Mesozoic and Tertiary Palaeobotany of Great Britain

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Chapter 8

Early and early middle Eocene (Ypresian–Lutetian) Palaeobotany of Great Britain

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INTRODUCTION

The early and middle part of the Eocene Epoch included a thermal maximum and prolonged warmth ('greenhouse world') when vegetation across southern England was similar to modern tropical rain forests bordered by a coastal *Nypa*-dominated mangrove (Figure 8.1; Collinson, 1996b, 2000 a,b). These floras are represented in the London Clay Formation and associated deposits, the Poole Formation (traditionally known as the 'Dorset Pipe Clay') and the Bracklesham Group, and are among the best-known early Tertiary floras in the world. The apparent presence of a 'tropical rain forest' in Britain, combined with the abundance of the fossils at coastal exposures, has meant that sites such as Sheppey have attracted collectors since at least the 18th century. The Poole Formation and Bracklesham Group sites have not yielded such diverse assemblages and have not therefore been as extensively studied. However, they represent different sedimentary facies to the London Clay and thus complement the fossil floras found in the latter deposits.

HISTORY OF RESEARCH

Plant fossils have been noticed in the London Clay for over 300 years, especially in coastal exposures such as Sheppey, where the large *Nypa* fruits are difficult to ignore. The early research on the London Clay floras was very much concentrated at Sheppey and an outline of the work is given in the introduction to that site report later in this chapter (see also Reid and Chandler, 1933; Chandler, 1961a; Andrews, 1980). The first extensive study was by Reid and Chandler (1933), who described nearly 300 species, mainly from Sheppey, and placed the London Clay firmly on the palaeobotanical map. Additions to this work were made by Chandler (1961a, 1964, 1978) and an identification guide to the fossils has been prepared by Collinson (1983b). The 'twig' floras have been reviewed and studied by Wilkinson (1981, 1984, 1988) and Poole (1992, 1993a,b).

Being so near to large centres of population and having such extensive coastal exposure, it is not surprising that the London Clay attracted considerable attention from collectors, especially after Reid and Chandler (1933) had drawn attention to the diversity of the floras that it contains. For instance, a local collector, D.J. Jenkins, was largely responsible for uncovering the palaeobotanical interest at Herne Bay. Another local collector, E.M. Venables, discovered the plant beds at Bognor. In more recent years, the Tertiary Research Group has focused much of the attention on the London Clay palaeobotany and their journal (*Tertiary Times*, later renamed *Tertiary Research*) has contained

Figure 8.1 Modern *Nypa* mangrove, Kapuas delta, Kalimantan, Indonesia. (Photo: M.E. Collinson.)

many useful papers on the subject. In most cases, the fossils found by these collectors have found their way into museums and have been incorporated into the body of knowledge on the early Eocene vegetation of southern Britain, as presented by Chandler (1961a, 1964) and Collinson (1983b), among others.

In the eastern Hampshire Basin, the London Clay is succeeded by the Bracklesham Group. Dixon (1850) first reported the presence of plant fossils in these beds and Carruthers (in Dixon, 1878) published a summary of the flora. Gardner (1884), Rendle (1894) and Reid (1897) described individual specimens from these deposits and Chandler (1961b) reviewed the then-available information. The most recent account has been by Collinson (1996b), who described new material from Bracklesham, documented the stratigraphical distribution of the different species, and reconstructed the vegetation and palaeoecology.

The Poole Formation (traditionally referred to as the 'Dorset Pipe Clays') in the western part of the Hampshire Basin is a fluviatile succession that is at least partly time-equivalent to the Bracklesham Group. Sites such as Studland and Corfe yielded numerous leaf fossils, such as the well-known remains of the fan-palm named *Trachycarpus* (Brodie, 1853; Gardner, 1877, 1886a; Gardner and von Ettingshausen, 1879; Chandler, 1962). The Alum Bay plant beds on the Isle of Wight also attracted some attention (see La Harpe and Salter (in Bristow, 1862), Gardner (in Reid and Strahan, 1889) and Crane, 1977, 1978). The less obvious fruit and seed flora, first discovered in the Poole Formation in the 1930s, has proved to be of considerable scientific interest, providing a complement to the London Clay flora (Chandler, 1962; Collinson, 1996b). Fragmentary fern fossils have also attracted some interest (Chandler, 1955; Collinson, 1996a, in press a).

PALAEOGEOGRAPHICAL SETTING

The palaeogeography of early Eocene times was generally similar to that of the Palaeocene (Figure 8.2). The most notable difference in the region near the British Isles is the separation of Greenland from Europe, which broke the land connection between Europe and North America that allowed plant migration.

Much of south-eastern England was under shallow sea during early Eocene times, which resulted in the deposition of the Thames and Bracklesham Groups (Figure 8.3). Lower

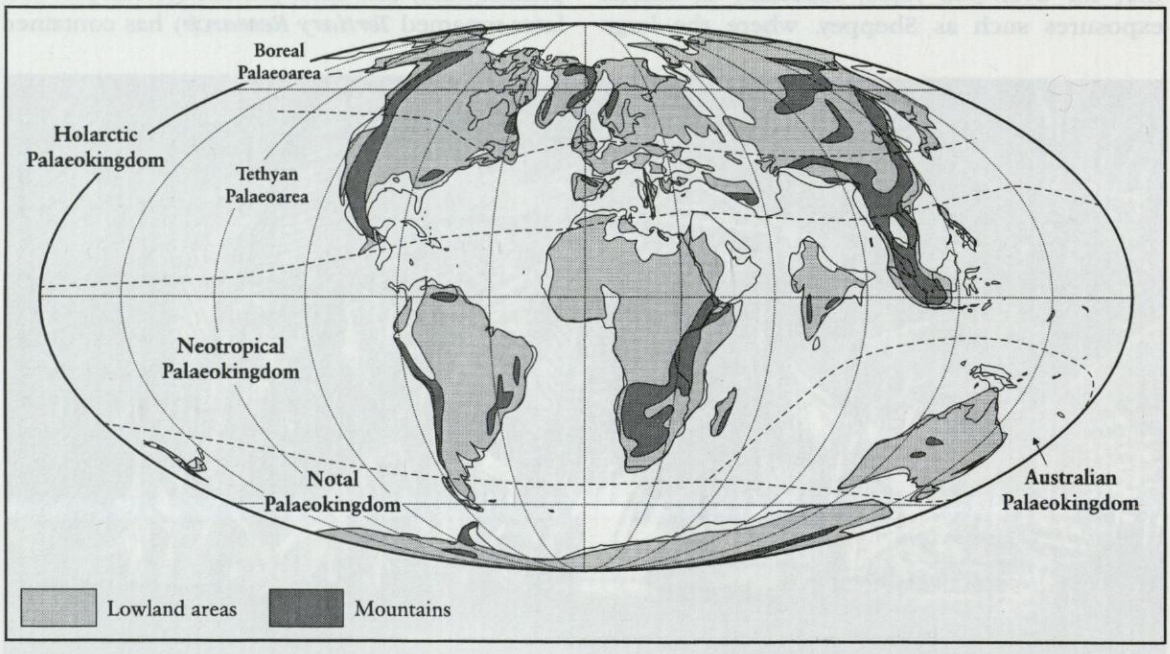

Figure 8.2 Palaeogeography of the Early Eocene world, showing main areas of land and mountains. Based on Smith *et al.*, 1994. Also shown are the main palaeofloristic areas, based on Akhmetyev (1987).

