Mesozoic and Tertiary Palaeobotany of Great Britain

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Chapter 7

The palaeobotany of the Palaeocene and Palaeocene–Eocene transitional strata in Great Britain

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INTRODUCTION

The Palaeocene Epoch and Palaeocene–Eocene transition was a time of climatic warmth with polar broad-leaved deciduous forests extending high into the Arctic Circle (Wolfe, 1977, 1985; Basinger *et al.*, 1994). The palaeobotanical evidence shows variations in vegetation through this interval. During deposition of the Woolwich Formation and Reading Formation, southern Britain supported freshwater mires and relatively low-diversity (cf. Eocene plant diversity), often patchy, forest–woodland with deciduous flowering plants together with more warm-loving elements (Collinson and Hooker, 1987; Collinson, 2000a). Similar deciduous flowering plants were associated with more conifers and ferns at Ardtun in the North (Boulter and Kvaček, 1989). In the latest part of this interval (Oldhaven Beds and division A1 of the London Clay Formation of King, 1981) the floras indicate the early development of vegetation similar to modern tropical rain forests that became fully established in the Eocene Epoch (Collinson, 1983b, 2000a). These floras are the earliest recognizably 'modern' examples from this country. There are none of the groups normally associated with the Mesozoic Era, such as the bennettites, caytonias and cycads (the latter have survived to the present day, but there is no post-Mesozoic macrofossil record of them from Britain).

HISTORY OF RESEARCH

Until recently, there has been relatively little interest in the Palaeocene palaeobotany of southern Britain, mainly because there is little good exposure. There are records of silicified pine cones (Prestwich, 1854; Gardner, 1883–1886a; Chandler, 1961a) and fern stems (Carruthers, 1870b, 1872; Kidston and Gwynne-Vaughan, 1907; Chandler, 1961a) from the Thanet Formation at Herne Bay. Ward (1978) and Collinson (pers. obs.) have reported fruits from these deposits, including several distinctive but as yet unidentified forms, and Collinson *et al.* (1985) described numerous megaspores. Crawley (in press) has revised the wood from these deposits.

The overlying Reading Formation suffers from generally poor exposure, which has limited the amount of palaeobotanical work done here. Occasional records from temporary exposures mainly in the London and Reading areas demonstrated the presence of leaf beds (e.g. Hooker, 1854), while fruits and seeds were described by Chandler (1961a), who also reviewed the earlier history of palaeobotanical research on these beds. However, the full potential of the Reading Formation was not established until the work by Crane, especially at Cold Ash near Newbury (see the Cold Ash GCR site report for details of the relevant publications). More recently, a diverse fruit and seed flora has been described from Felpham in West Sussex by Collinson (in Bone, 1986).

The youngest floras covered in this chapter originate from the Oldhaven Beds and the A1 division of the London Clay. Johnson (1901) was the first to report the presence of fossil fruits and seeds in these beds but there were no detailed records of the species present until Chandler (1961a, 1964) studied the Herne Bay and Walton-on-the-Naze floras. Brett (1972) described wood fossils from Harwich.

The Ardtun flora from Mull in Scotland is far more remote from centres of population and might well have gone unnoticed were it not for the local landowner (the Duke of Argyll) being a geologist and, at one time, the President of the Geological Society of London. He had the resources to arrange for extensive collecting at the site during the early 19th century, and later encouraged further collecting by the well-known palaeobotanist Gardner (1887a). Nevertheless, the palaeobotany at Ardtun remained largely unpublished until very recently, when Boulter and Kvaček (1989) produced the first monograph, based partly on an unpublished manuscript by Seward and Edwards. Boulter and Kvaček (1989) also give a comprehensive review of the history of work at Ardtun.

PALAEOGEOGRAPHICAL SETTING

The palaeogeography of early Tertiary times in the Northern Hemisphere shared many similarities with the geography of the present day (Figure 7.1). However, during most of the Palaeocene Epoch, there was a land connection between Europe and North America allowing plant migration. The North Atlantic started to 'open up' in late Palaeocene times, inducing an area of extensive igneous activity known as the 'Brito-Arctic Igneous Province' (BIP), which acted as a partial barrier to plant migration

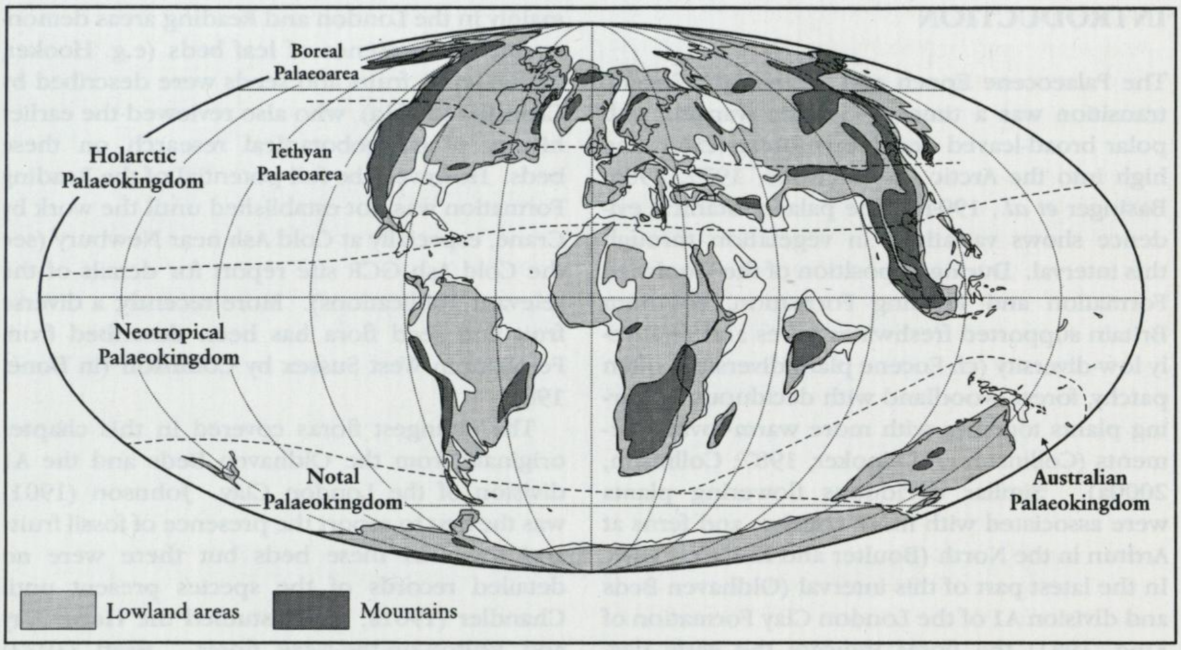

Figure 7.1 Palaeogeography of the Palaeocene world, showing main areas of land and mountains. Based on Smith *et al.* (1994). Also shown are the main palaeofloristic areas, based on Akhmetyev (1987).

(Boulter and Kvaček, 1989).

In southern Britain, Palaeocene and Palaeocene–Eocene transition deposits mainly occur in two areas known as the 'London Basin' and the 'Hampshire Basin'. These are purely structural basins, and these two areas were originally part of the same depositional basin that covered much of the present-day North Sea, Belgium, north-east France and south-east England (Figure 7.2). It was predominantly a shallow marine basin with mainly mud deposition, but with alluvial-plain deposits forming on the western margins.

STRATIGRAPHICAL BACKGROUND

Most of the sites dealt with in this chapter occur in south-eastern England. We have in part adopted the Ellison *et al.* (1994) lithostratigraphical classification of these strata (Figure 7.3) as this is used in the *British Tertiary Stratigraphy* GCR volume (Daley and Balson, 1999). The lower part of the sequence is divided into four major units: the basal Thanet Formation, the Upnor Formation, and the overlying Woolwich Reading formations. These are in turn overlain by what King (1981) termed the A1 division of the London Clay Formation (i.e. the Harwich, Swanscombe and Harefield Members as well as the Oldhaven Beds and the Blackheath Beds). Ellison *et al.* (1994) applied the name 'Harwich Formation' to these lowest members of the London Clay Formation. However, this interval as interpreted by Ellison *et al.* includes a wide variety of lithologies, and is in essence a time-slice rather than a true lithostratigraphical unit (Ward, 1995; Hooker, 1998, explanation to fig. 20.1). In this account, we have therefore retained the older lithostratigraphical nomenclature for discussion of these floras, as this serves to emphasize the different lithologies and hence different facies, which were key factors in ensuring different palaeoenvironments were included in the GCR network.

The chronostratigraphy of the lower Palaeogene has been somewhat problematic (Curry *et al.*, 1978), but, in the scheme currently accepted by the Internation Union of Geological Sciences (IUGS), the Palaeocene Series is divided into three stages, the Danian, Selandian and Thanetian. The Thanet Formation belongs to the Thanetian and is Palaeocene (Berggren and Aubry, 1998). The Woolwich Formation and Reading Formation and all succeeding strata beneath the A2 division of the London Clay Formation (King, 1981) fall

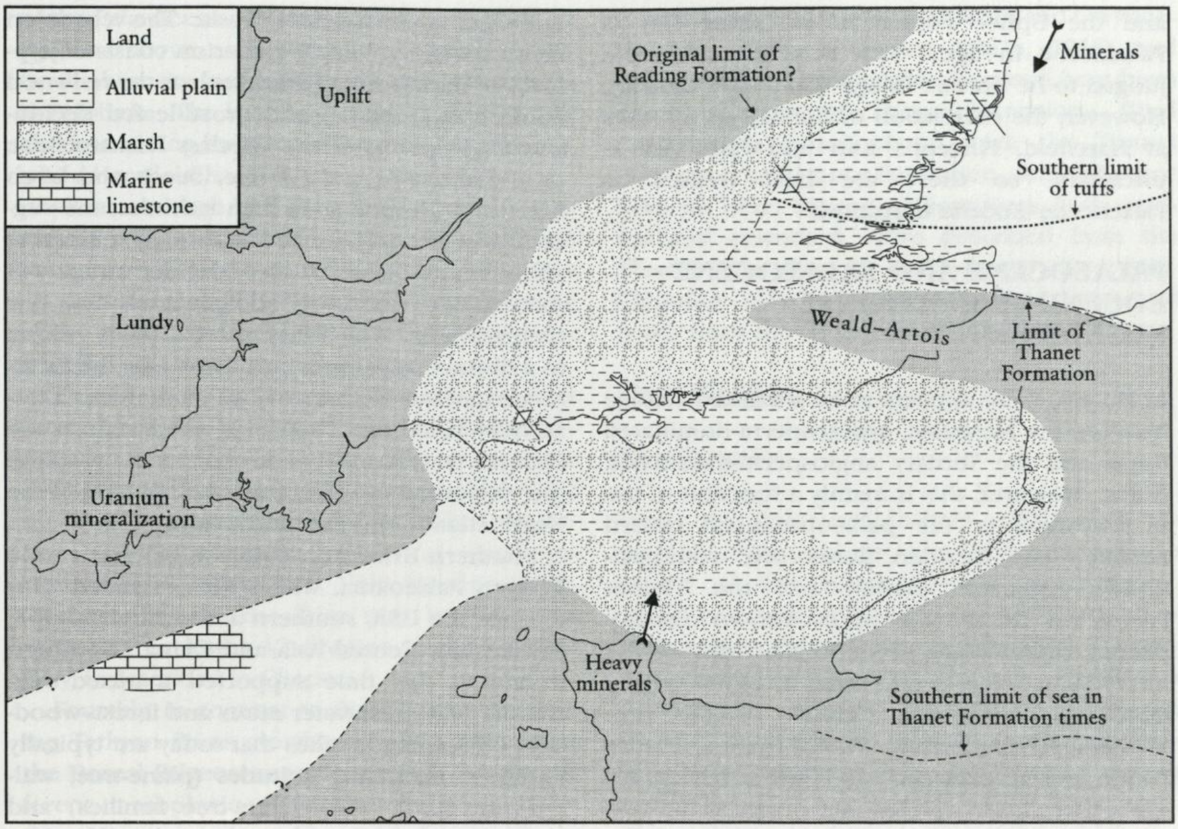

Figure 7.2 Palaeogeography of southern England during the Palaeocene. (After Murray, 1992.)

Group	Formation
Thames Group	London Clay Formation
	Oldhaven Formation
Lambeth Group	Reading Formation / Woolwich Formation
	Upnor Formation
	Thanet Formation

Figure 7.3 Lithostratigraphical classification of the Palaeocene and lower Eocene (Ypresian) deposits of the London and Hampshire basins. (Adapted from Curry *et al.*, 1978; King,1981; and Ellison *et al.*, 1994.)

within the Palaeocene–Eocene boundary interval currently under discussion by the International Geological Correlation Programme (IGCP 308) (Berggren and Aubry, 1998). These strata are treated here as Palaeocene–Eocene transitional interval. The London Clay division A2 and above are Eocene in age (Berggren and Aubry, 1998). The Ardtun flora has been dated as earliest Ypresian on palynological evidence (Jolley, 1997), but also falls within the disputed Palaeocene–Eocene boundary interval currently under discussion.

At the time that the present volume was going to press, the Palaeogene subcommission of the International Commission on Stratigraphy (ICS) voted to place the Palaeocene–Ecoene boundary at the base of the Carbon Isotope Excursion (CIE), which occurs within lower Reading Mottled Clay (see summary in Collinson, 2000a). This means that the Oldhaven Beds at Herne Bay and the London Clay division A1 at Harwich and Walton are Eocene in age (since they are stratigraphically higher than the Reading Formation) and the Upnor Formation at Herne Bay is Palaeocene in age. The Felpham strata are judged to be Eocene in age (Collinson, 2000a). However, the correlation of the CIE to the sites at Harefield, Pincent's Kiln and Cold Ash is uncertain, so these are best treated as Palaeocene–Eocene transition.

PALAEOCENE AND PALAEOCENE–EOCENE TRANSITIONAL VEGETATION

In Britain, there appears to be a marked change between the Mesozoic, gymnosperm-dominated floras and the Tertiary angiosperm-dominated floras. However, this is mainly a function of the major break in the palaeobotanical record between the Wealden floras (the youngest-known Mesozoic plants) and the Thanet Formation floras (the oldest-known Tertiary plants), representing some 50 Ma. Most of the intervening time is represented by either marine deposits (mainly the Chalk), or the pre-Thanetian unconformity. Where there is a more continuous record, such as North America, we see a more gradual transition between the two types of flora (Lidgard and Crane, 1990).

