Sequoiadendron fordii* Chandler, *Sequoia coutsiae* Heer (see Footnote 2 to Table 8.2, this volume), *Pinus fordii* Chandler and *P. sp.*. So far, no fern remains have been found here. The plants are preserved as carbonaceous fossils, often (but not always) covered by a layer of amorphous pyrites.

Interpretation

These are the youngest plant remains in the Palaeogene deposits of southern Britain. As with most other floras of the Bouldnor Formation, the flora here is dominated by aquatic plants, especially of the water soldier, water lily and pondweed families. It shares many species with the aquatic floras of the lower Bouldnor Formation, such as at Thorness Bay and Hamstead Ledge, but there are some differences, suggesting that climatic changes were continuing (Collinson, 1990b). Most notable is the appearance of two new *Stratiotes* species, *S. websteri* and *S. acuticostatus*. Collinson *et al.* (1981) state that *Stratiotes neglectus* becomes extinct at these higher levels. Chandler (1963a) described well-preserved specimens of this species but there was some question as to whether they actually originated from this horizon. *Potamogeton pygmaeus*, which is common and characteristic of the earlier Eocene-Oligocene transitional floras, has become extinct in Britain by Hamstead Member times and is replaced by *P. tenuicarpus*, which had made its first appearance in the Bembridge Marls (Collinson, 1983a; Collinson *et al.*, 1993a). Chandler (1963a) argued that *Typha latissima* extended through into the Hamstead Member but Collinson (1978a) suggested that these stratigraphically higher specimens belonged to a new and still unnamed species. *Acrostichum anglicum* is lost in the post-Grande Coupure floras, possibly due to continuing climate change or to other factors associated with the terminal Eocene event.

Unlike most of the other British Tertiary flo-



Figure 9.35 A foreshore exposure of in-situ logs covered with seaweed, preserved low in the Hamstead Member near Bouldnor. (Photo: M.E. Collinson.)

ras, fruits and seeds from the surrounding forest vegetation here are rare. Instead, pyritized leafy shoots, cones and logs are relatively abundant, especially of palms and conifers (Figure 9.35). The most completely known is the taxodiaceous conifer *Sequoiadendron fordii*, for which leafy shoots, cones and seeds are known (Chandler, 1978), and for which this is the only known locality. In contrast, the *Pinus* and *Sequoia* species are only known from cones. The palm fossils are mainly leaves, especially that described as *Sabal major* (probably not in fact a true *Sabal*) but one fruit has also been found.

Chandler (1978) described the remains of an unidentified flower preserved in pyrite from Bouldnor Cliff. Although a detailed description was given, no attempt was made to establish its affinities. Remains of flowers are extremely rare in the Tertiary deposits of Britain.

In summary, during the formation of the Hamstead Member this area was probably covered by a bulrush-dominated marsh, also supporting a range of other aquatic plants. Surrounding the marsh were probably forests dominated by taxodiaceous conifers. Together, this invites comparison with the cypress swamps of south-eastern USA. The site offers considerable research potential because the floras are associated with mammalian faunas and together these can track environmental changes across the Eocene–Oligocene boundary (Collinson and

Hooker, 1987).

Conclusions

Bouldnor Cliff has yielded the youngest known plant macrofossils from southern Britain. They originated from the lower Oligocene Hamstead Member and are c. 33–34 Ma old. Aquatic plants, including bulrushes, water soldiers, water lilies and pondweeds, dominated the flora. There are also some remains of forest plants, especially of taxodiaceous conifers. The vegetation of this part of Britain during early Oligocene times therefore has some similarities with that of the American cypress swamps of today. The British exposures of the Bouldnor and Hamstead sites are the only places in Europe where it is possible to study the association of plant and mammal fossils, enabling the study of land environments across the Eocene–Oligocene transition, a time of major global change.

BEES NEST (SK 241 546)

Introduction

Bees Nest in Derbyshire (Figure 9.36) has yielded the only known Neogene macroflora from Britain. It includes the remains of leaves, seeds and wood, and represents vegetation dominated



Figure 9.36 The Bees Nest GCR site as seen in 1967. (Photo: M. C. Boulter.)

by conifers.