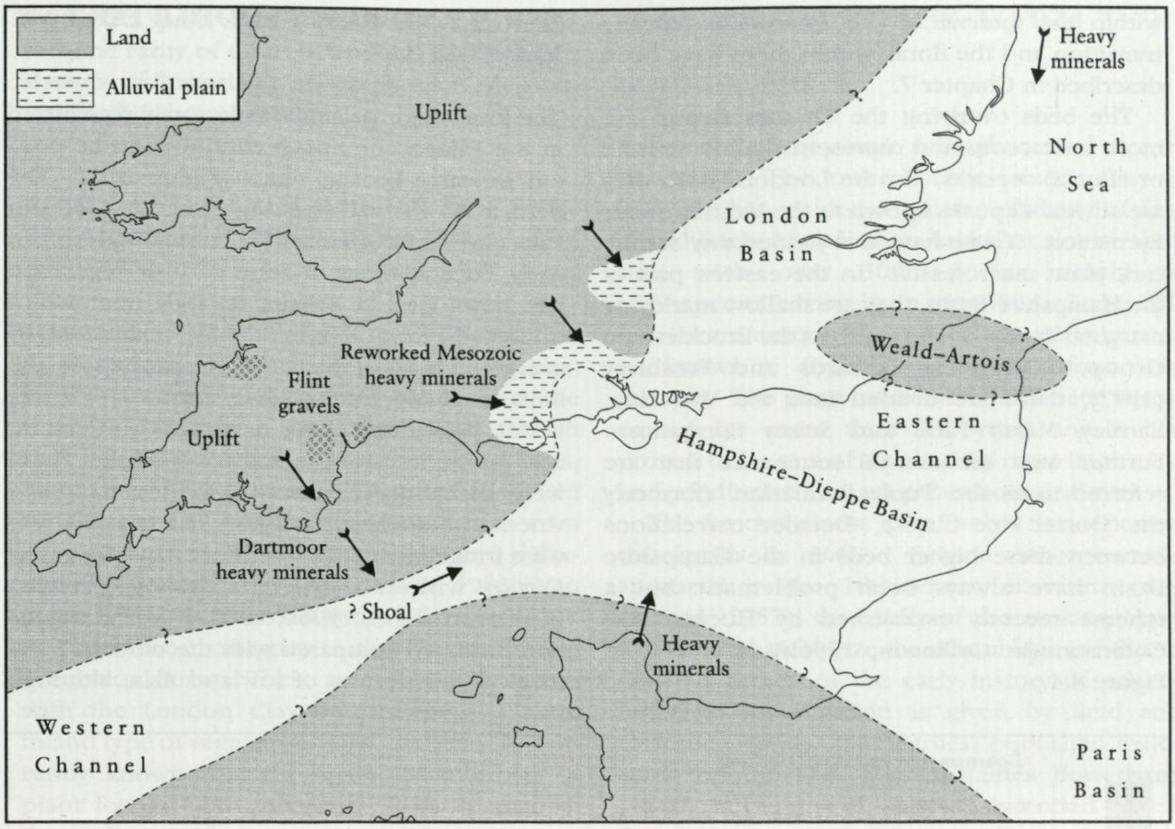

Figure 8.3 Palaeogeography of southern England during early Eocene times. (After Murray, 1992.)

Eocene deposits mainly occur in two areas known as the 'London Basin' and '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, north-east France, and south-east England (Figure 8.3). It was mainly a shallow marine basin with mainly mud deposition, but with alluvial-plain deposits forming on the western margins, the latter represented by the Poole Formation.

STRATIGRAPHICAL BACKGROUND

There has been much disagreement about the lithostratigraphical classification and correlation of these deposits in southern England, at least partly because of the difficulties in relating the marine and non-marine sequences that occur in different parts of the area. Terms such as the 'London Clay', 'Bracklesham Beds' and 'Dorset Pipe Clay' have been widely used in the literature, but often with very loose definitions.

The most comprehensive revision of the London Clay part of the sequence was by King (1981), who attempted detailed correlations of the sequences in different parts of south-eastern England. He referred to all of the London Clay (*sensu lato*) as the Thames Group. Below the classic London Clay sequences are more sandy beds sometimes referred to as the Basement Beds, which were formally identified as the Oldhaven Formation. The London Clay proper was divided into five informal divisions, termed 'A' to 'E', with divisions 'A' and 'B' being further subdivided into two and three subunits, respectively. He also recognized members within his London Clay Formation, defined on local developments of distinctive facies. However, the informal divisions were defined by discontinuities within the sequence, which he claimed to be able to recognize throughout most of south-eastern England, and these have tended to be most widely used by subsequent authors. The only significant alteration to King's scheme has been by Ellison *et al*. (1994), who combined the Oldhaven Formation and King's A1 subdivision to form the Harwich Formation. These strata fall within the interval of the Palaeocene–Eocene transition and the floras within them have been described in Chapter 7.

The beds overlying the Thames Group are more arenaceous and represent shallow marine or alluvial deposits. In the London Basin they are alluvial deposits known as the Virginia Water Formation. These have not yielded any significant plant macrofossils. In the eastern part of the Hampshire Basin, they are shallow marine or marginal deposits referred to as the Bracklesham Group. Following Edwards and Freshney (1987), these are divided into the Wittering, Earnley, Marsh Farm and Selsey Formations. Further west are alluvial sequences that are referred to as the 'Poole Formation' (formerly the 'Dorset Pipe Clays'). Detailed correlations between these higher beds in the Hampshire Basin have always been problematic but a scheme recently established by Hooker and Collinson (in Collinson, 1996b) is shown in Figure 8.4.

EARLY AND EARLY MIDDLE EOCENE VEGETATION

The four major palaeofloristic zones recognized in the Palaeocene Epoch continued to be present in early Eocene times (Figure 8.2). The British floras all belong to the Tethyan Palaeoarea of the Holarctic Palaeokingdom. In early Eocene times, a zone of lush vegetation had developed in Britain, strongly reminiscent of today's tropical rain forests, dominated by evergreen trees of the sumac, custard apple, dillenia, dogbane, frankincense, flacourtia, icacina, laurel, palm, sabia, soap berry and tea families, and mastic trees of the dogwood family. There were also abundant lianas of the icacina, grape vine and moonseed families. The coastal areas were fringed by dense stands of mangrove palms (*Nypa*) with rare true mangroves (*Ceriops*) (Collinson, 1993, 1996b, 2000a,b). The vegetation has been compared with the modern paratropical rain forests of lowland Asia, although

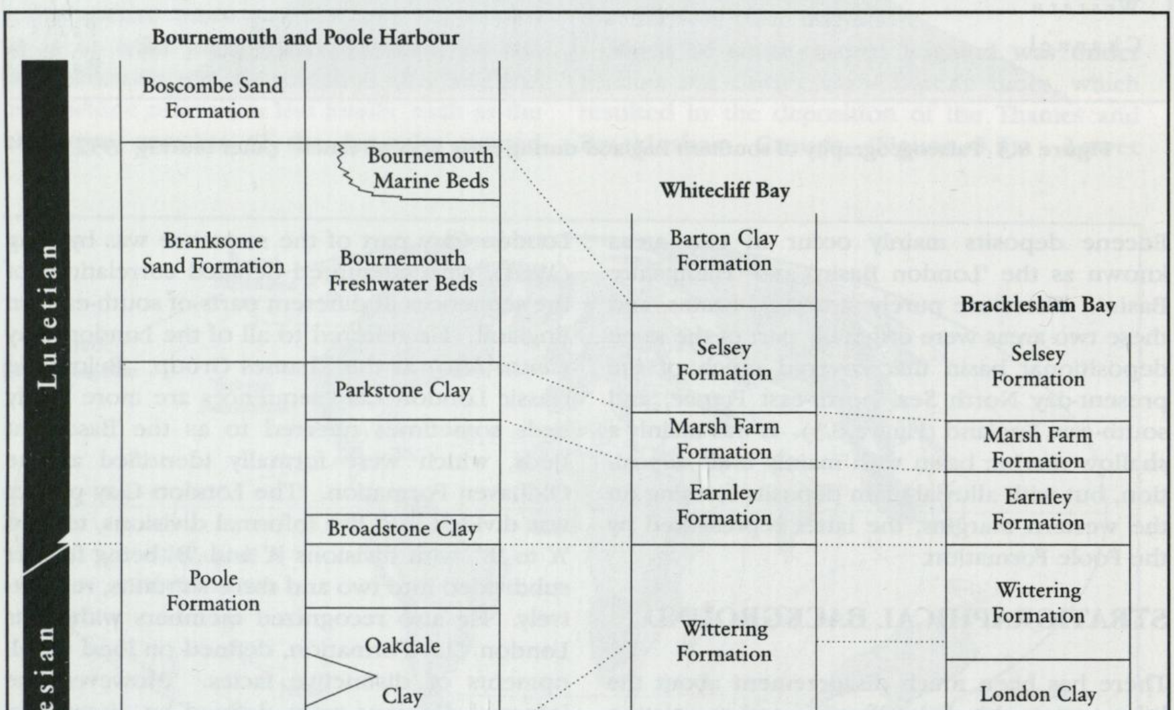

Figure 8.4 Correlation of the Bracklesham Group and Poole Formation in the Hampshire Basin. (After Hooker and Collinson, in Collinson, 1996b.)

there are some clear differences, such as the extreme rarity of dipterocarps and the apparent absence of flowering plant epiphytes (Collinson, 1983b, 2000b, in press b).