The Cretaceous–Tertiary (K/T) 'extinction' event seems to have been much less marked for plants than for animals. While there is evidence of significant perturbation of the vegetation at the K/T boundary, most notably the presence of widespread wildfire followed by a marked increase in ferns (Wolfe, 1991), plant life seems to have relatively quickly recovered and there were few major taxonomic extinctions (Boulter *et al.*, 1988). The bennettites and caytonias did not survive into the Tertiary, but they were already rapidly declining in Late Cretaceous times and the K/T event may have done little more than act as a *coup de grâce*. Among the angiosperms, a second radiation and modernization seems to have taken place after the K/T event, where partially reconstructed whole plants and individual organs are very similar to, or indistinguishable from, those of living genera (Collinson, 1990a, 2000b).

The Palaeocene world is divided into four major palaeofloristic zones: the Holarctic, Tropical, Notal and Australian Palaeokingdoms (Figure 7.1; Akhmetyev, 1987). Britain belongs to the first of these. Two palaeoareas are recognized within the Holarctic. The Boreal Palaeoarea includes Canada, northern Britain, Scandinavia and much of Russia. The vegetation represented by this phytochorion consisted typically of deciduous conifers such as the redwood family (Taxodiaceae) and broad-leafed deciduous angiosperms of the subclass Hamamelidae (e.g. plane tree, walnut tree, beech and birch families). Despite such high latitudes, the vegetation seems to have had essentially temperate affinities and the adoption of deciduousness was more a matter of restricted light levels than low temperatures. The British Boreal floras belong to a distinct palaeoprovince, known as the Brito-Arctic Igneous Palaeoprovince (sometimes alternatively called the 'Thulean'), which reflects the extreme conditions that developed as a result of the volcanicity resulting from the opening of the North Atlantic (Boulter and Kvaček, 1989).

Southern Britain, in contrast, belongs to the Tethyan Palaeoarea, which also extended over most of the USA, southern and central Europe, Kazakhstan, Central Asia and China. Southern Britain at this time supported a mixed vegetation, with freshwater mires and forest–woodland containing families that today are typically found in temperate latitudes (plane-tree, walnut-tree, birch and katsura-tree families) and subtropical to tropical latitudes (palms, frankincense, tea, icacina, moonseed, grape and squash families) (Collinson and Hooker, 1987; Collinson, 2000a). The vegetation towards the end of the interval covered in this chapter (A1 division of the London Clay, Oldhaven Beds) became very similar to that of the overlying Eocene Series (Collinson, 1983b). A distinctive flora characterizes the slightly older 'late Palaeocene' thermal maximum (Collinson, 2000a).

PALAEOBOTANICAL SITES IN THE PALAEOCENE AND PALAEOCENE–EOCENE TRANSITION OF BRITAIN

These palaeobotanical sites can be broadly divided into four categories. The first includes floras from the Thanet Formation of southern England. Plant remains are generally rare in these deposits and only one site, Herne Bay, has yielded a sufficiently diverse assemblage to merit selection as a GCR site. Herne Bay has also yielded a few plants (Ward, 1978) from the Upnor Formation, in the lowest part of the Palaeocene–Eocene transitional interval (Berggren and Aubry, 1998).

Secondly, there are sites from the middle part of the Palaeocene–Eocene transition in southern England known as the 'Reading Formation'. By far the best site for fruits and seeds in these beds is Felpham. The best 'leaf beds' (in fact lenses, also containing fruits and seeds) are at Cold Ash, while Harefield has yielded an interesting charophyte assemblage. All three have been selected as GCR sites. A fourth site, at Pincent's Kiln, has been incorporated within the GCR network, not so much for yielding a diverse flora, but because of the palaeoecological insights that it provides into the vegetation.

Thirdly, there are several sites that preserve floras from the latest part of the Palaeocene–Eocene transitional interval. These are the Oldhaven Beds at Herne Bay, and division A1 of the London Clay at Harwich and Walton-on-the-Naze, which are more or less of equal age (Ellison *et al.*, 1994; Ward, 1995; Hooker, 1998). Wrabness, where the flora may be from the upper A1 or lower A2 division of the London Clay, is described in Chapter 8.

Fourthly, in contrast to these sites representing Tethyan floras, northern Britain belongs to the Boreal Palaeoarea and preserves a quite different, mesophytic vegetation. Only one site in Great Britain, Ardtun, has yielded a significant assemblage of these Boreal floras and this has been included as the representative Hebridean site for the GCR.

HERNE BAY (TR 185 685–TR 224 693)

Introduction

Herne Bay is one of the most important Palaeogene sites in the London Basin and has been independently selected as a GCR site for its stratigraphical interest (Daley in Daley and Balson, 1999, p.34). It is also of considerable interest for palaeobotany, yielding the only significant flora from the Thanet Formation. It contains the only unequivocal Palaeocene flora known from Britain.

Plant fossils have been reported from several stratigraphical levels, the best documented being fruits and seeds from the A2 division of the London Clay Formation (see Herne Bay GCR site report in Chapter 8). However, the palaeobotany of the underlying Tertiary deposits has not been investigated to the same extent. Silicified pine cones (Prestwich, 1854; Gardner, 1883–1886a; Chandler, 1961a), fern stems (Carruthers, 1870b, 1872; Kidston and Gwynne-Vaughan, 1907; Chandler, 1961a, 1965) and angiosperm wood (Crawley, in press) have been described from the Thanet Formation. Ward (1978) lists other plants from the Thanet Formation and Upnor Formation, although none have yet been figured. Megaspores, both original and reworked, were described from the Thanet Formation by Collinson *et al.* (1985). Chandler (1961a, 1964) described fruits and seeds from the Oldhaven Beds.

Description

Stratigraphy

Daley (in Daley and Balson, 1999) gives an account of the geology at Herne Bay, including a review of the complexities of the lithostratigraphical nomenclature. Using the classification proposed by Ellison *et al.* (1994), the section here consists of 17.5 m of Thanet Formation, overlain by 5.6 m of Upnor Formation. This in turn is overlain unconformably by deposits of the Thames Group (Oldhaven Beds and London Clay Formation). The sequence is shown in Figure 7.4, which also identifies the levels of the main plant beds.

Palaeobotany

Chandler (1961a) described from the Thanet Formation here two species of pinacean cone, *Pinus prestwichii* Gardner and *P. macrocephalus* Gardner, and a silicified stem of the fern *Osmunda dowkeri* (Carruthers) Miller (Figure 7.5; see also Carruthers 1870b, 1872; Kidston and Gwynne-Vaughan, 1907; Chandler, 1965; Collinson, in press a). From the *Astarte tenera* Bed in the middle Thanet Formation, Ward (1978) recorded *Canticocculus* sp. and *Iodes multireticulata* Reid and Chandler), together with a fragment of the pine cone *Pinus macrocephalus* Gardner. Later he reported (in Daley and Balson, 1999) that these beds have yielded a rich seed flora, and Collinson (pers. obs.) has found distinctive but so far unidentified fruits and seeds from here. There is clearly considerable research potential here.

Ward (1978) also recorded *Iodes multireticulata* from the *Corbula regulbiensis* Bed near the top of the Thanet Formation, while Brett (1960) described wood from this level. The overlying Upnor Formation (lowermost Palaeocene–

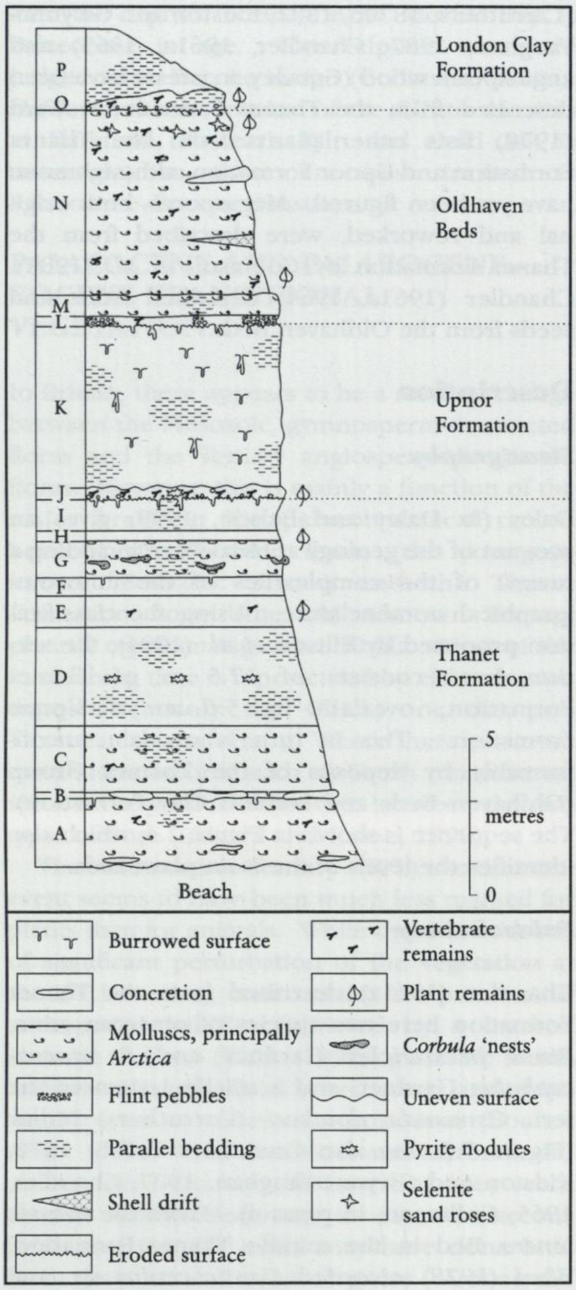

Figure 7.4 Sequence exposed in the cliffs and foreshore at Herne Bay. (After Ward, 1978).

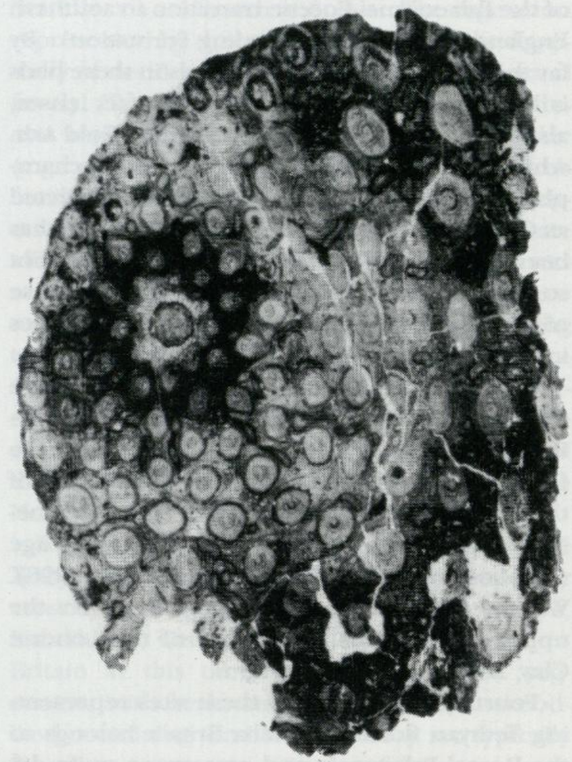

Figure 7.5 Stem of the fern *Osmunda dowkeri* permineralized by silica, hence showing anatomical detail, × 1.8 (see Chandler, 1965) (specimen number BMNH V.29629c). The specimen was found at Herne Bay and judged to have been derived from the Thanet Formation. The specimen is the holotype of this species. (Photo: Natural History Museum, London.)

Eocene transition interval) has yielded *I. multireticulata*, *P. macrocephalus* and seeds of *Vitis* sp..

Collinson *et al.* (1985) described numerous megaspores from the Thanet Formation at Herne Bay. Many were reworked from Mesozoic and Palaeozoic strata, and suggested that the sediments of the Thanet Formation were derived by longshore drift from the eastern coast of Britain. However, there were also original Tertiary megaspores here, including *Minerisporites glossoferus* (Dijkstra) Tschudy emend. Batten and Collinson (in press) and *Erlansonisporites* sp. (both of lycophyte origin) and *Azolla* cf. *teschiana* Flörschutz. Following a revision of the type material, Batten and Collinson (in press) have shown the presence of both *M. glossoferus* and *M. mirabilis* (Miner) Potonié emend. Batten and Collinson in the Thanet Formation Flora (Figure 7.6).

Chandler (1961a, 1964) described a number of species from the Oldhaven Beds at Herne Bay, some new to science. This flora comes from the latest part of the Palaeocene–Eocene transitional

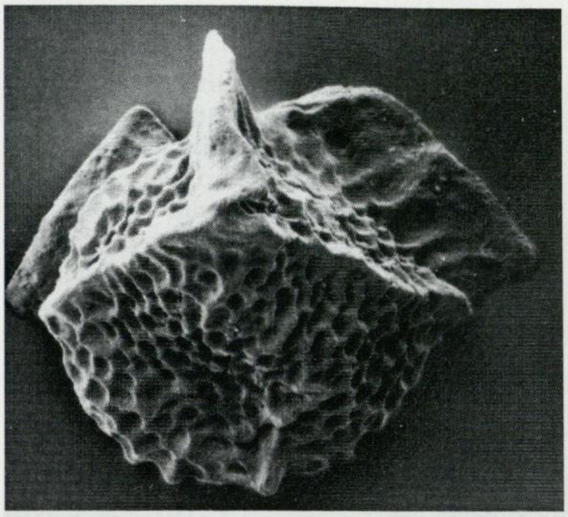

Figure 7.6 Megaspore of *Minerisporites mirabilis*, an early member of the species tending towards *M. glossoferus* morphology, × 120 (see Batten and Collinson, in press). From the Thanet Formation, Herne Bay. (Photo: M.E. Collinson.)

interval. For those species marked below with '*', Herne Bay is the type locality.