There are no major sedimentary sequences in Britain that post-date the lower Oligocene strata of the Hampshire Basin. There are some areas of Neogene marine deposits, such as the Coralline Crag in East Anglia, and the St Erth Beds in Cornwall (Curry *et al.*, 1978; but see Balson in Daley and Balson, 1999, p 239). However, the only reported terrestrial deposits are the so-called 'pocket deposits' in solution cavities within Carboniferous Limestone, mainly in northern England. Plant macrofossils were first reported from here by Chaloner (1961) and have been the subject of detailed description by Boulter (1969, 1970, 1971a,b, 1974) and Boulter and Chaloner (1970).

Description

Stratigraphy

Stratigraphical details of the Brassington Formation at Bees Nest are given by Boulter *et al.* (1971) and a general discussion on the sedimentology is provided by Walsh *et al.* (1972).

The sequence is c. 43 m thick and includes all three of the members recognized in the Brassington Formation (Figure 9.37). They are interpreted as deposits that were let down into subsidence hollows in a karstic landscape, and were thus protected from subsequent erosion. The plant remains occur in the grey clays of the Kenslow Member near the top of the sequence. Based on the palynology, these deposits have been dated as late Miocene to early Pliocene in age (Boulter, 1971c).

Palaeobotany

Conifer foliage and wood dominate this macroflora. The most extensively studied is the taxodiacean conifer *Cryptomeria anglica* Boulter, for which details of the shoot anatomy have been established (Boulter, 1969; Boulter and Chaloner, 1970). Also found in association are taxodiaceous wood (Figure 9.38) and a possible taxodiaceous seed. Logan and Thomas (1987) investigated the composition of lignin present in this wood. Boulter and Chaloner (1970) also briefly described shoots that they