EARLY AND EARLY MIDDLE EOCENE PALAEOBOTANICAL SITES IN BRITAIN

These palaeobotanical sites can be divided into three categories. The first group yields the classic Tethyan floras of division A2 and above of the London Clay. There are four principal Britiish sites that have this flora, Sheppey, Bognor Regis, Herne Bay and Wrabness. Although all four yield broadly similar assemblages, each has its own particular strengths and each occurs at a different stratigraphical level (Collinson, 1983b), so that all must be included in the GCR network.

The second category is sites for the Poole Formation floras. These are contemporaneous with the London Clay but represent a more inland type of vegetation. Only two sites are currently known to yield significant numbers of plant fossils, Lake and Arne. Because each of these sites yields a somewhat different assemblage, they have both been selected for inclusion in the GCR network.

In the Bracklesham Group, the only place to have yielded any quantity of plant macrofossils is Bracklesham Bay, which has therefore been selected as a GCR site. Whitecliff Bay has yielded some plant macrofossils, as well as making a major contribution to the palynological record. Normally, sites with dominant palynological interest are not included within the relevant GCR palaeobotany network, but the palynological evidence from Whitecliff Bay is so important for enhancing the understanding of vegetational change in the Eocene Epoch of Britain, that an exception has been made. Other palaeobotanical sites in the Bracklesham Group, such as those mentioned by Collinson (1996b), have yet to be studied in detail and some were temporary exposures.

The historically important site of Bournemouth Cliffs (Daley in Daley and Balson, 1999) is no longer accessible (Collinson, pers. obs.). The palaeobotanical interest (using museum collections) was summarized by Collinson (1996b, p. 195) and McElwain (1998) used leaves to deduce elevated CO_2 levels during the Eocene 'greenhouse world'.

SHEPPEY (TQ 955 738–TQ 024 717)

Introduction

This is one of the classic palaeobotanical sites in the world. The lower Eocene London Clay at Sheppey has yielded a greater diversity of fossilized Eocene seeds than any other similar-aged site, with over 300 species mainly of angiosperms having been identified. Some 200 species are unique to this locality and 35 genera are known in fossil form in Britain from only this site. The plant fossils here have been investigated for more than 300 years and it has proved to be one of the world's most important and productive Tertiary palaeobotanical sites.

The famous diarist John Evelyn first reported the fossils in 1668. Several other records appeared in the 18th-century literature (e.g. Parsons, 1757), especially of the striking *Nypa* fruits that characterize the assemblage (a full and detailed review of the early history of palaeobotanical investigation is given by Reid and Chandler, 1933). The earliest published major study on the flora was by James Bowerbank (1840), in the first of what was intended to be a five-part monograph (the other four parts were never published). He described 103 species from Sheppey and, although many of these taxa have been subsequently synonymized, it was the first publication that gave a true impression of the diversity of the flora. Bowerbank described how many specimens were collected by locals, who scoured the beach for pyrite and selected out any fossils for sale to tourists, who came here by boat from London (see also Thomas, 1977).

The site was visited during the 1870s by the Austrian palaeobotanist, Constantin von Ettingshausen, who shortly after started to collaborate with the British palaeobotanist Starkey Gardner on a monograph of the Sheppey flora. Unfortunately, however, the collaboration was marred by personal disagreements, and in the end only the first volume was published, dealing with the ferns (Gardner and von Ettingshausen, 1879–1882). Gardner (1883–1886a) on his own later produced a monograph on the conifers of Sheppey, but the angiosperms, which form by far the largest part of the assemblage, did not receive a comprehensive analysis until the work by Eleanor Reid and Marjorie Chandler. Their classic 1933 monograph describes 289 angiosperm and 5 conifer species, based mainly

Figure 8.5 Cliffs and foreshore at Sheppey, as seen looking west from Warden Point. (Photo: M.E. Collinson.)

on seeds and fruits; fossil wood was noted as occurring at Sheppey, but was regarded as lying outside of the scope of their already enormous work. Supplements to this work were published by Chandler (1961a, 1964, 1978), in which a further 62 angiosperm species and one conifer species are described, together with some fragmentary fern and lycopsid remains. Chandler (1964) made a detailed comparative analysis of the flora and placed it in the wider context of other contemporary floras. The most recent documentation of the main taxa in this flora is by Margaret Collinson (1983b). Other studies include those by Tralau (1964), Brett (1972), Collinson and Ribbins (1977), Ribbins and Collinson (1978), Wilkinson (1981, 1983, 1984, 1988), Manchester (1988), Crawley (1989, in press), Collinson (1993), Poole (1992, 1993a,b, 1996, 2000) Poole and Wilkinson (1992, 1999, 2000), and Poole and Page (2000).

Description

Stratigraphy

Davis (1936), Holmes (1981) and King (1984) have described the geology at Sheppey. The exposed strata (Figure 8.5) belong to the upper part of the London Clay Formation (divisions C to E in the classification of King, 1981, 1984), and are thus Ypresian in age (Figure 8.6). They are low-energy marine shelf deposits, containing marine invertebrates and fishes, as well as the plants and insect remains that were washed in from neighbouring land. According to Collinson (1983b), this land was probably at least 80 km away.

The clay cliffs here can be very dangerous, and it is easy to sink up to the waist if care is not taken. Reid and Chandler (1933) claimed never to have seen fossils *in situ*, but an extensive search by Davis (1936) eventually revealed plant remains in the clay (e.g. Figure 8.11). The plant fossils are most easily found loose on the foreshore (Figure 8.7), having been washed out of the clay by the action of the waves. This action by the waves can cause some damage to the fossils, but has the advantage of concentrating them on the foreshore. This is a key factor in making Sheppey an important site as it makes collecting the fossils so much easier than many other sites. At the Clarno Nut Bed (Oregon, USA;

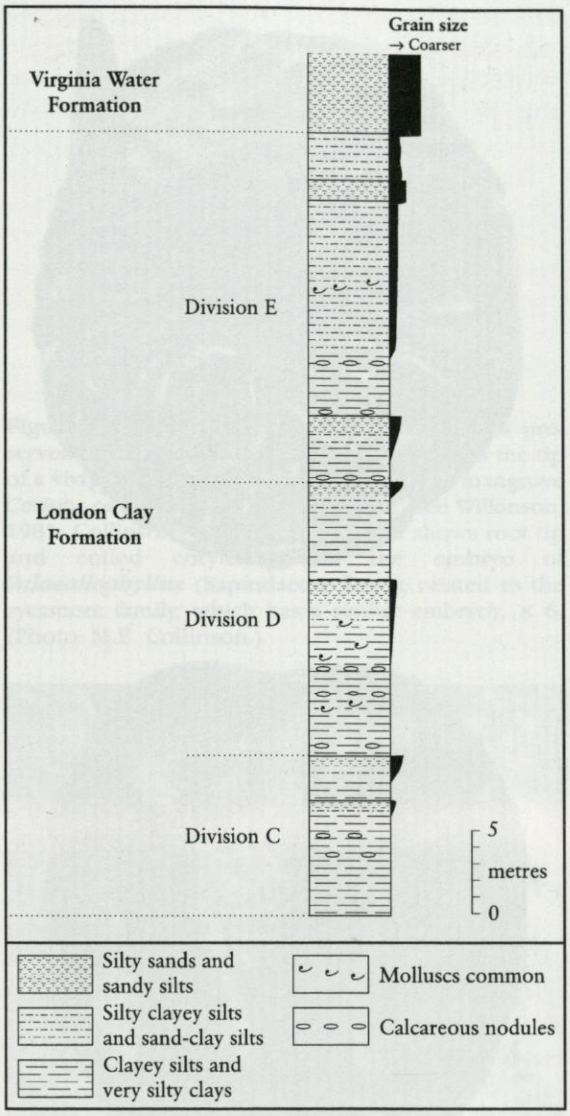

Figure 8.6 Lithostratigraphy of the London Clay Formation exposed at Sheppey. Division C is based on King (1984). (After King, 1981)

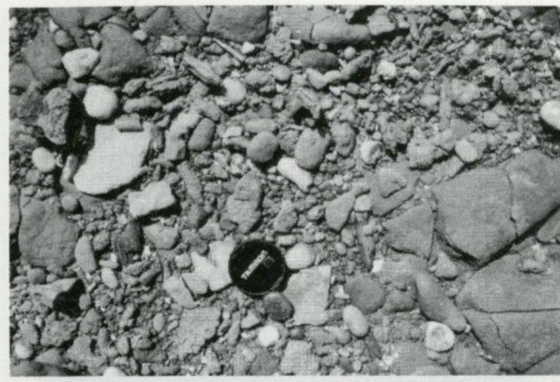

Figure 8.7 Pyrite concentration and in-situ clay in the foreshore at Sheppey, including a *Nypa* fruit and a twig. (Photo: M.E. Collinson.)