Icacinaceae
Natsiatum eocenicum Chandler (see footnote to Table 8.1)
Lauraceae
Laurocarpum sp. (*Cinnamomum*?)
L. spp.
Menispermaceae
**Cocculus cooperi* (Chandler) Mai 1987
**C.? serratus* (Chandler) Chandler
Tinospora excavata Reid and Chandler
Potamogetonaceae
**Limnocarpus cooperi* Chandler (see Collinson, 1982a)
**L.? magnus* Chandler
L. sp.
Symplocaceae
?*Symplocos* sp.
Rutaceae
Zanthoxylon sp.
Theaceae
**Cleyera? cooperi* (Chandler) Chandler
C.? variable (Ludwig) Chandler
Vitaceae
Vitis spp.

In addition, there were generically unattributable examples of ?palm, epacris, spurge and buckthorn families.

Brett (1966) described a wood of the cashew nut family from a loose beach specimen judged, on the basis of sediment infillings of *Teredo* borings, to have come from the Woolwich Formation (Palaeocene–Eocene transition) at Herne Bay.

Interpretation

Herne Bay is of outstanding palaeobotanical interest for yielding plant fossils from the Palaeocene and early Eocene strata, providing insight into the stratigraphical changes in the plant fossil record through this interval. However, it is significant that each of the three main plant-bearing units (Thanet Formation, Oldhaven Beds and the A2 division of the London Clay Formation) yields significant floras and each is worthy of selection as a GCR site on its own merit. The last is dealt with in the next chapter.

Herne Bay is the only known site to yield plant macrofossils from the Thanet and Upnor formations, making them the oldest known Tertiary plant fossils in Britain. The best documented are the silicified osmundacean fern stem (Figure 7.5) and two pine cones (Carruthers 1870b, 1872; Kidston and Gwynne-Vaughan, 1907; Chandler, 1961a, 1965).

Herne Bay is the type locality for *Osmunda dowkeri*. Two silicified pieces of stem have been found here, one described by Carruthers (1870b, 1872), the other by Chandler (1961a). The detailed anatomy was very finely preserved, including starch grains within the cells, and there is no doubt as to its osmundacean affinities (Miller, 1967, 1971). The stem is important for confirming the presence in the Tertiary deposits of Europe of the subgenus *Plenasium*, which today is restricted to East and Southeast Asia (Collinson, in press a). Other fossil evidence of this subgenus in Europe comes from sterile and fertile fronds known as *Osmunda lignitum* (Giebel) Stur from the Eocene to Miocene deposits of Europe (Barthel, 1976; Collinson, in press a).

The pine cones are known from both silica petrifactions and carbonaceous fossils. Two species have been distinguished on size and shape of the cone and on the form of swellings on the cone scale; for one of these species (*P. prestwichii*) Herne Bay is the type locality. The anatomy of both species is well preserved and unequivocally shows that they belong to the genus of living pines, *Pinus*.

Ward (1978) stated that the *Astarte tenera* Bed in the Thanet Formation yields abundant fossilized seeds. They are of considerable potential significance, being the oldest known Tertiary seed-flora in Britain, but they have yet to be described in the literature. Collinson (pers. obs.) has also found determinable wood in the Upnor Formation here but it has yet to be described. The megaspores from this horizon described by Collinson *et al*. (1985) provide some of the best evidence of lycophytes from the Tertiary rocks of Britain, including isoetalean forms and *Selaginella*-like forms. They confirm the importance of heterosporous lycophytes and water ferns in the British Palaeocene record, as in the floras of the same age in continental Europe (Collinson and Hooker, 1987; Batten and Collinson, in press).

From the Oldhaven Beds flora at Herne Bay, Chandler (1961a) described three types of seed thought to belong to the pondweed family, and which she assigned to the genus *Limnocarpus* Reid. Collinson (1982a) reviewed this genus and argued that it should be restricted to those species known to have had paired fruits. The Herne Bay species have endocarps with straight ventral margins and so may have originally been paired, but they have never been found preserved in pairs. Collinson thus argued that they can only be regarded as tentatively assigned to *Limnocarpus*. They are nevertheless of interest as the only known examples of this aquatic family from the Thames Group, and the oldest known from Britain.

Three species of the form-genus *Myrtospermum* were recognized by Chandler (1961a). One was later provisionally transferred to the palms (Chandler, 1964), while the other two (*M. cooperi* and *M. variabile*) were placed in the tea family. Chandler (1964) suggested that the latter two species might belong to the living genus *Cleyera* although Collinson (1983b) stated that they could equally belong to *Eurya*.

Chandler (1961a) assigned a seed of the moonseed family with a prominent serrated ornamentation to *Menispermicarpum serratum*. However, she subsequently discovered that the living *Cocculus* can also have such ornamentation and so provisionally transferred the Herne Bay species to this genus (Chandler, 1964). Mai (1987) also transferred Chandler's *Canticocculus cooperi* to the genus *Cocculus*.

Conclusions

The Thanet Formation at Herne Bay yields the oldest known flora from Britain containing angiosperm fruits and seeds, and heterosporous plants, *c*. 55 Ma old. It has also yielded petrified fern stems and conifer cones, which show details of their anatomy. Herne Bay is the only site to have yielded a fossil flora from the Oldhaven Beds, a distinctive lithology that is essentially coeval with the division A1 of the London Clay at Walton-on-the-Naze and Harwich, and with the Harefield Member at Harefield.

FELPHAM (SZ 949 993)

Introduction

Felpham is the only known site to yield a diverse assemblage of fossil fruits and seeds from the middle part of the Palaeocene–Eocene transition beds in the Reading Formation of Britain. Four new genera and 16 new species have been found here. Felpham is the only available site where floras can be studied near the 'late Palaeocene' thermal maximum, and which provide an important contrast with the later Eocene floras. It is also the only known site where in-situ palms can be seen (see Figure 7.10).

The Reading Formation is best known for its leaf floras, such as that found at Cold Ash. However, these do not produce the variety of evidence on reproductive structures that is necessary for comparison with other floras. Some seeds have been reported from Cold Ash, but the only place where a reasonably diverse fruit and seed assemblage has been found is Felpham. Full details of the palaeobotany here have yet to be published, but Collinson (in Bone, 1986) has given a preliminary report and it is briefly referred to by Collinson and Hooker (1987), and Collinson (1990b, 1996a, 2000a). Van Bergen *et al*. (1993) include specimens from here in their study of *Salvinia* microspore massulae and megaspores.

Description

Stratigraphy

The foreshore exposures at Felpham, (Figure 7.7) whose geology was described by Bone (1986), are represented in Figure 7.8. About

Figure 7.7 Felpham foreshore looking almost north across the near-shore part of the area of Bed 3, including the lignite bed and the channel infill, and showing new sea defences in foreground and at right. In this photograph most of the strata are underwater or are covered by modern beach deposits. Taken in 1999. (Photo: M.E. Collinson.)

17 m of mainly mottled clays disconformably overlie Chalk deposits. Bone (1986) estimated that a further 12 m of mottled clays are obscured by alluvium, which are in turn overlain by brown clays probably of the London Clay Formation. There are no biostratigraphically useful animal macrofossils in the clays. However, lithostratigraphical correlation is with the Reading Formation, which indicates that they are in the Palaeocene–Eocene boundary interval and slightly post-dating a record of the carbon isotope excursion (CIE) that indicates the 'late Palaeocene' thermal maximum (Collinson, 2000a).

In the upper part of the exposed Reading Formation here is a 1.6-m thick lignite bed, which is one source of the plant fossils. There is also a channel deposit that cuts down into the lignite and has also yielded plant fossils.

Palaeobotany

Knowledge of the Felpham flora is mainly derived from 'a preliminary report' by Collinson (in Bone, 1986) and Collinson (2000a). From the clays in the lignite bed and from the channel deposit, she reports a diverse assemblage of fruits and seeds. The most abundant are from aquatic plants. In the clays associated with the lignite bed are the remains of the sedge *Caricoidea obovata* Chandler, a water lily *Sabrenia* sp. nov. and a water soldier *Stratiotes* sp. nov. (see Collinson, 1990a, pp. 50–1). This suggests shallow-water vegetation in a marsh setting. In contrast, the channel mainly yielded the water fern *Salvinia* sp. (see also van Bergen *et al.*, 1993) and the loosestrife *Decodon* sp. nov., which Collinson suggested as growing on water margins.

Less abundant, but more diverse, are the remains of forest trees and lianas, including the angiosperms of the frankincense, dogwood, squash, icacina, moonseed, rue, tea and grape families. The only named species were *Natsiatum eocenicum* Chandler, *Icacinicarya inornata* Chandler and *Vitis* sp.. However,

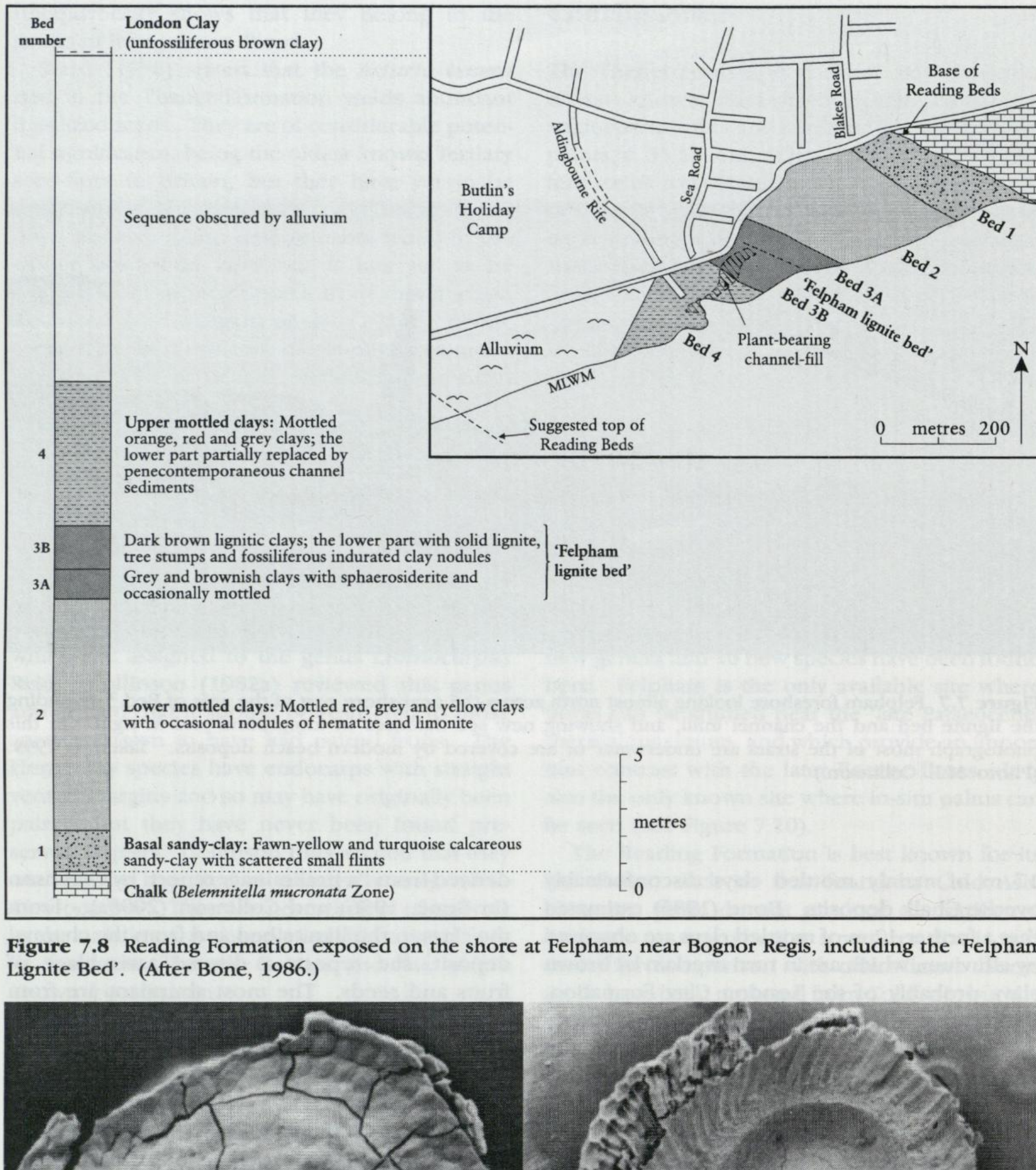

Figure 7.8 Reading Formation exposed on the shore at Felpham, near Bognor Regis, including the 'Felpham Lignite Bed'. (After Bone, 1986.)

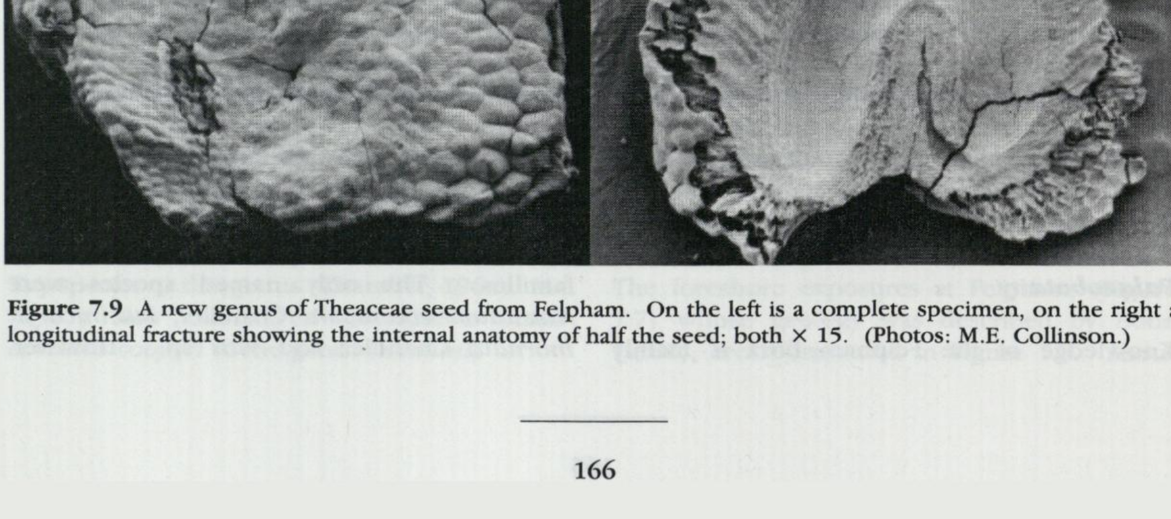

Figure 7.9 A new genus of Theaceae seed from Felpham. On the left is a complete specimen, on the right a longitudinal fracture showing the internal anatomy of half the seed; both × 15. (Photos: M.E. Collinson.)