Bartonian–Rupelian and Miocene palaeobotany

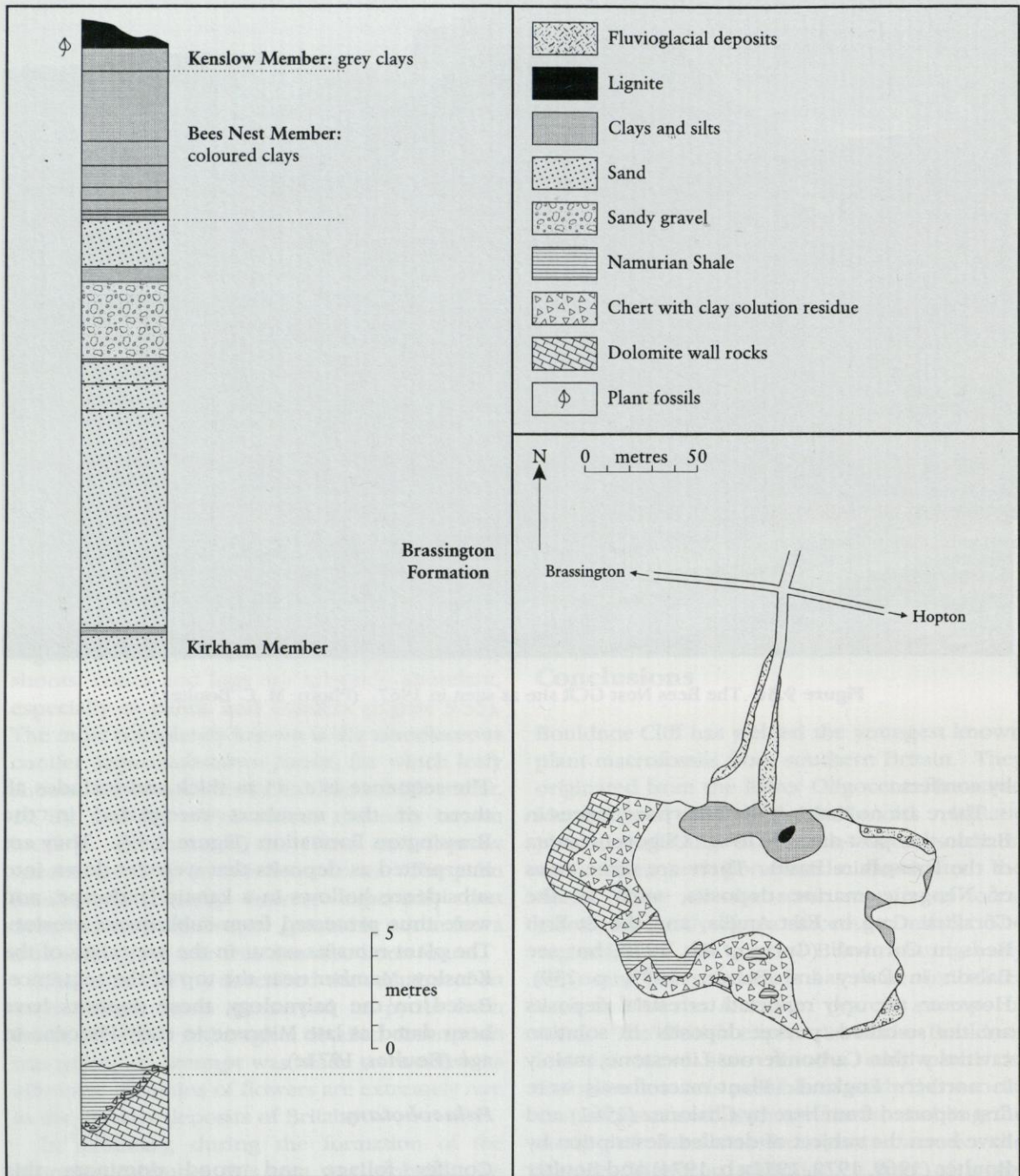


Figure 9.37 Left shows the Neogene deposits exposed at Bees Nest, including the plant-bearing Kenslow Member. Right shows the geographical distribution of the principal deposits within the quarry. (After Boulter *et al.*, 1971.)

assign to the conifers *Sciadopitys tertiaria* Menzel and *Abies alba* Miller, and wood of *Picea* and *Pinus*. The only non-coniferous macrofossils found are of the moss *Muscites lanceolata* Boulter (1974).

Boulter (1971c) has also described the palynology of these deposits. This also revealed a forest-dominated flora, although there was a greater taxonomic diversity, including a range of broad-leafed angiosperms.