Manchester, 1994), for instance, the fossils have to be removed from chert by sledgehammers, and at Messel and Gieseltal (Germany) they are obtained by searching over bedding planes.

Palaeobotany

The plant fossils from Divisions D and E here are preserved mainly as pyrite petrifactions (Figures 8.7–8.10, 8.12), although some partly carbonaceous fossils also occur (Figure 8.11). The pyrite fossils yield anatomical detail (Figures 8.10 and 8.12) and internal structures such as embryos (Figure 8.9). Listed in Table 8.1 are 276 species of angiosperm fruits and seeds. In addition to these are woods, fern rachides (Figure 8.10), conifer leafy shoots and cones, fragments of tap roots, a (?)tuber, spines, twigs (Figure 8.12) and other assorted plant debris. Finally, Chandler (1968) described one specimen of silicified false-stem of the tree fern *Tempskya* from loose material on the beach at Sheppey. This was probably derived from Cretaceous deposits, although no such strata are exposed in the vicinity of Sheppey (it may have been dumped from ships' ballast), and should not be accepted as evidence of *Tempskya* in the Tertiary record (Collinson, 1996a, in press a).

Interpretation

The immense diversity of the Sheppey Eocene flora is partly due to the long history of collecting here. However, it is also probably because it represents different types of vegetation from mangroves, deltaic and extra-basinal habitats. The most abundant plant fossils are the palm fruits *Nypa burtinii*. The modern *Nypa fruticans* van Wurmb (known as the 'mangrove palm') fringes coastal areas in south-eastern Asia (Figure 8.1), and there is every reason to believe that the Sheppey fossils were also from shoreline vegetation (Collinson, 1993, 1996b, 2000b). The morphology and taphonomy of the Sheppey fruits has been examined by Collinson (1993), who found that they are very similar to those of the extant species, but tended to be smaller than those of other Eocene floras. Tralau (1964), Gee (1990) and Collinson (2000b) summarize the fossil distribution of *Nypa* and show that it

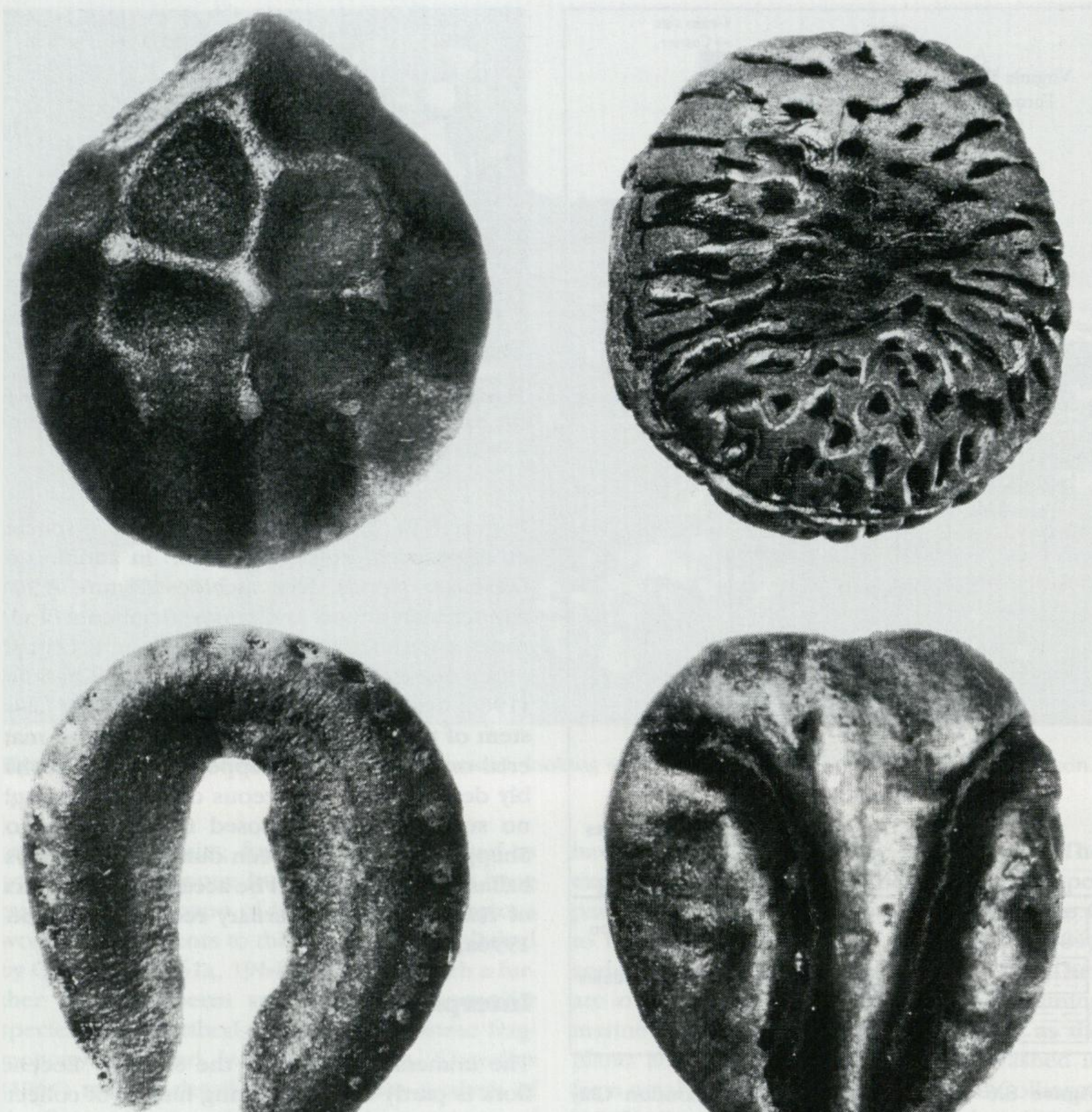

Figure 8.8 Pyritized internal casts of fruits and seeds of families typical for the London Clay flora at Sheppey (see Collinson, 1983b). Upper left shows *Iodes corniculata* (icacina family), × 12. Upper right shows *Anonaspermum cerebellatum* (custard apple family), × 14. Lower left shows *Diploclisia auriformis* (moonseed family), × 14. Lower right shows *Parthenocissus monasteriensis* (grape vine family), × 23. (Photos: M.E. Collinson.)

occurs extensively in the Eocene deposits of Europe, from Britain through to the Ukraine, as well in the rest of the world south to about 65° south (e.g. Tasmania – Pole and Macphail, 1996). It disappears from Britain in the late Lutetian (late Middle Eocene) (Collinson, 2000a).

Numerous and diverse but less abundant palms occur at Sheppey. Species have been assigned to the extant genera *Corypha, Livistonia, Oncosperma, Sabal* and *Serenoa*, all but the last of which today grow in south-eastern Asia. The *Sabal* are of interest in that they are associated with what may be fragments of leaf (the others are known only from their fruits).

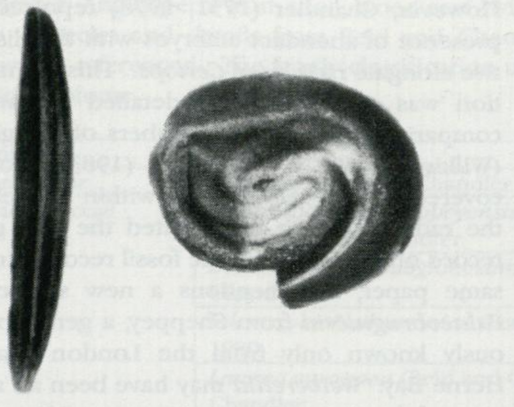

Figure 8.9 Pyritized preservation of embryos preserved in the London Clay at Sheppey. Left is the tip of a viviparous embryo ('sea pencil') of the mangrove *Ceriops cantiensis*, about natural size (see Wilkinson, 1981; Collinson, 1983b, 1993). Right shows root tip and coiled cotyledons of the embryo of *Palaeallophyllus* (Sapindaceae family, related to the sycamore family, which has a similar embryo), × 6. (Photo: M.E. Collinson.)

Figure 8.11 Leafy shoot of the conifer *Araucarites* sp., × 3.7 (see Collinson, 1983b). This is a rare example of an in-situ fossil from the clay sediment at Sheppey. (Photo: M.E. Collinson.)