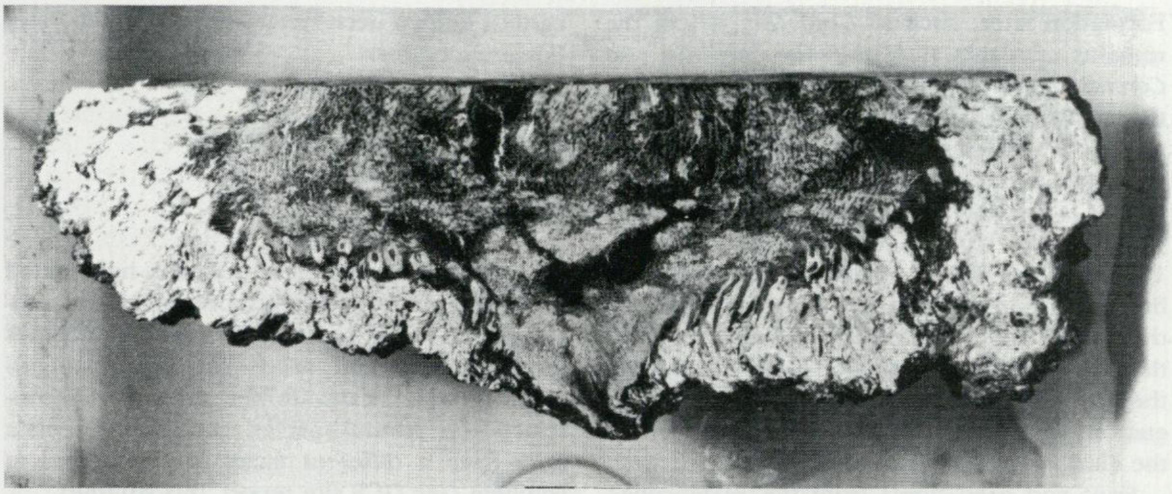

Figure 7.10 Longitudinal polished cut surface of lower part of a partly pyritized palm stump, collected *in situ* at Felpham, × 0.3 (see Collinson in Bone, 1986; Collinson, 1990a). (Photo: Natural History Museum, London.)

Collinson mentioned that the elements of the frankincense, rue and grape families were probably conspecific with forms found in the early and middle Eocene deposits. In contrast, among the squash, moonseed and tea families, there are at least three new genera and several new species (Collinson, 2000a). In particular, a *Trichosanthes*-like seed, a new genus of Theaceae seed, (Figure 7.9) and a *Decodon*-like seed characterize the flora of the 'late Palaeocene thermal maximum' (LPTM). Also abundant are *Rhamnospermum bilobatum* Chandler, whose affinities remain totally obscure. Also present here are fertile pinnules of the schizeaecean fern *Anemia poolensis* Chandler (Collinson, 1990a, 1996a, in press a). There are a number of other floral elements that have not yet been identified (Collinson, pers. obs.).

Sideritic nodules within the lignite bed have yielded leaf adpressions of probable lauralean affinities, small compound fruits, petrified fern rachises very similar to those of the London Clay, and coniferous (?redwood) cones. The lignite bed also contains in-situ petrified tree stumps yielding palm anatomy (Figure 7.10; Collinson, 1990a) and large compressed logs as yet unidentified (Bone, 1986).

Interpretation

This is the only site in Britain to yield a diverse suite of fruit and seed fossils from the Palaeocene–Eocene boundary beds, and it provides the only opportunity to compare the vegetation of this time with the later Eocene floras (see Chapter 8). The bulk of the flora represents palm-dominated swamp vegetation, quite different from the London Clay floras, such as from Sheppey. A number of essentially tropical families found in the London Clay also occur here, including the frankincense, dogwood, squash, icacina, moonseed, rue, tea and grape families. However, most of the tropical families that characterize the Ypresian floras do not occur at Felpham, suggesting that the paratropical rain forests had not yet fully developed in southern England.

The aquatic vegetation, whose remains dominate the Felpham flora, also differs from that represented in the Ypresian and Lutetian. The commonest species here, *Carcoidea obovata*, is unknown from horizons above the Reading Formation, and the new species of *Sabrenia* and *Stratiotes* are not known from anywhere else in Britain. *'Scirpus' lakensis*, which is a diagnostic element of the Ypresian and Lutetian aquatic floras, is unknown from Felpham, or from any other Reading Formation locality.

Felpham has yielded the only example of the water fern *Salvinia* from a conservable site in Britain and is one of the few early records of this genus in Europe. The chemistry of these fossils has been studied by van Bergen *et al.* (1993).

There appears to be a marked contrast with the adpression floras from other Reading

Formation sites, such as Cold Ash, where the remains of plants such as *Palaeocarpinus* and *Cercidiphyllum*-like plants dominate. However, this is probably because the Felpham deposits represent a marsh setting, which was unsuited to those two plants (see Collinson, in Bone, 1986).

This is the only known site in Britain to have yielded palm stumps (Bone, 1986; Collinson, 1990a; Figure 7.10). Their identity was confirmed through observations on the anatomy of the trunk. Collinson (in Bone, 1986) reported that they occur at intervals of 1–4 m, suggesting they were dominant elements in the swamp vegetation, which was thus similar to some areas of the Florida Everglades of today.

Fruit and seed floras from the Palaeocene–Eocene transition are extremely rare worldwide, making Felpham a site of international importance. Detailed comparisons are difficult because, although known for well over a decade, the flora has not been fully described in the literature. However, Collinson (in Bone, 1986) remarked that for several genera, Felpham represented the earliest known occurrence and was thus potentially important for understanding the early evolution of the relevant groups.

Collinson (2000a) has recognized that the distinctive flora at Felpham characterizes the interval near, or at, the 'late Palaeocene thermal maximum' (LPTM). Comparable floras were also identified from temporary exposures at St Pancras and Croydon, but Felpham is the only conservable site to yield the assemblage. The site is therefore of international importance for understanding global climatic change near the Palaeocene–Eocene boundary.

Conclusions

The foreshore at Felpham is the only site in Britain to yield a diverse assemblage of fruits and seeds from the Palaeocene–Eocene transition beds, *c.* 54 Ma old. It is one of the very few such floras of this age known worldwide and is thus of international importance for understanding the global climatic and vegetational changes taking place at this time. It represents a mainly marsh community dominated by aquatic plants (e.g. sedge-like plants), but also includes remains of paratropical rain forest trees and lianas. Of additional interest is the presence of in-situ stumps of palm trees, the first such stumps found in Britain. Although still to be fully studied, Felpham seems to represent the earliest known occurrences of several genera of flowering plants.

COLD ASH (SU 500 714)

Introduction

The Reading Formation at Cold Ash has yielded a diverse flora from the Palaeocene–Eocene transition. It is important because it includes foliage, fruits and seeds (of mainly angiosperms), which have allowed the partial reconstruction of several species. It also represents a flora from a different facies to that found at Felpham (see GCR site report, this volume).

There is a long history of records of plant fossils from the Reading Formation, mostly from temporary exposures in Berkshire (Chandler, 1961a). Cold Ash seems to have been first identified as a major source of palaeobotanical material in the mid-1970s by Roland Goldring and Peter Crane, when the site was undergoing expansion as a source of sand. These workings finished in 1980 and most of the pit has been infilled. However, one of the pockets of plant-bearing mudstones has been conserved by English Nature and provides for the continuing interest in the site (Crane and Goldring, 1991). Most of the published palaeobotanical work on the site has been by Crane and his colleagues (Crane, 1978, 1981, 1984, 1989a; Collinson and Crane, 1978; Smith and Crane, 1979; Crane and Jarzembowski, 1980; Crane and Manchester, 1982; Collinson *et al.*, 1985; Crane and Stockey, 1986; Manchester, 1987; Jarzembowski, 1989; Herendeen and Crane, 1992). Collinson (1978a) also included some specimens from the site in an unpublished thesis.

Description

Stratigraphy

An outline plan and stratigraphical sequence for when the site was at its maximum extent is shown in Figure 7.11. The bulk of the section consisted of poorly consolidated cross-bedded sands of the Reading Formation, which is in the transition interval between the Palaeocene and the Eocene series (see 'Stratigraphical Background' earlier in this chapter). The underlying Upnor Formation and the Chalk were sometimes revealed during commercial

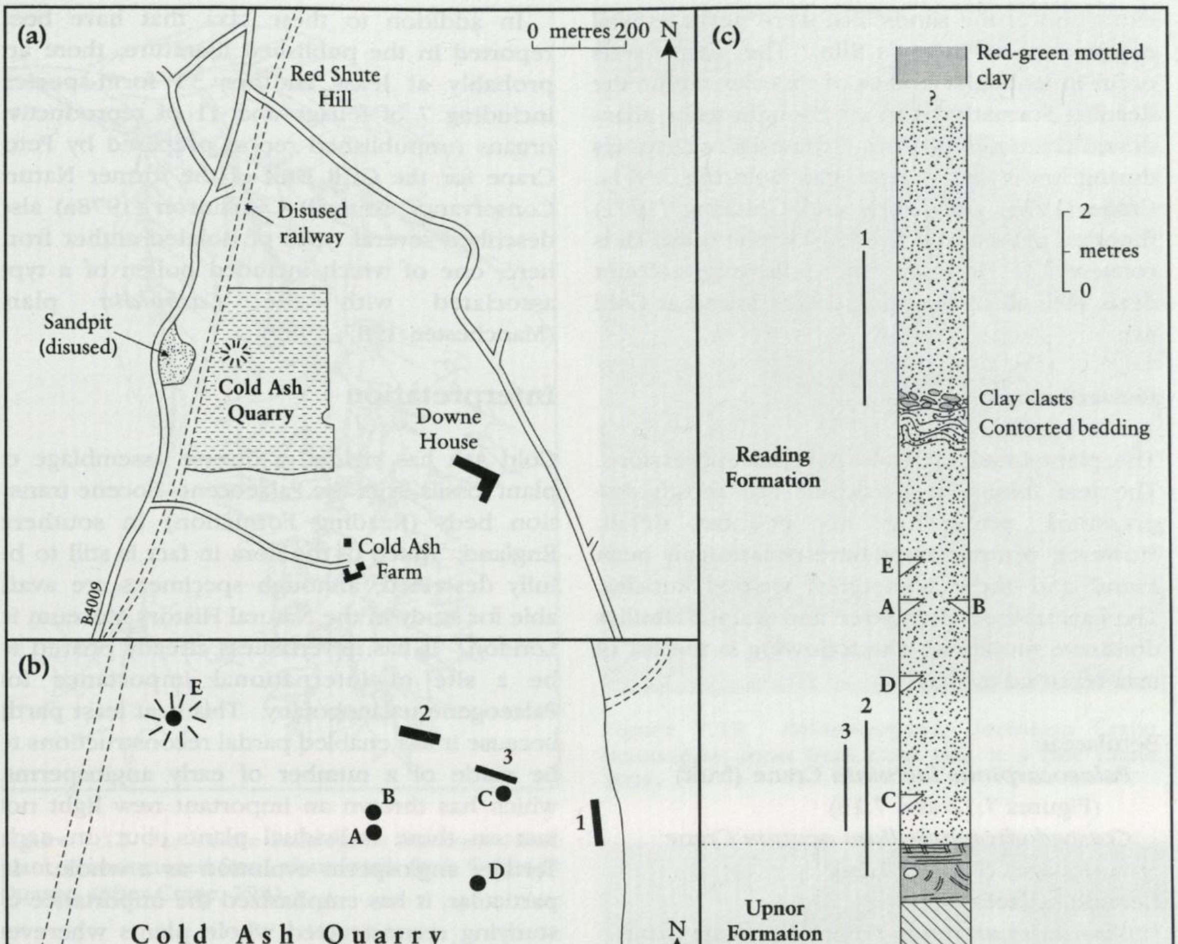

Figure 7.11 Cold Ash Quarry in the early 1980s; (a) and (b) show plans of the site and include the location of the sections 1–3 represented in (d). Also shown are the locations of the main plant-bearing lenses (A–E); (c) is a composite stratigraphical section for the site. (After Crane and Goldring, 1991.)

extraction of the sands, but were never as well exposed as at Pincent's Kiln. The plant fossils occur in lenticular bodies of silty clay within the Reading Formation and are thought to be abandoned channel fills or mud deposits in channels during low water (Crane and Goldring, 1991). Crane (1978) and Crane and Goldring (1991) reported plants from five lenses, one of which is conserved. However, the following account deals with all of the plant fossils found at Cold Ash.

Palaeobotany

The plant fossils at Cold Ash are adpressions. The leaf fossils in particular are mostly impressions preserving no cellular detail. However, compressions have occasionally been found and these sometimes yielded cuticles. The katsura-tree, plane-tree and walnut families dominate the flora. The following is the list of taxa reported to date:

Betulaceae
- *Palaeocarpinus laciniata* Crane (fruit) (Figures 7.12 and 7.13)
- *Craspedodromophyllum acutum* Crane (foliage) (Figures 7.14)

Cercidiphyllaceae
- *Nyssidium arcticum* (Heer) Iljinskaja (fruit)
- *Trochodendroides prestwichii* (De la Harpe) Crane (foliage)

Ericaceae
- *Rhododendron newburyanum* Collinson and Crane (seeds) (Figure 7.15)
- Cf. *Vaccinium* sp. (seeds)

Juglandaceae
- *Casholdia microptera* Crane and Manchester (fruit)
- *Dicotylophyllum* sp. (foliage)

Lauraceae
- *Lauraceaephyllum stenolobatus* Koch (foliage)

'Legumes'
- *Leguminocarpon gardneri* (Chandler) Herendeen and Crane (fruit)

Platanaceae
- *Platanus schimperi* (Heer) Saporta and Marion (foliage) (Figure 7.16)

Theaceae
- Cf. *Cleyera* sp. (seeds)

Incertae sedis
- *Rhamnospermum bilobatum* Chandler

In addition to these taxa that have been reported in the published literature, there are probably at least another 35 form-species, including 7 of foliage and 11 of reproductive organs (unpublished report prepared by Peter Crane for the GCR Unit of the former Nature Conservancy Council). Collinson (1978a) also described several types of isolated anther from here, one of which included pollen of a type associated with the *Casholdia* plant (Manchester, 1987, 1989).