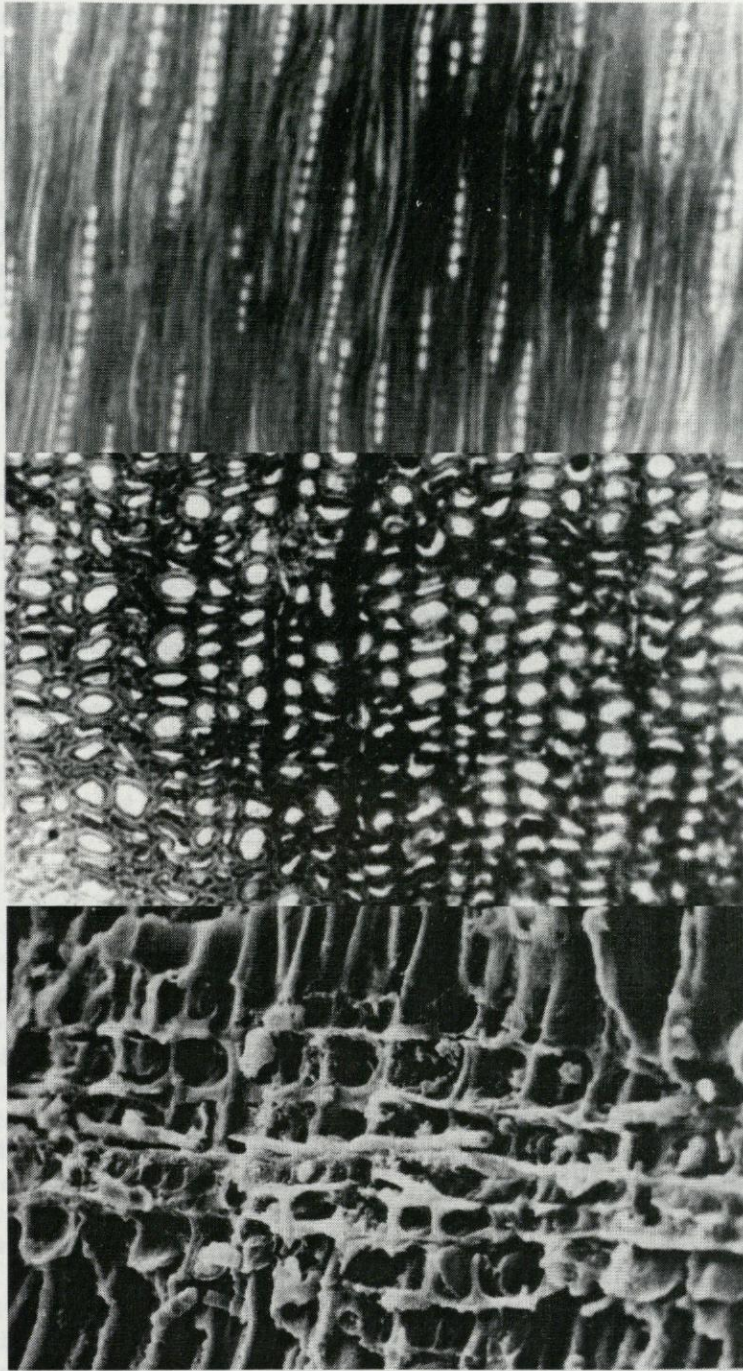


Figure 9.38 Taxodiaceous wood. Sections cut in transverse (top $\times 130$), radial longitudinal (bottom $\times 200$) and tangential longitudinal (middle $\times 75$) alignment show radially aligned tracheids and uniseriate medullary rays with both parenchyma cells and ray tracheids. The upper two photographs were taken using light microscopy, the bottom photograph under Scanning Electron Microscopy

Interpretation

A number of other British sites have yielded Nerogene palynofloras of this age, such as the nearby Kenslow Top pit (Boulter, 1971c), as well

as in Cornwall, Pembrokeshire and Anglesey (Walsh *et al.*, 1987, 1996, 1999), but this is the only locality so far to have yielded plant macrofossils. It thus provides a unique insight into late Tertiary vegetation of Britain, as it moves

from the relatively warm conditions of the Palaeogene times to the ice-house conditions of the Pleistocene.

Boulter (1969) argued that *Cryptomeria* was a major component of the Arcto-Tertiary Flora in Europe, having been reported from Germany and the Caucasus, as well as Derbyshire. Unlike many other extant taxodiaceous genera (see Manchester, 1999, for a review), however, there are no reliable records of it from North America, suggesting that it originated in the Old World. Today, *Cryptomeria* is restricted to China, Japan and Korea, and it is probable that its distribution had declined significantly as a result of climatic cooling in late Neogene and Quaternary times.

Bees Nest is the only locality to yield macrofossils of *Cryptomeria anglica*. The foliage, including the epidermal structure, is very similar to that of the sole living species, *C. japonica* Don. The main difference was that the living species does not have such thickened walls in the cuticle at the outer edge of the stomatal subsidiary cells. Poorly preserved cones and a seed associated with this fossil foliage are also very similar to those of *C. japonica*.

Full systematic descriptions of the other conifers have not been published, although Boulter and Chaloner (1970) have figured and discussed some of the specimens.

The specimen of moss described by Boulter (1974) was compared with a number of extant families, including the Hypnodendraceae, Rhizogoniaceae and Mniaceae, but could not be accommodated within any of them. Boulter suggested that it might represent a moss family that became extinct during the Quaternary glaciations.

Conclusions

Bees Nest is the only site in Britain to yield plant macrofossils of Neogene age. It preserves remains of forests growing in inland Britain 5–6 Ma ago, which consisted mainly of taxodiaceous conifers. However, unlike the earlier (Palaeogene) floras, the dominant taxodiaceous conifer was *Cryptomeria*. This was a widespread tree in Neogene times in Europe, but today is restricted to parts of China, Japan and Korea.