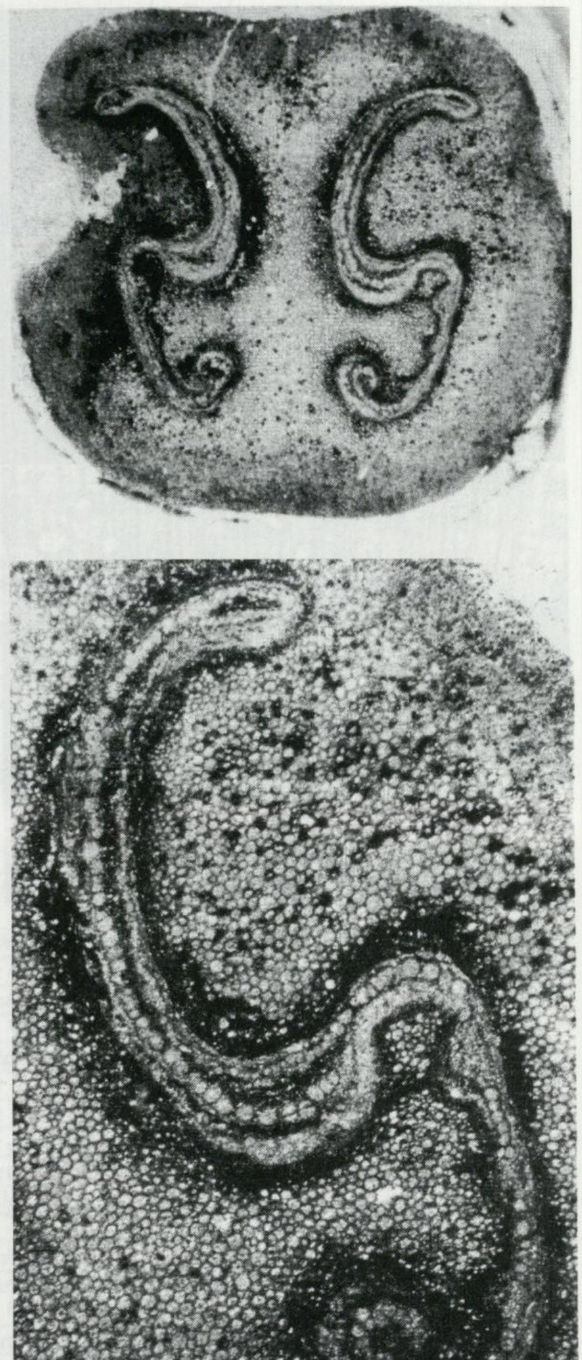

Figure 8.10 Anatomical preservation by pyrite permineralization of the axis of a fern frond (a possible dennstaedtioid fern) (see Collinson, in press a). The uppermost picture is of a polished, transverse section of the axis, × 14. Below is a close-up showing cell detail, even in the delicate parenchyma of the cortex surrounding the conducting tissue × 33. From the Sheppey GCR site. (Photos: M.E. Collinson.)

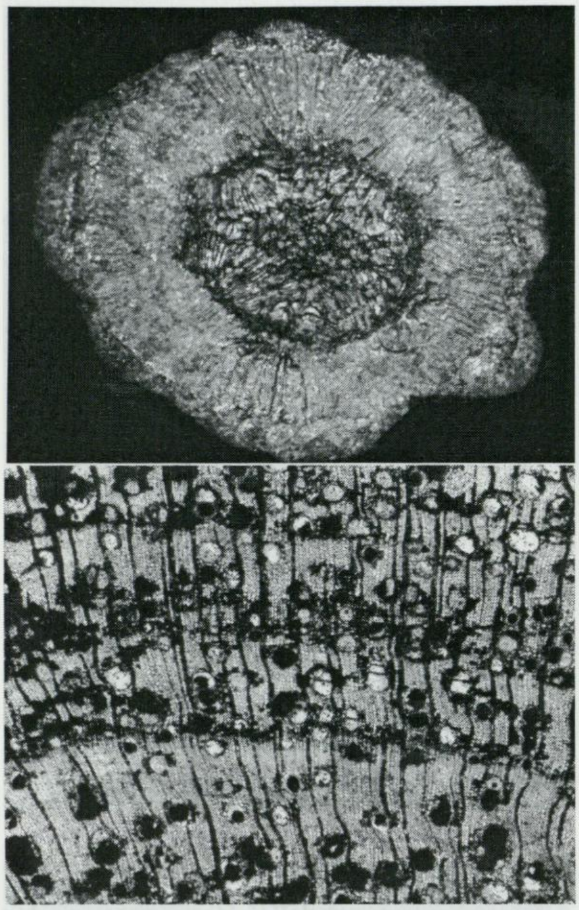

Figure 8.12 Low- and high-powered images of the twigs *Sapindoxylon guioaoides* Poole and Wilkinson from Sheppey. The long dimension of the specimen at the top is 3.75 mm, the field of view of the high powered image is 900 microns across. (Photo: I. Poole.)

Caryotispermum is similar to fruits of the extant palm *Caryota* except that the fossils have three seeds per fruit rather than two, and the embryo is nearer the ventral scar (Reid and Chandler, 1933, p. 104). In addition, there are a number of types of fruit that are undoubtedly of palms but are otherwise of unknown affinity, and so are assigned to *Palmospermum*. This makes Sheppey the most diverse of the early palm floras, with much potential for interpreting the early evolutionary history of this group.

Also abundant at Sheppey are remains of *Ceriops* (Figure 8.9), an extant genus of the mangrove family (Rhizophoraceae) that today grows in areas adjacent to the *Nypa* mangroves in south-east Asia. Complete fruits or seeds have not been reported, which explains why Reid and Chandler (1933) did not record this genus. However, Chandler (1951, 1978) reported the presence of abundant embryos with the distinctive elongate radicles of *Ceriops*. This identification was confirmed by a detailed anatomical comparison with extant members of the genus (Wilkinson, 1981). Wilkinson (1983) also discovered casts of starch grains within the cells of the radicles, which represented the first good record of such grains in the fossil record. In the same paper, she mentions a new species of *Palaeobruguieria* from Sheppey, a genus previously known only from the London Clay at Herne Bay. *Wetherellia* may have been an associate of the ancient *Nypa* mangroves (Mazer and Tiffney, 1982; Collinson, 1993, 1996b) and occurs abundantly at Sheppey (Collinson and Hooker, 1987; Collinson, 1990b).

Other families that today occur in tropical or subtropical habitats, but which occur abundantly as fossils at Sheppey, include the sumac, custard apple, dogbane, frankincense, flacourtia, icacina, laurel, moonseed, soap berry, tea and grape families, and mastic trees of the dogwood family and *Rehderodendron* of the storax family (the present-day distribution of many genera within these families found at Sheppey is reviewed by Tiffney, 1994 and Manchester, 1999). Today, the sumac family includes some of the tall canopy trees in tropical rain forests. Several different types of fruit of this family occur at Sheppey. Two have been assigned to living genera (*Dracontomelon*, *Lannea*), while the rest appear to belong to extinct genera. Although there are a few temperate members of this family living today, the Sheppey fossils all seem to be related to the section Spondieae, which is exclusively tropical.

The laurel family also includes many canopy trees in today's tropical rain forests. Fossil fruits of this family are often difficult to assign to living genera because of the lack of taxonomically useful characters. Most of the Sheppey fossils have therefore been assigned to generalized form-genera for laurel fruits (e.g. *Laurocarpum*) although many species have been assigned to the living genera *Cinnamomum* and *Beilschmiedia*.

Associated with these remains of what were probably canopy trees are fruits of families that today are tropical lianas: icacinas, moonseeds and grapes. The Sheppey icacinas include fruits of two living genera, *Iodes* and *Natsiatum*. Reid and Chandler (1933) and Chandler (1961a) described a high diversity of moonseed fruits but

Table 8.1 Angiosperm fruit, seed, wood and twig fossils from the Eocene London Clay GCR sites. Species and details from Reid and Chandler (1933) and Chandler (1961a), unless otherwise referenced. The family classification used here is summarized in Chapter 1 of the present volume.