Interpretation

Cold Ash has yielded a diverse assemblage of plant fossils from the Palaeocene–Eocene transition beds (Reading Formation) in southern England. Much of the flora in fact is still to be fully described, although specimens are available for study in the Natural History Museum in London. It has nevertheless already proved to be a site of international importance for Palaeogene palaeobotany. This is at least partly because it has enabled partial reconstructions to be made of a number of early angiosperms, which has thrown an important new light not just on these individual plants, but on early Tertiary angiosperm evolution as a whole. In particular, it has emphasized the importance of studying reconstructed whole plants wherever possible, to obtain the maximum information on the relationship of the early angiosperms to living genera.

The most abundant fossil plants at Cold Ash are the leaves *Trochodendroides prestwichii*, which are closely associated with the fruits *Nyssidium arcticum*. Largely as a result of Crane's (1984) study on the Cold Ash fossils, this became one of the best-understood early Palaeogene dicotyledons, which is widely known as the '*Cercidiphyllum*-like plant' (see also Crane and Stockey, 1985, 1986). It was evidently a woody plant with large rounded leaves and rigid axes bearing paired female fruits (the male structures are unknown), and shares many features with the extant *Cercidiphyllum*. Today, the katsura-tree family (Cercidiphyllaceae) consists of just one genus with two species, found only in Japan and China. However, in Palaeogene times, a *Cercidiphyllum*-like plant was one of the commonest constituents of the middle and high latitudes floras of the Northern Hemisphere (Crane, 1989a; Friis and Crane, 1989). In Britain, it is not only found in the Reading Formation

Figure 7.12 Part of the Palaeogene *Palaeocarpinus* plant, reconstructed from plant fossils from Cold Ash Quarry. (After Crane, 1981.)

(Chandler, 1961a, 1964; Crane, 1984), but is also known (under the name *Jenkinsella apocynoides* Reid and Chandler in older publications) from the Oldhaven Beds and London Clay (Chandler, 1961a; Cooper, 1977; George and Vincent, 1977; Crane, 1984) and the lower Headon Formation (Crane, 1984). In the Palaeocene deposits of North America there is a very similar genus, *Joffrea*, which is distinguished from *Nyssidium* mainly on the inflorescences of the former having been borne on short shoots.

Also based on evidence of association, Crane (1981) argued that *Palaeocarpinus laciniata* (Figure 7.13) was the fruit of the plant that bore the leaves *Craspedodromophyllum acutum* (Figure 7.14). This was the first partial reconstruction of an angiosperm from Cold Ash and was at the time one of the best-known early Palaeogene dicotyledons. The leaves are of a type that has been normally assigned to the birch family, although Crane (1981) pointed out

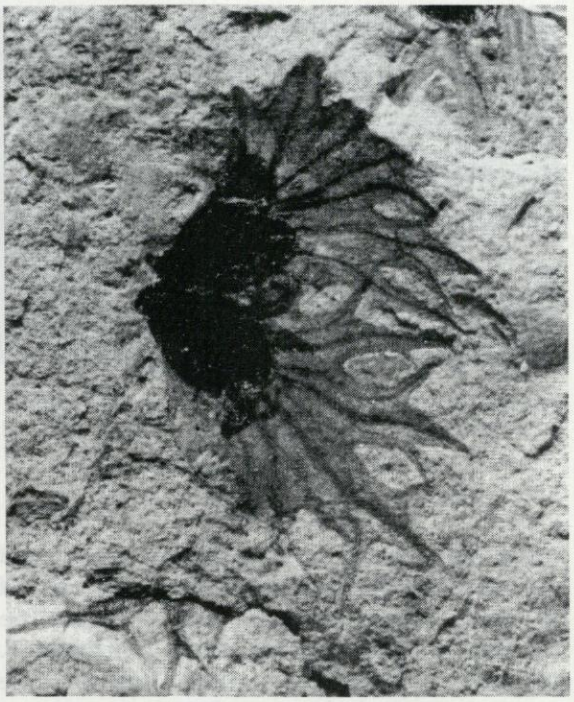

Figure 7.13 *Palaeocarpinus laciniata* Crane. Betulaceous fruits from Cold Ash, × 4 (see Crane, 1981).

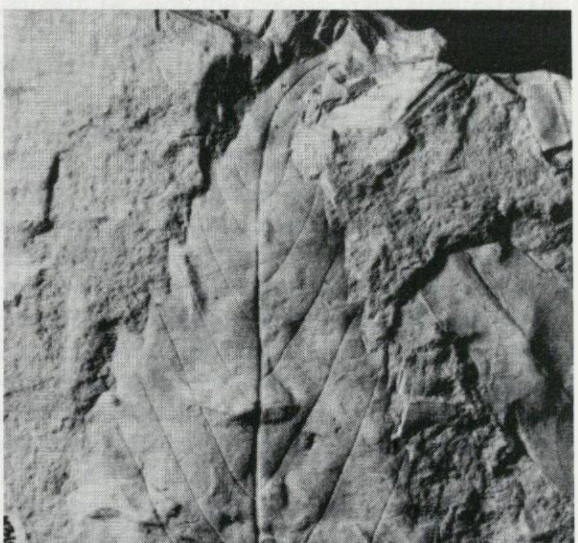

Figure 7.14 *Craspedodromophyllum acutum* Crane. The apical portion of a leaf attributed to the Palaeocarpinus plant from Cold Ash × 1.2 (see Crane, 1981).

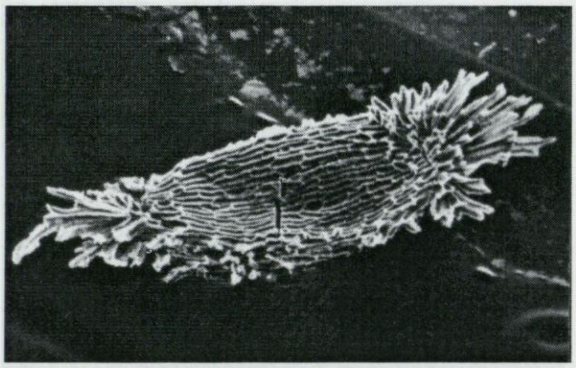

Figure 7.15 Seeds of *Rhododendron newburyanum*, × 50 (see Collinson and Crane, 1978), from the Cold Ash GCR site. (Photo: M.E. Collinson.)

that there are other families that have this type of foliage. The fruit is more clearly diagnostic of the birches, in particular of the tribe Coryleae (including the hazels and hornbeams). However, Crane (1981) pointed out that the winged nut is most comparable to *Carpinus* (hornbeam), while the arrangement of the involucral bracts is more similar to *Corylus* (hazel). Hence, although the nuts or the bracts may on their own suggest affinities with living genera, the combination of characters (especially when taken with the foliage) clearly separates the Cold Ash plant from anything living today. This combination of characters fits in well with the predictions of a cladistic analysis of extant birch family by Crane (1989b).

There have subsequently been many other *Palaeocarpinus* plants described. These have shown that the genus had a circum-boreal occurrence in the Palaeocene and Palaeocene–Eocene transition, occurring in Britain, France, China and North America. In the Eocene Epoch, it persisted in North America and eastern Asia (Manchester, 1999). The Cold Ash flora thus contains the type material upon which a global palaeobiogeography has been built. *Palaeocarpinus* is also important because of its diversity and because it is the earliest known member of the tribe Coryleae, which subsequently became specialized for animal dispersal (Collinson and Hooker, 1987; Manchester, 1987; Collinson, 1999).

Crane and Manchester (1982) described an unusual fruit of the walnut family as *Casholdia microptera* (see also Manchester, 1987). It is the oldest known fruit from this family from Eurasia, and is only marginally younger than *Polyptera*

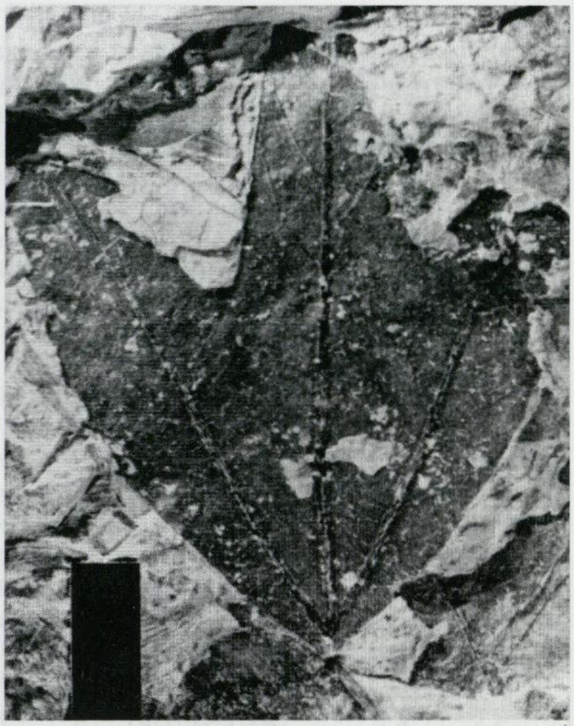

Figure 7.16 *Platanus schimperi* (Heer) Saporta and Marion. A platanoid leaf from Cold Ash. (Photo: P.R. Crane.)

manningii Manchester and Dilcher from Wyoming. Unlike most other fossil walnut fruits, *Casholdia* cannot be assigned definitely to one of the extant tribes of that family, but on the whole it has more in common with the Engelhardieae. However, there is associated foliage that shows closer similarities to the Juglandeae, while associated pollen suggests the Platycaryeae. While the connection between the fruit, foliage and pollen has not been proven, the Cold Ash fossils seem to represent a primitive member of the walnut family, sharing characters of more than one of the extant tribes.

Cold Ash is the best locality for the legume fruits *Leguminocarpon gardneri* (Herendeen and Crane, 1992). They clearly show affinities with the subfamily Caesalpinioideae (sometimes regarded as a distinct family) and are the oldest reliable evidence of this subfamily in the fossil record. However, in the absence of evidence of other parts of the plant, it is difficult to be certain if it can be assigned to an extant genus, hence Herendeen and Crane placed it in a form-genus for isolated legume fruits. Isolated leaflets of legume-like compound leaves have been found at Cold Ash, but descriptions have not been published.

Collinson and Crane (1978) described numerous isolated *Rhododendron* seeds with very distinctive dissected terminal wings, which they made the basis of a new species, *Rhododendron newburyanum* (Figure 7.15). They are very similar to those of many living rhododendrons, especially those that grow as trees and shrubs in lowland forests. Associated with the seeds are leaves with a similar outline to some extant *Rhododendron* species but the venation is too poorly preserved to confirm their identity. Collinson and Crane suggested that the seeds may have been transported some distance from their parent plant. They appear to be the only recorded examples of Palaeogene *Rhododendron* from anywhere in the world.

Other common leaf fossils at Cold Ash are ***Platanus schimperi*** (Figure 7.16) and ***Lauraceaephyllum stenolobatus***. Although not described in detail in the published literature, Crane (1989a, fig. 12A) figured a drawing of what was claimed to be a fruitlet associated with the *Platanus* leaves. However, no evidence has been found here of the *Platanus*-like fruit-cluster ***Liquidambar paleocenica*** Chandler described from other localities in the Reading Beds (Chandler, 1961a).

Crane and Jarzembowski (1980) and Jarzembowski (1989) have described leaf mines from here. Although leaf mines and galls have been described from the Branskome Sand Formation at Bournemouth Cliffs (Scott *et al.*, 1994; Lang *et al.*, 1995) these were based only on museum collections, the sites having long been obscured by amenity and sea-defence work. Cold Ash is therefore the only available site at which insect and plant co-evolution can be documented from leaf trace fossils in the British Tertiary record.

Much work clearly remains to be done at Cold Ash, with only about a third of the flora having been described in detail. There is also potential for wider palaeoecological studies, building on the work on fungi (Smith and Crane, 1979) and leaf taphonomy (Crane and Jarzembowski, 1980). However, it is already clear that the flora is of great significance.

The Cold Ash flora is similar to the assemblages from other Reading Formation localities around Reading described by Chandler (1961a). However, except for Felpham (see GCR site report, this volume), this is the only place where there is still at least the potential to collect further material; the Pincent's Kiln exposures are unlikely to yield any quantities of new specimens. There is a some similarity at the family level with the Palaeocene–Eocene transitional interval floras of the Brito-Arctic Igneous Province, such as from Ardtun, although there are no species in common and the latter tends to have a greater diversity of ferns and conifers. This similarity may be partly a function of both the Cold Ash and Ardtun floras including a large proportion of riparian elements. However, it also holds true for many other circum-arctic floras of this age and so the similarity in the fossils may reflect a more fundamental similarity in the original vegetation.

The Eocene Thames Group, such as the London Clay at Sheppey (see GCR site report, this volume), yields quite a different flora to that at Cold Ash, including the remains of trees and shrubs of a more obvious tropical character. Significantly, there is no evidence in the Palaeocene–Eocene transitional floras of the mangroves that dominated the Ypresian vegetation of southern England (Collinson, 2000a). This difference cannot be explained merely by the London Clay being a marine deposit, whereas the Reading Formation is non-marine; the Poole Formation, which is a non-marine equivalent of the London Clay, also yields a markedly different flora from that found at Cold Ash (or Felpham). There appears to have been a real difference between the Reading Formation and London Clay vegetation in southern England, the latter being of a significantly more tropical aspect. There is evidence of a short-lived increase in atmospheric CO_2 at the Palaeocene–Eocene boundary, which may have elevated temperatures (Beerling and Jolley, 1998). This may have favoured the change from mixed-mesophytic to paratropical vegetation, with a distinctive flora characterizing the transitional interval (Collinson, 2000a).

Outside of Britain, the closest comparison with Cold Ash seems to be with sites in continental Europe such as Menat in France (Piton, 1940), which yield the remains of similar paratropical vegetation. As pointed out by Kvaček (1994), however, there are also elements (e.g. *Lauraceaephyllum*) that allow a comparison with the Tertiary floras of higher latitudes. According to Kvaček, the Reading Formation and Brito-Arctic Igneous Province floras are reflecting the migration of high-latitude elements into the paratropical forests of central Europe and are thus crucial for developing our understanding of the Tertiary vegetational history of Europe.