Family	Species	Herne Bay	Bognor	Sheppey
Alangiaceae	*Alangium jenkinsii* Chandler	×		
Anacardiaceae	*Chaerospondias sheppeyensis* (Reid and Chandler) Chandler	×		×
	Dracontomelon subglobosum Reid and Chandler	×	×	×
	Edenoxylon? atkinsoniae Crawley, 1989			×
	Lannea europaea (Reid and Chandler) Chandler		×	×
	L. jenkinsii (Reid and Chandler) Chandler	×	×	×
	L. (?) *subreniformis* Reid and Chandler			×
	Lobaticarpum variabile Reid and Chandler	×	×	×
	Pentoperculum minimus (Reid and Chandler) Manchester, 1994		×	×
	Pseudosclerocarya lentiformis Reid and Chandler	×		×
	P. subalata Reid and Chandler			×
	Spondiaecarpon operculatum Chandler		×	×
	Spondicarya trilocularis Reid and Chandler			×
	Xylocarya trilocularis Reid and Chandler			×
Anonaceae	*Anonaspermum anoniforme* Reid and Chandler			×
	A. cerebellatum Reid and Chandler			×
	A. commune Reid and Chandler			×
	A. complanatum Reid and Chandler			×
	A. complicatum Chandler			×
	A. corrugatum Reid and Chandler			×
	A. minimum Reid and Chandler		×	×
	A. obscurum Reid and Chandler			×
	A. pulchrum Reid and Chandler	×		×
	A. punctatum Reid and Chandler			×
	A. rotundatum Reid and Chandler			×
	A. rugosum Reid and Chandler			×
	A. subcompressum Reid and Chandler			×
	Uvaria ovale (Reid and Chandler) Chandler, 1978		×	×
Apocynaceae	*Ochrosella ovalis* Reid and Chandler			×
	Ochrosoidea sheppeyensis Reid and Chandler	×		×
Araceae	*Epipremnum* sp. (Chandler, 1978)		×	
Arecaceae	*Caryotispermum cantiense* Reid and Chandler			×
	Corypha wilkinsonii Chandler, 1978			×
	Livistonia atlantica Mai, 1976			×
	L.? minima Reid and Chandler			×
	Nypa burtinii (Brongniart) Ettingshausen (Collinson, 1993, 1996b)	×	×	×
	Oncosperma? anglica Reid and Chandler			×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Arecaceae – *contd.*	*Palmospermum cooperi* Chandler (= ?*Sabal* – Mai, 1976)	×		
	P. davisii Chandler	×	×	×
	P. elegans Chandler			×
	P. excavatum Reid and Chandler	×	×	×
	P. minutum Chandler	×	×	
	P. ornatum Chandler	×		
	P. ovale Chandler			×
	P. parvum Reid and Chandler			×
	P. pulchrum Chandler	×		×
	P. subglobulare Chandler			×
	P. sp.	×	×	×
	Sabal grandisperma Reid and Chandler			×
	S. jenkinsii (Reid and Chandler) Manchester, 1994	×		×
	Sabal sp.	?	?	×
	Serenoa eocenica Reid and Chandler		×	×
	?*Trachycarpus* sp. (Chandler, 1978)		×	
?Asteraceae	Indet. genus (Chandler, 1978; Collinson *et al.*, 1993b)		×	
Boraginaceae	*Ehretia clausentia* Chandler (see Chandler, 1964)		×	
Burseraceae	*Bursericarpum aldwickense* Chandler		×	
	B. angulatum Reid and Chandler			×
	B. bognorense Chandler		×	
	B. ovale Chandler		×	
	B. venablesii Chandler		×	
	Palaeobursera bognorensis Chandler		×	
	Protocommiphora europea Reid and Chandler		×	×
	Tricarpellites communis Bowerbank	×	×	×
Capparidaceae	Genus? (Chandler, 1978)		×	
Celastraceae	*Canticarpum celastroides* Reid and Chandler			×
	Cathispermum pulchrum Reid and Chandler			×
cf. Cercidi-phyllaceae	*Celastrinoxylon ramunculiformis* Poole and Wilkinson, 1999			
	Nyssidium arcticum (Heer) Iljinskaja[1]	×	×	×
Cornaceae (including Mastixiaceae)	*Beckettia mastixioides* Reid and Chandler[2]	×	×	×
	B. bognorensis (Chandler) Knobloch and Mai, 1986[3]	×	×	×
	Dunstania ettingshausenii (Gardner) Reid and Chandler[4]	×	×	×
	D. multilocularis Reid and Chandler[4]	×	×	×
	Langtonia bisulcata Reid and Chandler[5]	×		×
	Mastixia cantiensis Reid and Chandler	×	×	×
	M. grandis Reid and Chandler		×	
	M. parva Reid and Chandler	×	×	×
Cucurbitaceae	*Cucurbitospermum cooperi* Chandler	×	×	
	C. equilaterale Chandler		×	
	C. sheppeyense Chandler		×	
	C. triangulare Chandler		×	

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Cyperaceae	*Polycarpella caespitosa* Reid and Chandler *emend.* Chandler, 1978		×	×
Dilleniaceae	*Hibbertia bognorensis* Chandler		×	
	Tetracera(?) *cantiensis* Reid and Chandler			×
	T. croftii Chandler	×		
	T. eocenica Reid and Chandler	×	×	×
	T. (?) *sheppeyensis* Reid and Chandler			×
Dipterocarpaceae	*Anisopteroxylon ramunculiformis* Poole, 1993b			×
Elaeocarpaceae	*Echinocarpus priscus* Reid and Chandler	×		×
	E. sheppeyensis Reid and Chandler	×		×
Epacridaceae	*Leucopogon quadrilocularis* Reid and Chandler	×	×	×
Euphorbiaceae	*Euphorbiospermum ambiguum* Reid and Chandler			×
	E. bognorense Chandler		×	
	E. cooperi Chandler	×		
	E. crassitestum Reid and Chandler			×
	E. eocenicum Reid and Chandler	×	×	×
	E. latum Reid and Chandler			×
	E. obliquum Reid and Chandler			×
	E. obtusum Reid and Chandler			×
	E. subglobulare Chandler		×	
	E. subquadratum Reid and Chandler			×
	E. truncatum Reid and Chandler			×
	E. venablesii Chandler		×	
	Euphorbiotheca minima Chandler	×		
	E. minor Reid and Chandler			×
	E. obovata Reid and Chandler			×
	E. obscura Reid and Chandler			×
	E. sheppeyensis Reid and Chandler			×
	E. (?) *pentalocularis* Reid and Chandler			×
	Lagenoidea trilocularis Reid and Chandler			×
	Wetherellia variabilis Bowerbank (see Collinson, 1993, 1996b)	×	×	×
Flacourtiaceae	*Oncoba variabilis* (Bowerbank) Reid and Chandler	×	×	×
	Saxifragispermum spinosissimum Reid and Chandler	×		×
	Oncobella polysperma Reid and Chandler			×
Haloragaceae	*Haloragicarya quadrilocularis* Reid and Chandler			×
Hamamelidaceae	*Corylopsis venablesii* Chandler		×	
	C. (?) *bognorensis* Chandler		×	
	C. (?) *latisperma* Chandler		×	
	C. sp.			×
	Steinbauera subglobosa Presl (see Mai and Walther, 1985)[6]		×	×
Icacinaceae	*Faboidea crassicutis* Bowerbank	×		×
	Icacinicarya amygdaloidea Chandler	×		
	I. bognorensis Reid and Chandler		×	
	I. echinata Chandler			×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Icacinaceae – *contd.*	*I. elegans* (Bowerbank) Reid and Chandler			×
	I. emarginata Chandler			×
	I. forbesii Chandler			×
	I. foveolata Reid and Chandler	×		×
	I. glabra Chandler			×
	I. jenkinsii Reid and Chandler	×		×
	I. minima Reid and Chandler	?	×	×
	I. mucronata Chandler			×
	I. nodulifera Reid and Chandler	×		×
	I. ovalis Reid and Chandler			×
	I. ovoidea Reid and Chandler	×		×
	I. platycarpa Reid and Chandler	×	×	×
	I. reticulata Chandler	×	×	×
	I. rotundata Reid and Chandler			×
	Iodes corniculata Reid and Chandler	×	×	×
	I. eocenica Reid and Chandler			×
	I. multireticulata Reid and Chandler	×	×	×
	Natsiatum eocenicum Chandler[7]		×	×
	Palaeophytocrene ambigua Reid and Chandler			×
	P. foveolata Reid and Chandler	×	×	×
	Sphaeriodes ventricosa (Bowerbank) Reid and Chandler			×
	Stizocarya communis Reid and Chandler			×
	S. oviformis Reid and Chandler			×
Juglandaceae	*Juglandicarya cantia* Reid and Chandler			×
	J. cooperi Chandler	×		
	J. crassa (Bowerbank) Reid and Chandler			×
	J. depressa Reid and Chandler	×	×	×
	J. lubbockii Reid and Chandler	?		×
	J. minuta Chandler	×		×
	Platycarya richardsonii (Bowerbank) Chandler, 1964	×	×	×
	Pterocaryopsis bognorensis Chandler[8]		×	
	P. elliptica Chandler, 1978		×	×
Lauraceae	*Beilschmiedia bognorensis* Chandler		×	
	B. bowerbankii Reid and Chandler			×
	B.? crassicuta Reid and Chandler			×
	B. eocenica Reid and Chandler			×
	B.? fibrosa Reid and Chandler			×
	B. gigantea Reid and Chandler			×
	B. oviformis (Bowerbank) Reid and Chandler	×		×
	B. pyriformis Reid and Chandler	×		×
	Cinnamomum globulare Reid and Chandler	×	×	×
	C. grande Reid and Chandler	×	×	×
	C. oblongum Chandler	×	×	×
	C. ovoideum Chandler	×	×	×
	Crowella globosa (Bowerbank) Reid and Chandler	×	×	×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Lauraceae – *contd.*	***Endiandra crassa*** Reid and Chandler			×
	Laurocalyx bowerbankii Reid and Chandler			×
	L. dubius Reid and Chandler			×
	L. fibrotorulosus Reid and Chandler			×
	L. globularis Reid and Chandler	×		×
	L. magnus Reid and Chandler			×
	Laurocarpum crassum Reid and Chandler			×
	L. cupuliferum Chandler	×		
	L. davisii Chandler			×
	L. inornatum Chandler	×		×
	L. minimum Reid and Chandler	×	×	×
	L. minutissimum Reid and Chandler	×	×	×
	L. ovoideum Reid and Chandler	×		×
	L. paradoxum Reid and Chandler	×	×	×
	L. proteum Reid and Chandler	?		×
	L. pyrocarpum Reid and Chandler			×
	L. sheppeyense Reid and Chandler	×		×
	Litsea pyriformis Reid and Chandler	×	×	×
	Protoravensara sheppeyensis Reid and Chandler	×	×	×
'Legumes'	***Leguminocarpon nervosum*** (Reid and Chandler) Chandler			×
Linaceae	***Decaplatyspermum bowerbankii*** Reid and Chandler			×
Lythraceae	***Cranmeria trilocularis*** Reid and Chandler			×
	Minsterocarpum alatum Reid and Chandler			×
	Pachyspermum quinqueloculare Reid and Chandler			×
	Tamesicarpum polyspermum Reid and Chandler	×	×	×
Magnoliaceae	***Magnolia angusta*** Reid and Chandler	×	×	×
	M. crassa Reid and Chandler	×	×	×
	M. davisii Chandler			×
	M. enormis (Bowerbank) Reid and Chandler			×
	M. gigantea Chandler			×
	M. lata Chandler		×	
	M. lobata (Bowerbank) Reid and Chandler	×	×	×
	M. longissima (Bowerbank) Reid and Chandler			×
	M. oblonga Chandler	×	×	×
	M. pygmaea Chandler			×
	M. rugosa Chandler	×	×	×
	M. subcircularis Reid and Chandler	×	×	×
	M. subquadrangularis (Bowerbank) Reid and Chandler	×	×	×
	M. subtriangularis Reid and Chandler			×
	Talauma wilkinsonii Chandler, 1964	×		
Meliaceae	***Toona sulcata*** (Bowerbank) Reid and Chandler		×	×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Meliaceae – *contd.*	*Melicarya variabilis* Reid and Chandler			×
Menispermaceae	*Atriaecarpum deltiforme* Chandler, 1978			×
	A. venablesii (Chandler) Chandler, 1978		×	
	Bowerbankella tiliacoroidea Reid and Chandler			×
	Calycocarpum(?) *jenkinsii* Chandler	×		
	Davisicarpum gibbosum Chandler (see also Chandler, 1978)			×
	Diploclisia auriformis (Hollick) Manchester, 1994[9]		×	
	Eohypserpa parsonii Reid and Chandler			×
	Jatrorrhiza gilliamii Chandler, 1964		×	×
	Menispermum(?) *taylorii* Chandler, 1964		×	
	Microtinomiscium foveolatum Reid and Chandler			×
	Palaeosinomenium venablesii Chandler		×	×
	Parabaena bognorensis Chandler, 1964		×	
	Tinomiscium taylorii Chandler	×	×	
	Tinomiscoidea scaphiformis Reid and Chandler	×		×
	Tinospora excavata Reid and Chandler	×	×	×
	T. rugosa Reid and Chandler	×		
	T. wilkinsonii Chandler	×		
	Wardensheppeya davisii (Chandler) Eyde, 1970	×	×	×
	Menispermoxylon sp. (see Poole and Wilkinson, 2000)			×
Moraceae	*?Morus* sp. (see Collinson, 1989)			×
Myrsinaceae	*Ardisia*(?) *eocenica* Reid and Chandler			×
?Myrtaceae / Theaceae	*Aldwickia venablesii* Chandler	×	×	×
	Palaeorhodomyrtus subangulata (Bowerbank) Reid and Chandler			×
Nymphaeaceae	*Protobarclaya eocenica* Reid and Chandler			×
Nyssaceae	*Nyssa oviformis* Reid[10]	×		×
	N. cooperi Chandler	×		
	N. sp.	×	×	×
	Palaeonyssa multilocularis Reid and Chandler[11]	×	×	×
Olacaceae	*Erythropalum europaeum* Reid and Chandler			×
	E. jenkinsii Chandler	×		
	E. (?) *striatum* Reid and Chandler			×
	E. turbinatum Chandler			×
	Olax depressa Reid and Chandler	×		×
Onagraceae	*Palaeeucharidium cellulare* Reid and Chandler		×	×
Platanaceae	*Plataninium decipiens* Brett, 1972	×		×
Posidoniaceae	*?Posidonia parisiensis* (Brongniart) Fritel (see Collinson, 1983b)	×		

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Rhizophoraceae	*Ceriops cantiensis* Chandler			×
	Palaeobruguieria elongata Chandler	×		
	P. alata Chandler	×		
	P. sp. nov. (Wilkinson, 1983)			×
Rosaceae	*Rubus* sp.		×	
Rutaceae	*Canticarya gracilis* Reid and Chandler			×
	C. ovalis Reid and Chandler			×
	C. sheppeyensis Reid and Chandler	×		×
	C. ventricosa Reid and Chandler	×		×
	C. sp.		×	×
	Caxtonia elongata Chandler			×
	C. glandulosa Reid and Chandler		×	×
	C. rutacaeformis Reid and Chandler			×
	Citrispermum sheppeyense Chandler	×		×
	Clausenispermum dubium Reid and Chandler			×
	Eozanthoxylon glandulosum Reid and Chandler			×
	Rutaspermum minimum Chandler		×	
	R. bognorense Chandler		×	
	Shrubsolea jenkinsii Reid and Chandler	×		
Sabiaceae	*Bognoria venablesii* Chandler		×	
	Meliosma cantiensis Reid and Chandler	×	×	×
	M. jenkinsii Reid and Chandler	×	×	×
	M. sheppeyensis Reid and Chandler	×	×	×
Sapindaceae	*Cupanoides grandis* Bowerbank	×		×
	C. tumidus Bowerbank	×		×
	Palaealectryon spirale Reid and Chandler			×
	Palaeallophylus minimus Chandler	×		×
	P. ovoideus Reid and Chandler			×
	P. rotundatus Reid and Chandler	×		×
	Sapindospermum cooperi Chandler	×		
	S. davisii Chandler			×
	S. grande Reid and Chandler			×
	S. jenkinsii Reid and Chandler	×	×	
	S. ovoideum Reid and Chandler	×		
	S. revolutum Chandler	×		
	S. subovatum (Bowerbank) Reid and Chandler			×
	S. taylorii Chandler, 1978		×	
	Sapindoxylon guioaoides Poole and Wilkinson, 1992			×
	S. koelreuteroides Poole and Wilkinson, 1992			×
Sapotaceae	*Sapoticarpum dubium* Reid and Chandler			×
	S. latum Reid and Chandler			×
	S. rotundatum Reid and Chandler			×
	Sapotispermum sheppeyense Reid and Chandler			×
	Sapotoxylon atkinsoniae Crawley, 1989			×
Solanaceae	*Cantisolanum daturoides* Reid and Chandler			×
Staphyleaceae	*Tapiscia chandleri* Mai, 1976			×
	T. elongata (Chandler) Mai, 1976			×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Staphyleaceae–*contd.*	*T. ornata* (Chandler) Mai, 1976			×
	T. pusilla (Reid and Chandler) Mai, 1976 (see also Manchester, 1988, 1994)	×	×	×
Sterculiaceae	*Sphinxia ovalis* Reid and Chandler	×		×
	Sterculia subovoidea (Reid and Chandler) Mai in Mai and Walther 1985[12]			×
Styracaceae	*Rehderodendron stonei* (Reid and Chandler) Mai[13]	×		×
Symplocaceae	*Symplocos curvata* Reid and Chandler			×
	S. quadrilocularis Reid and Chandler			×
	S. trilocularis Reid and Chandler			×
	S. (?) *bognorensis* Chandler		×	
Theaceae	*Hightea elliptica* Bowerbank	×	×	×
	H. turgida Bowerbank	×	×	×
Thymelaeaceae	*Aquilaria bilocularis* (Reid and Chandler) Mai[14]	×		×
Tiliaceae	*Cantitilia lobata* Chandler			×
	C. polysperma Reid and Chandler	×		×
Trochodendraceae	*Trochodendron* (?) *paucisseminum* Reid and Chandler			×
?Urticaceae	*Urticicarpum scutellum* Reid and Chandler (see Collinson, 1989)			×
Vitaceae	*Ampelopsis crenulata* Reid and Chandler		×	×
	A. monasteriensis Kirchheimer (see Mai, 1987, 1999)	×	×	×
	A. turneri Chandler			×
	Palaeovitis paradoxa Reid and Chandler	×	×	×
	Parthenocissus monasteriensis (Reid and Chandler) Chandler	×	×	×
	Tetrastigma corrugata Chandler		×	
	T. davisii Chandler			×
	T. (?) *elliottii* Chandler			×
	T. globosa Reid and Chandler			×
	T. sheppeyensis Chandler		×	×
	Vitis arnensis Chandler, 1978			×
	V. bilobata Chandler		×	×
	V. bognorensis Reid and Chandler		×	×
	V. bracknellensis Chandler		×	×
	V. elegans Chandler		×	×
	V. excavata Chandler, 1978			×
	V. longisulcata (Reid and Chandler) Chandler	×	×	×
	V. magnisperma Chandler	×	×	×
	V. obovoidea Chandler		×	
	V. platyformis Chandler			×
	V. pygmaea Chandler			×
	V. rectisulcata Chandler		×	×
	V. semenlabruscoides Reid and Chandler		×	×
	V. subglobosa Reid and Chandler	×	×	×
	V. venablesii Chandler		×	
	V. sp. (tendrils)	×		
	Vitaceoxylon ramunculiformis Poole and Wilkinson, 2000			×