Conclusions

Cold Ash has yielded an internationally significant fossil flora from the Palaeocene–Eocene transition beds (Reading Formation) of southern Britain, dominated by plants related to the planes, caesalpinias, hazels, rhododendrons and walnuts, as well as the now rare katsura-tree family. It provides important insights into the vegetation that flourished here about 54 Ma ago and which seems to be less 'tropical' in nature than the succeeding London Clay vegetation, such as preserved at Sheppey. It is one of the few sites in Europe where it has proved possible to partly reconstruct some of the early Tertiary angiosperms and has provided important evidence as to the early evolution of flowering plants.

PINCENT'S KILN (SU 651 720)

Introduction

This small, disused quarry on the north-east side of Theale, Berkshire, is now in the grounds of a hypermarket but some exposure has been retained (Figures 7.17a and 7.18). It is one of the few sites where plant macrofossils can be collected from sandy and muddy sediment low in the Reading Formation of southern England. The site is of especial interest as it shows the relationship between the plant-bearing levels and the unconformity with the underlying Chalk.

There has been little published work on the palaeobotany of this site. Plant fossils were mentioned by Collinson *et al.* (1985) and a list of species was published by Crane and Goldring (1991), who also placed the plant-bearing levels in a stratigraphical context.

Description

Stratigraphy

The geology of the site has been described by Whitaker (1872), Blake (1903), Crane and Goldring (1991), and Daley (in Daley and Balson, 1999, p. 78). Approximately 4.5 m of Palaeogene deposits overlie Chalk (Figures 7.17 and 7.18), the contact being a planar unconformity with extensive burrowing (Figures 7.17b and 7.19). The basal 1 m of the Palaeogene strata here consists of glauconitic sands and pebbles of the Upnor Formation, which are interpreted as shallow marine. The Chalk is extensively burrowed by *Glyphichnus* Bromley and Goldring (1992), a probable crustacean burrow. The overlying Reading Formation (Figures 7.17 and 7.18) is mainly medium to coarse sands with some mudstone lenses. These upper beds cut down into the Upnor Formation and were deposited by a prograding fluvial system.

Palaeobotany

The Reading Formation here has yielded a range of plant fossils (Crane and Goldring, 1991), including the leaves *Lauraceaephyllum stenolobatus* Koch and *Platanus schimperi* (Heer) Saporta and Marion. An important but as yet undescribed fruit and seed flora occurs in sandy scours and fills. Crane and Goldring mention the fruit *Leguminosites gardneri* Chandler (= *Leguminocarpon gardneri* (Chandler) Herendeen and Crane, 1992) and seeds of *Vitis* sp. and an undetermined menispermacean. Collinson *et al.* (1985) described the lycophyte megaspores *Mineriporites mirabilis* (Miner) Potonié and *Erlansonisporites* sp. (Figure 7.20) from the sandy unit.

Interpretation

Pincent's Kiln is one of the very few places where plant macrofossils have been found at low levels in the Palaeocene–Eocene transition beds of southern Britain. Although collecting anything more than small specimens is now difficult, it is the only place where the plant-yielding horizons can still be seen in their stratigraphical context with the underlying Upnor Formation and Chalk. The sediments containing the fruits, seeds and megaspores are sandy scours and fills. It therefore complements the Cold Ash site, which has yielded a more diverse assemblage from silty-clay channel fills, and thus helps in the overall interpretation of the Palaeocene–Eocene transition vegetation of southern England.

The lycophyte megaspores *Erlansonisporites* (Figure 7.20) from here have been found to show iridescence comparable to that of precious opal (Hemsley *et al.*, 1994 and references quoted therein). This has led to the establishment of a model of self-assembly in biological systems

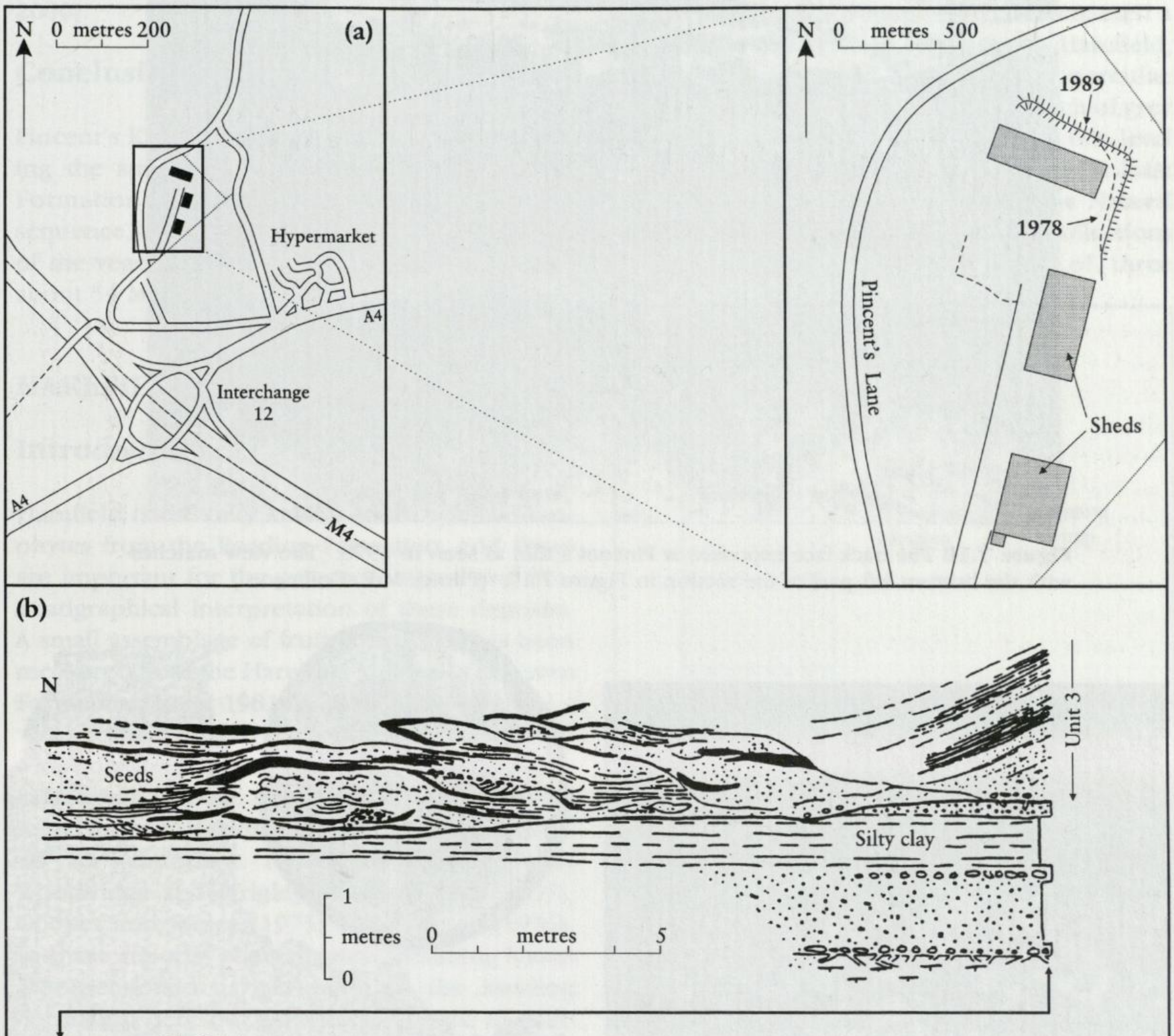

Figure 7.17 (a) Location and plan of Pincent's Kiln, with faces as at 1978 and 1989. (b) Face as exposed in 1978, with Palaeogene deposits lying unconformably on Chalk. Horizons indicated as marine are the Upnor Formation, non marine are the Reading Formation. (After Crane and Goldring, 1991.)

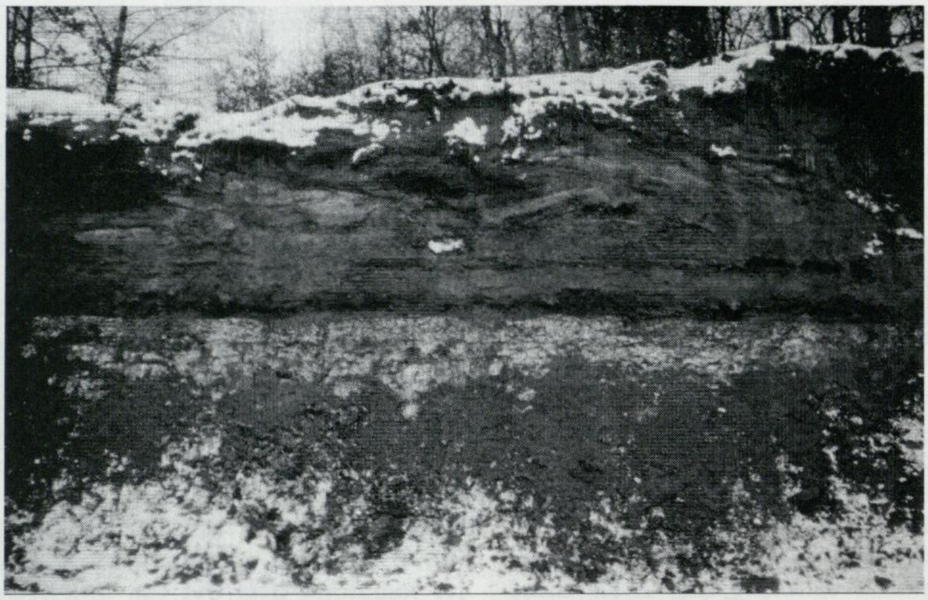

Figure 7.18 The back face exposure at Pincent's Kiln as seen in 1978. The view matches with the bottom left part of the section in Figure 7.17. (Photo: M.E. Collinson.)

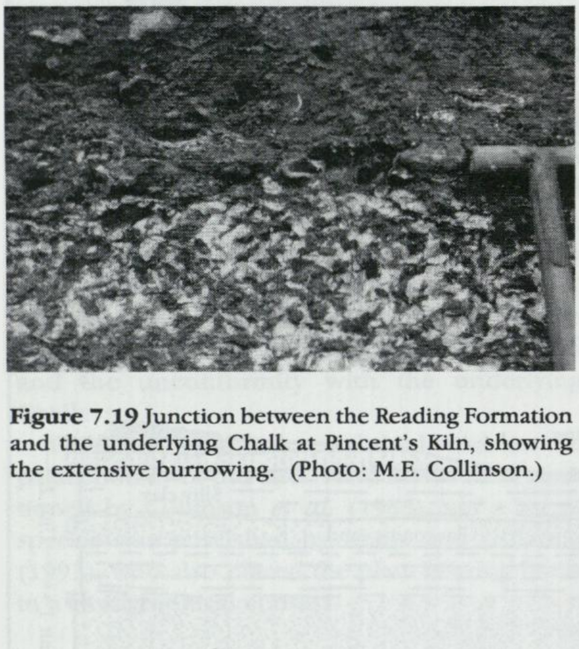

Figure 7.19 Junction between the Reading Formation and the underlying Chalk at Pincent's Kiln, showing the extensive burrowing. (Photo: M.E. Collinson.)

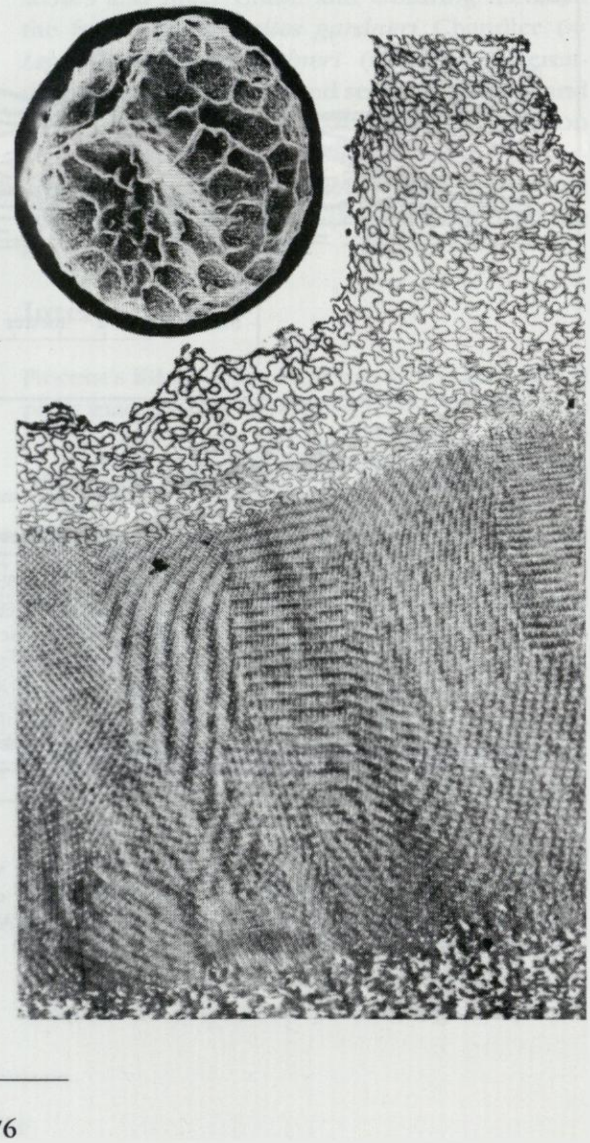

Figure 7.20 Megaspore of the lycophyte *Erlansonisporites*. The main picture is a Transmission Electron Microscope image of the wall structure showing a central layer with colloidal crystal-like organization, × 2520. The inset shows a Scanning Electron Microscope image of the whole spore, × 60. Observation of this spore has led to a major research project testing the hypothesis that spore wall organization can arise through self assembly (see Hemsley *et al.*, 1994, 1998, 2000). (Photo: M.E. Collinson.)

(Hemsley *et al.*, 1994), currently being investigated experimentally (Hemsley *et al.*, 1998, 2000).

Conclusions

Pincent's Kiln is the best available site for showing the stratigraphical context of the Reading Formation plant-bearing levels low in the sequence, and thus helps in the reconstruction of the vegetational habitats of southern Britain, about 54 Ma ago.

HAREFIELD (TQ 049 898)

Introduction

Harefield is the only known site to yield charophytes from the Reading Formation, and these are important for the palaeoecological and biostratigraphical interpretation of these deposits. A small assemblage of fruits and seeds has been recovered from the Harefield Member, Oldhaven Formation (King, 1981).

'Harefield Cement Works Pit' or 'Great Pit' is a well-known geological site, in which Palaeocene–Eocene Reading Formation can be seen lying unconformably on Chalk. It has yielded an abundant fauna as described by Wooldridge and Wrigley (1930), Curry (1957), Cooper and James (1975) and Cooper (1976). In these reports, plant remains including leaves are mentioned as occurring in the Reading Formation here but no descriptions or identifications are given. The only published palaeobotanical work is on the charophytes (Riveline, 1984a,b).

The overlying Harefield Member has yielded some fossil fruits and seeds similar to those found in the overlying London Clay (Reid and Chandler, 1933; Chandler, 1961a).

Description

Stratigraphy

Daley (in Daley and Balson, 1999) reviews the geology of this site. In summary, there is a thin development of Upnor Formation lying unconformably on chalk, which in turn is overlain by about 10 m of Reading Formation (Figure 7.21). The top of the section is the basal Thames Group.

Palaeobotany

Curry (1957) and Cooper (1976) documented a level within the Reading Formation at Harefield, containing bithyniid gastropod operculae together with leaves, in a lenticular patch of grey sandy-silty clay. Sieved residues from this level yielded about 30 charophytes, including at least three taxa (Collinson, pers. obs.). The Natural History Museum, London, has in its collections (V. 36337–9) about 15 specimens of three

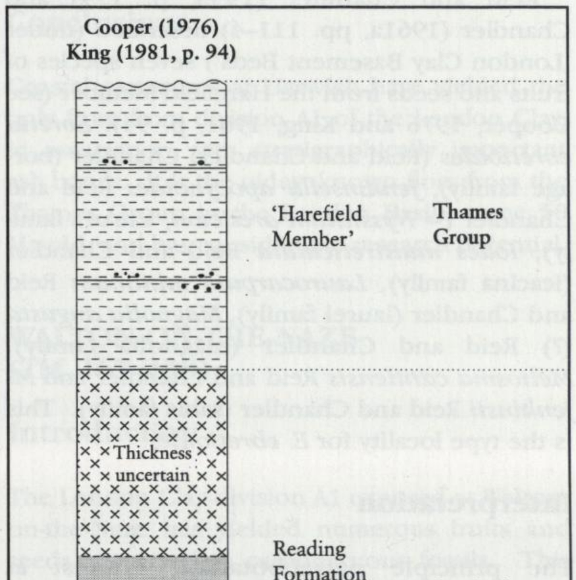

Figure 7.21 Stratigraphical succession at Harefield. (After Daley and Balson, 1999, fig. 4.2.)

charophyte taxa, collected and presented in 1958 by D. Curry. Curry (pers. comm., 1981) indicated that these specimens and others (four taxa) still in his collection originated from 0.3 m above the base of the Reading Formation. According to Curry, they have been tentatively identified as species of *Peckichara*, cf. *Tectochara* and *Harrisichara* by Grambast. The *Peckichara* (Figure 7.22) closely resembles *P. disermas* Grambast (Grambast, 1977; Collinson, pers. obs.; see also Riveline, 1984a,b).

Reid and Chandler (1933, p. 179) and Chandler (1961a, pp. 111–4) described (under 'London Clay Basement Beds') seven species of fruits and seeds from the Harefield Member (see Cooper, 1976 and King, 1981, p. 94): *Ehretia ehretioides* (Reid and Chandler) Chandler (borage family), *Jenkinsella apocynoides* Reid and Chandler (= *Nyssidium arcticum*, katsura family), *Iodes multireticulata* Reid and Chandler (icacina family), *Laurocarpum minimum* Reid and Chandler (laurel family), *Magnolia angusta* (?) Reid and Chandler (magnolia family), *Meliosma cantiensis* Reid and Chandler and *M. jenkinsii* Reid and Chandler (sabia family). This is the type locality for *E. ehretioides*.

Interpretation

The principle palaeobotanical interest at Harefield is that it is the only known locality to have yielded charophyte fossils from the Reading Formation (Curry, 1957; Riveline, 1984a,b; Collinson, pers. obs.). Charophytes (stoneworts) are a group of green algae with a fossil history extending back to the Silurian and are potential candidates for being ancestral to the vascular plants (Graham, 1985). However, the interest of these Palaeocene examples is that they are very sensitive palaeoenvironmental indicators, being mainly restricted to freshwater conditions (a few modern forms have been reported in high salinity conditions in the Baltic). They provide good evidence that the Reading Formation is non-marine, in contrast to the laterally equivalent marine Woolwich Formation. Hooker (1991) used the presence of similar charophyte remains in the Suffolk Pebble Bed as evidence that the latter (and its associated mammal fauna) was reworked from the Reading Formation. Hooker (1991, 1996, 1998) used the recognition of the *disermas* charophyte zone at Harefield as pivotal in the interpretation of the stratigraphy of the Palaeocene–Eocene transitional interval and for correlation with continental Europe.

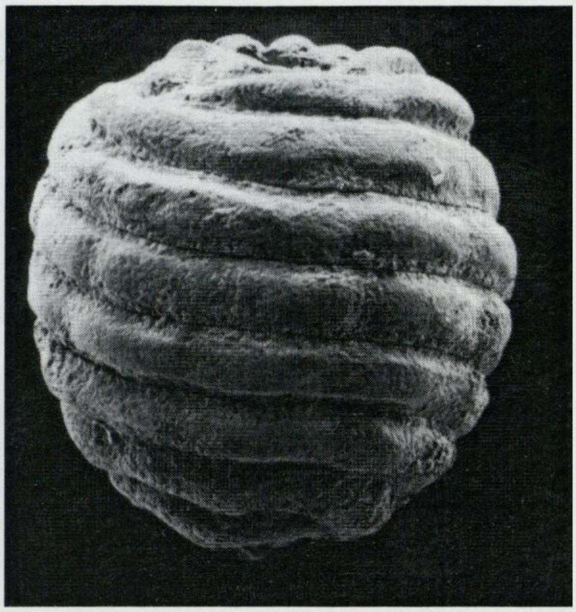

Figure 7.22 Gyrogonite of charophyte ?*Peckichara*, × 80 from the Reading Beds, Harefield. (Photo: M.E. Collinson.)

The Thames Group here has yielded a relatively poor fruit and seed flora. It is nevertheless of interest in being the only known site to yield such plant fossils (Chandler, 1961a) from the Harefield Member, which is more or less contemporaneous with, but in a different facies from, the Oldhaven Beds at Herne Bay and the A1 division of the London Clay at Walton-on-the-Naze and Harwich.

Conclusions

Harefield is the only British locality to yield remains of stoneworts (charophyte algae) from the Reading Formation, which is about 55 Ma old. They provide good evidence that the beds in which they occur formed under freshwater conditions. They are also critical for correlating these rocks with similar-aged deposits in continental Europe.

HARWICH (TM 263 320)

Introduction

The stretch of coast between Beacon Cliff and The Guard at Harwich, Essex, exposes plant-bearing deposits in division A1 of the London Clay Formation (King, 1981), yielding the stratigraphically oldest plant fossils from the Thames Group in the London Basin. There is no detailed published account of the flora here, the only records in the literature being by Elliott (1970), Brett (1972) and Collinson (1983b).

Description

Stratigraphy

Elliott (1970) has described the geology along this stretch of coast (see also Daley in Daley and Balson, 1999, p.61). The plant-bearing beds consist of clayey silts associated with ash bands. These ash bands allow the plant beds to be accurately positioned within the lowest division of the Thames Group (division A1 of the London Clay of King, 1981) and hence they fall in the Palaeocene–Eocene transitional interval (see 'Stratigraphical Background' earlier in this chapter). The plant fossils can be extracted from the plant bed when it is exposed. However, collecting is easier from loose material on the foreshore, which has been washed out of the plant bed.

Palaeobotany

Collinson (1983b) mentions that nine species have been found here, but only two were specifically named: *Platycarya richardsonii* (Bowerbank) Chandler (walnut family) and *Vitis magnisperma* Chandler (grape family). The fossils are mostly preserved as pyrite petrifactions. Chesters (reported by Elliott, 1970) also recorded the presence of possible examples of *Anonaspermum*, *Cinnamomum*, *Dunstania*, *Langtonia/Mastixia* and *Sapindospermum*, but the preservation was insufficient to establish species.

Brett (1972) described fossil wood from here as *Platanus*, which was very similar to the trunk wood of modern *Platanus*. Also described was possible root wood, under the name *Plataninium*.

Interpretation

The plant beds at Harwich are associated with volcanic ash bands that can be traced throughout the London Basin (Elliott, 1971). This allows them to be placed confidently in what King (1981) called the A1 division of the London Clay Formation.

The full list of species occurring here has yet to be published but the flora is similar to that of the overlying Eocene London Clay (Collinson, pers. obs.). In the absence of a full list of taxa found here, it is impossible to give a detailed comparative analysis for this site. However, its low stratigraphical position relative to the classic London Clay plant fossil sites makes it a site of considerable research potential.

Conclusions

Coastal exposures at Harwich have yielded the only flora from division A1 of the London Clay, in association with stratigraphically important ash bands. It is the oldest known flora from the Thames Group in the London Basin, some 50 Ma old, and has considerable research potential.

WALTON-ON-THE-NAZE (TM 267 238)

Introduction

The London Clay division A1 exposed at Walton-on-the-Naze has yielded numerous fruits and seeds preserved as carbonaceous fossils. This mode of preservation makes it easier to compare the fossils with other early Tertiary fruit and seed floras, and with the fruits of living plants. It is also important as one of the few places where bulk samples of a Palaeocene–Eocene plant bed with fruits and seeds can be collected from a cliff section.

The presence of fossil fruits and seeds here was first noted by Johnson (1901) in a local naturalists' journal. They appear to have been overlooked by Reid and Chandler (1933) in their classic work on the 'London Clay' plant fossils, but were noted by Chandler (1961a) in her first supplement to that monograph. George and Vincent (1977) also briefly mention them in a field guide to the area. Collinson (1983b) lists most of the species at that time known from here and figured several specimens.

Description

Stratigraphy

Davis and Elliott (1951), George and Vincent

(1977) and Daley (in Daley and Balson, 1999) have described the geology here. The plant bed here is within three to six metres of silty clays, which are exposed in the lower part of the cliff and the foreshore, underlying deposits of the Red Crag. The deposits are silty clay and were assigned by King (1981) to the uppermost A1 division of the London Clay, and hence fall in the Palaeocene–Eocene transitional interval (see 'Stratigraphical Background', earlier in this chapter).

Palaeobotany

In contrast to most London Clay Formation plant sites, the fruits and seeds here are preserved as carbonaceous fossils (Figure 7.23). Because of their mode of preservation, the fossils have not been concentrated on the beach by wave action (compare with the situation at Sheppey). The fossils must instead be carefully sifted from the mudstones and siltstones collected *in situ*. Collinson (quoted in George and Vincent, 1977) and Collinson (1983b) stated that 18 species are known from here, of which the following were listed:

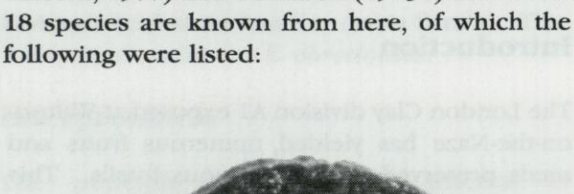

Figure 7.23 Endocarp of *Wardensheppeya davisii* (Menispermaeae) in carbonaceous preservation, × 38 (see Collinson, 1983b). Walton-on-the-Naze, London Clay Bed A1. (Photo: M.E. Collinson.)

Annonaceae
Anonaspermum commune Reid and Chandler
Cercidiphyllaceae
Nyssidium arcticum (Heer) Iljinskaja (= *Jenkinsella apocynoides*)
Cornaceae
?*Eomastixia* sp.
?Euphorbiaceae
Wetherelliia variabilis Bowerbank
Icacinaceae
Icacinicarya amygdaloidea Chandler
Iodes corniculata Reid and Chandler
Palaeophytocrene ambigua Reid and Chandler
Juglandaceae
Platycarya richardsonii (Bowerbank) Chandler
Lauraceae
Cinnamomum sp.
?*Litsea bournensis* Bandulska
Menispermaceae
?*Palaeococculus lakensis* Chandler
Tinospora excavata Reid and Chandler
Wardensheppeya davisii (Chandler) Eyde
Rutaceae
Rutaspermum spp.
Sapindaceae
?*Sapindospermum* sp.
Staphyleaceae
Tapiscia pusilla (Reid and Chandler) Mai
Symplocaceae
?*Durania* sp.
Vitaceae
Vitis pygmaea Chandler

See Table 8.1 for references to nomenclatural revisions.

Interpretation

Far fewer species have been reported from here compared with the more classic, slightly younger, Ypresian plant sites such as Herne Bay and Bognor. This is probably because the site has only recently been investigated and because the fossils have to be sifted from the mudstones and siltstones obtained from the in-situ plant bed, making it difficult to obtain the sorts of quantities that can be obtained where the fossils have been concentrated by the action of the sea. The general balance of the reported assemblage agrees with that normally found in the slightly younger London Clay sites with a predominance of 'tropical' elements, such as species of the custard apple, icacina, mastic trees of the dogwood family, moonseed and soapberry families, together with some taxa indicating cooler conditions, such as species of the walnut family.

What makes Walton-on-the-Naze palaeobotanically important is the preservation of the fossils. Ypresian fruits and seeds of the London Basin are normally preserved as pyrite petrifactions. This mode of preservation has many benefits for the palaeobotanist, not least that the fossils often preserve internal cellular detail, especially of the softer, pulpy tissue (Chandler, 1978; Wilkinson, 1983). As pointed out by Collinson (1983b), however, it also presents the palaeobotanist with some difficulties. The permineralizing fluids might produce only a partial replacement of the fruit, showing what appear to be quite different features from a fossil representing a complete fruit. The analogy given by Collinson (1983b) is what would happen if an orange were to be petrified by pyrite: the fossil might be a cast of the whole orange, a cast of the inside of the skin (i.e. a cast whose outer surface looks like the inside of the skin), a cast of the orange minus the skin showing the segments, a cast of the cavity in the fruit where the seed was positioned, or a cast of the seed itself. Furthermore, a particular fossil might show more than one type of preservation, such as a cast of the whole orange, but with part of the skin removed. This is easy to interpret in the case of an orange, where we have prior knowledge of what we are looking at. However, in the case of extinct taxa where we only have the fruit, things are not so easy. The permineralization can also sometimes distort the cells, making the anatomy and sometimes even the morphology difficult to interpret (Chandler, 1978).

These problems can be partially overcome by the study of carbonaceous fossils, where there has been little or no pyrite replacement. Walton-on-the-Naze is the best available site for London Clay carbonaceous fruits and seeds in the London Basin. They are obviously not so robust as their pyritized counterparts and they fragment more easily. Some of the internal cellular detail may also be lost, but these fossils will often demonstrate the gross morphology of the fruit or seed far more clearly than their pyritized counterparts, enabling more straightforward comparisons both with living relatives and fruits and seeds from other formations. By studying these carbonaceous fossils in tandem with the pyritized petrifactions, a far more complete understanding can be obtained of the London Basin flora, especially of the fruits and seeds.

Conclusions

Walton-on-the-Naze is the best site for carbonaceous fossils of fruits and seeds from the uppermost part of the Palaeocene–Eocene transitional interval of the London Basin. The preservation of these fossils complements the better-known pyrite petrifactions in younger strata and provides an insight into the early stages of development of the 50 Ma old paratropical rain forest of Early and Middle Eocene times.

ARDTUN (NM 381 248)

Introduction

Ardtun, on the Isle of Mull in the Hebrides, is the only significant Tertiary palaeobotanical site in Scotland. It is the only site in Great Britain to yield Palaeogene plant macrofossils representing the Brito-Arctic Igneous Province. It provides a significant insight into the early Tertiary vegetation of the high northern latitudes and their relationship to the vegetation found further south in Europe.

A full account of the history of research here is given by Boulter and Kvaček (1989). The fossils were first discovered in the mid-19th century and were briefly described by Forbes in Argyll (1851). Gardner and Ettingshausen (1879–1882) and Gardner (1883–1886a) included material from here in their aborted series of monographs on the 'Eocene' floras of Britain, and Gardner (1887a) also undertook some additional collecting here, using explosives to remove the basalt overlying the plant bed.

The next major period of interest in the Ardtun flora was in the mid-20th century, which resulted in a number of short papers (Seward and Holtum, 1924; Johnson, 1935, 1937), plus an uncompleted monograph by Seward and Edwards. The latter was eventually incorporated into the only published full monograph on the Ardtun flora, which also contained palynological results on the Tertiary sediments exposed here (Boulter and Kvaček, 1989). In recent years, there has also been work on material from here by Crane (1988), Crane *et al.* (1988) and Jolley (1997).

Description

Stratigraphy

Details of the geology here can be found in Emeleus and Gyopari (1992). A thin succession of sedimentary rock occurs between two layers of basalt (Figure 7.24). The siliciclastics are mainly coarse grained, but there are three beds of silty sandstone and clay, which have yielded the plant fossils.

Palaeobotany

The plant fossils of the Ardtun plant bed are mainly adpressions, occasionally preserving cuticles. Foliage is predominant although some reproductive structures also occur. The following are the major taxa of macrofossils described by Boulter and Kvaček (1989):

Equisetaceae
Equisetum sp.
Dryopteridaceae
Onoclea hebridica (Forbes) Gardner and Ettingshausen
Ginkgoaceae
Ginkgo gardneri Florin
Taxodiaceae
Metasequoia occidentalis (Newberry) Chaney
Elatocladus campbellii (Forbes) Seward and Holttum
Glyptostrobus dunoyeri (Baily) Boulter and Kvaček
Cupressaceae
Cupressoconus machenryi (Baily) Boulter and Kvaček
Taxaceae
Amentotaxus gladifolia (Ludwig) Ferguson *et al.*

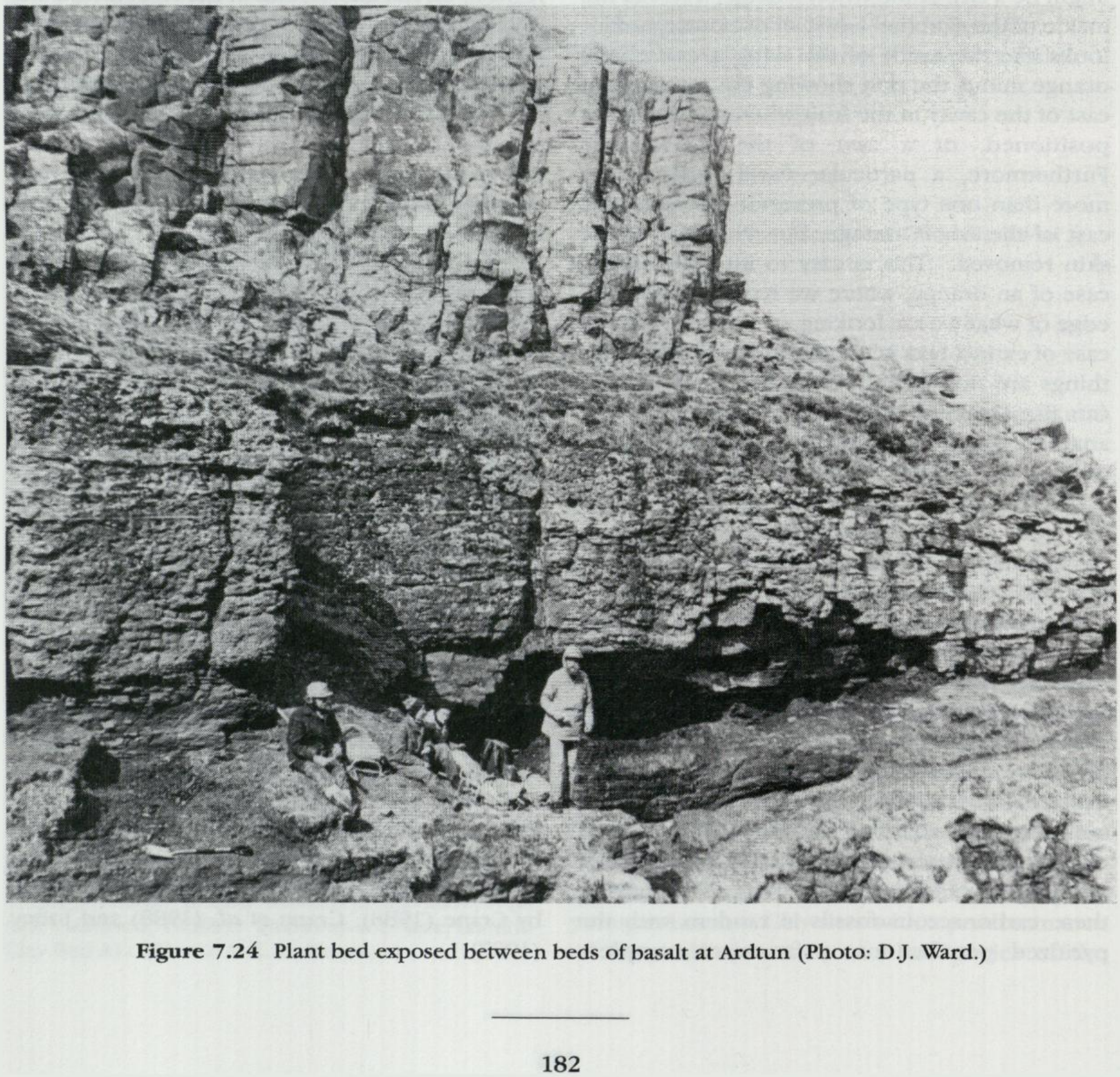

Figure 7.24 Plant bed exposed between beds of basalt at Ardtun (Photo: D.J. Ward.)

Platanaceae
Platanites hebridicus Forbes
Cercidiphyllales (incertae familiaris)
Trochodendroides antiqua (Gardner) Boulter and Kvaček
Fagales (*incertae familiaris*)
Corylites hebridicus Seward and Holttum
Fagopsiphyllum groenlandica (Heer) Manchester, 1999, p. 522
Juglandales (incertae familiaris)
Juglandiphyllites ardtunensis Boulter and Kvaček
J. finlayi (Johnson) Boulter and Kvaček
Hamamelididae (incertae familiaris)
Camptodromites major (Johnson) Boulter and Kvaček
C. multinervatus (Johnson) Boulter and Kvaček
Davidoidea hebridica Johnson
D. hebridica (Seward and Holttum) Boulter and Kvaček
?Rhamnales (incertae familiaris)
Vitiphyllum sewardii Boulter and Kvaček
Dicotyledonae (incertae ordnis)
Zizyphoides ardtunensis Johnson
Cornophyllum hebridicum (Johnson) Boulter and Kvaček
Calycites ardtunensis Crane

In addition to these vascular plants, Boulter and Kvaček (1989) describe some bryophyte remains from here, while Edwards (1922) had described fungal remains.

Boulter and Kvaček (1989) interpret the lower of the three plant beds (the Black Leaf Bed of Gardner, 1883–1886a, 1887a) as representing non-swampy riparian forest dominated by *Corylites* and *Trochodendroides*. The middle plant bed is, in contrast, dominated by taxodiaceous remains plus *Platanites* and *Camptodromites*, and was interpreted as representing a taxodiaceous swamp forest. No palaeoecological interpretation was given of the top leaf bed.

Interpretation

Ardtun is one of the 'classic' leaf floras from the Palaeocene–Eocene transition interval (Wolfe, 1997). It was formed in the Brito-Arctic Igneous Province (BIP), a belt of Palaeogene igneous rocks and intra-basaltic sediments that extends from Rockall to Spitsbergen, and which resulted from the initiation of the North Atlantic Ocean (Wenk, 1961). Several sites within the province have yielded plant fossils, but Ardtun is in many ways the most important (Boulter and Kvaček, 1989). It is the only British site to yield this important fossil flora. In Northern Ireland, similar floras are known from County Antrim, most notably Ballypalady and Glenarm (reviewed by Watts, 1970). These Irish sites are particularly important for conifers (especially reproductive structures) but do not yield the diversity of angiosperms as found at Ardtun.

Outside of Britain, plant macrofossils are known from eastern Greenland (Mathiesen, 1932; Seward and Edwards, 1941) and the Faeroes (Rasmussen and Koch, 1963), but these floras are generally poorly preserved and much less diverse than the Ardtun flora. The only known flora that matches that of Ardtun in diversity is from Spitsbergen (Schloemer-Jäger, 1958; Schweitzer, 1974, 1980; Budantsev, 1983; Kvaček and Manum, 1993). Spitsbergen has yielded 13 species of conifers and angiosperms, all but two (*Macclintockia dentata* Heer and *Haemanthophyllum nordenskioldii* (Heer) Boulter and Kvaček) also occurring at Ardtun (Boulter and Kvaček, 1989). However, the balance of the Spitsbergen flora is quite different, being dominated by *Metasequoia* and *Trochodendroides* that were growing in swamp forests, and quite different from the mainly riparian vegetation preserved at Mull. Spitsbergen has also yielded more ferns, with five species having been recorded based on macrofossils, three of which are unknown from the other BIP sites (*Osmunda macrophylla* Penhallow, *Coniopteris blomstrandii* (Heer) Kvaček and Manum, cf. *Dryopteris alaskana* (Hollick) Wolfe), although they are common in other circum-Arctic floras. The ferns from Ardtun, Spitsbergen and the other localities have been recognized as representing a biogeographically distinct Circum-Arctic Palaeocene–Eocene floristic group extending to high northern palaeolatitudes (Collinson, in press a).

The Ardtun flora differs from the similar-aged Reading Formation floras of southern Britain in being dominated by deciduous species of both conifers and the Hamamelidae. This may partly reflect the more northern latitudes of the BIP, and it is notable that most of the families found at Ardtun also occur in the high-latitude Cretaceous and early Tertiary floras of Alaska and northern Canada (Hickey *et al*., 1983; Spicer *et al*., 1987). However, these high-latitude floras do not represent cold-climate vegetation, but rather temperate (or even warm-temperate) vegetation, reflecting the generally warmer conditions that prevailed during very early Tertiary times. A more significant factor was probably that the BIP was an area of active volcanicity, producing highly disturbed habitats with poor soils and uneven water supply (Boulter and Kvaček, 1989).

The BIP and its flora have a crucial role in understanding the early Tertiary floristic development of Europe (Boulter and Kvaček, 1989; Kvaček, 1994). It acted as a selective filter to plants between the Boreal and Tethyan Palaeoareas, only allowing through those species that could tolerate its volcanically influenced habitats. Later in the Tertiary, the filter became a more complete barrier as the Atlantic opened up and prevented the spread of most plants with seeds as their disseminules. It is thus clear that the Ardtun flora has a key role in understanding the complex vegetational mosaic in the Tertiary deposits of Europe.

Of the individual species of plant macrofossils, only two have been subjected to detailed morphological description. Crane (1988) investigated some small fruits originally assigned to the living genus *Abelia* by Seward and Edwards in their unpublished manuscript. However, Crane showed that they were unlikely to belong to that genus and instead placed them in the artificial form-genus *Calycites*, of unknown angiospermous affinities.

Crane *et al*. (1988) reconstructed the entire leaf of *Platanites*, including the basal pair of leaflets crucial to the identification of this extinct genus. They also found associated fruits and infructescences. These are very similar to the reproductive organs of one of the living *Platanus* species and provided the first unequivocal evidence of an early member of the Platanaceae with pinnately compound leaves. This is essential for understanding the early evolution of this family, and of the possible relationship between the Hamamelidae and the Rosidae.

Conclusions

Ardtun is a classic Tertiary palaeobotanical locality, yielding plant fossils representing the warm-temperate vegetation of about 54 Ma ago (transition interval between the Palaeocene Series and Eocene Series). It is unique in Britain. Only in Spitsbergen has a comparable fossil flora been reported, but the Ardtun assemblage is generally more diverse, especially in conifers and flowering plants. It represents mainly deciduous trees growing in a disturbed volcanic terrain, and is crucial for understanding plant migration and the floristic evolution of Europe during early Palaeogene times.