Table 8.1 – *contd.*

Family	Species	Herne Bay	Bognor	Sheppey
Incertae sedis	*Carpolithus anthozoiformis* Chandler, 1964		×	
	C. bellispermus Chandler, 1978		×	
	C. bignoniformis Reid and Chandler			×
	C. bowerbankii Reid and Chandler			×
	C. crassus (Bowerbank) Reid and Chandler			×
	C. curtus (Bowerbank) Reid and Chandler			×
	C. ebenaceoides Reid and Chandler			×
	C. gracilis (Bowerbank) Reid and Chandler	×	×	×
	C. lentiformis (Bowerbank) Reid and Chandler			×
	C. lignosus Reid and Chandler			×
	C. monasteriensis Reid and Chandler			×
	C. olacaceoides Reid and Chandler			×
	C. quadripartitus Reid and Chandler			×
	C. scalariformis Reid and Chandler			×
	C. semencorrugatus Reid and Chandler	×		×
	C. subusiformis (Bowerbank) Reid and Chandler	×		×
	C. tessellatus (Bowerbank) Reid and Chandler			×
	C. thunbergioides Reid and Chandler	×		×
	Leyrida bilocularis Reid and Chandler	×	×	×
	L. subglobularis Reid and Chandler			×
	Neuroraphe obovatum Reid and Chandler	×		×
	Rhamnospermum bilobatum Chandler		×	×

1 Includes *Jenkinsella apocynoides* Reid and Chandler (see Crane, 1984).

2 Includes *Lanfrancia subglobosa* Reid and Chandler (see Knobloch and Mai, 1986; Mai, 1993).

3 Includes *Portnallia bognorensis* Chandler and *P. sheppeyensis* Chandler (see Knobloch and Mai, 1986; Mai, 1993).

4 *Dunstania* has been assigned to *Cornus* by some authors (e.g. Eyde, 1988) (see discussion in Manchester, 1994, p. 42).

5 The genus *Langtonia* is retained following Collinson (1983b) and Manchester (1994), in contrast to Mai (1993).

6 Includes *Protaltingia europea* Reid and Chandler (see Mai and Walther, 1985).

7 Kvaček and Bužek (1995) recombined *Natsiatum eocenicum* from the London Clay as *Palaeobosiea marchiaca* (Mai) Kvaček and Bužek. One key feature in this taxonomy was the absence of a papillate locule-lining in modern *Natsiatum* but its presence in the fossil. However, Manchester (1994, p. 52) noted the presence of a papillate locule-lining in modern *Natsiatum*. There is also some similarity with *Hosiea* (Mai, 1987; Manchester, 1994; Kvaček and Bužek, 1995). We have retained the original nomenclature pending further study of modern and fossil material.

8 *Pterocaryopsis* are probably isolated nutlets from fruiting heads of *Platycarya richardsonii* (see Manchester, 1987, explanation to fig. 10).

9 Includes *Diploclisia bognorensis* Chandler.

10 Includes *Nyssa bilocularis* (Reid and Chandler) Chandler (see Mai and Walther, 1985).

11 This may be ?*Nyssa* (see Manchester, 1994).

12 Includes *Euphorbiospermum obovoideum* Reid and Chandler (see Mai and Walther, 1985).

13 Includes *Durania stonei* (Reed and Chandler) Chandler (see Mai, 1970).

14 Originally *Lagenoidea bilocularis* Reid and Chandler, and also includes *Lagenella alata* Reid and Chandler (see Mai and Walther, 1985).

most are rare and only one belongs to a living genus (*Tinospora*). The grape family is also represented by many but mostly rare species, including representatives of the living genera *Vitis*, *Ampelopsis*, *Parthenocissus* and *Tetrastigma*, mainly recognized through the work of Chandler (1961a). Chandler (1978) later discussed the problems of distinguishing seeds of this family, especially when the determinations have to be based on just one or two specimens, but was nevertheless able to confirm her earlier observations on the diversity of this family in the London Clay.

The custard apple family is mostly represented by isolated seeds of a variety of forms, but one fruit has been placed in the living genus *Uvaria*. The flacourtia family is also represented here, by fruits of the living genus *Oncoba*. The dogbanes are today a mainly tropical family, with just a few members, such as periwinkle (*Vinca*), extending into temperate latitudes. The Sheppey fruits closely resemble those of the extant *Ochrosia* from Madagascar and northern Australia, and thus again give this flora a tropical tone. The Sheppey fossils assigned to the frankincense, soapberry and tea families cannot be referred to living genera.

The dogwoods (Cornaceae) are a family of mostly temperate plants, with just a few subtropical and tropical representatives. However, the commonest representatives in the Sheppey flora (*Mastixia* and *Beckettia*) belong to the section of the family that is exclusively tropical, the Mastixioideae, typically found today in south-eastern Asia.

Together with these essentially tropical elements are families that tend to be of a more temperate character. Among the fruits and seeds, the walnut and magnolia families come into this category. Since Reid and Chandler (1933) and Chandler (1961a) originally described them, the walnut family fruits from Sheppey have been studied by Wing and Hickey (1984) and Manchester (1987). According to Manchester, the fruit *Juglandicarya depressa* may in fact belong to the extant genus *Cyclocarya*, although no formal transference of the species was made. Much commoner, however, are fruits that can be assigned to two species of another extant genus, *Platycarya* (Manchester, 1987). Reid and Chandler (1933) commented that one of these (*P. richardsonii*, for which they used the name *Petrophiloides*) was the commonest species at Sheppey that indicated cooler conditions.

The magnolias, whose seeds are abundant in the London Clay (Chandler, 1978), might indicate cooler conditions, although many now have a tropical distribution. The seeds described to date all belong to the well-known extant genus *Magnolia*. The seeds of most living *Magnolia* species are very difficult to distinguish, often only differing on features such as size, which need large numbers of specimens to use reliably. Chandler (1978) noted that there were some of the Sheppey seeds that stood out as distinctive, such as the large *M. longissima* and *M. gigantea*, and *M. rugosa* with its ridged surface. Most of the rest, however, are very difficult to separate into anything more than morphological types, which may have little to do with the original species diversity. Nevertheless, Tralau (1963) claimed that the London Clay magnolias were clearly different from those of the Neogene deposits of central Europe, which he regarded as belonging to the extant species *Magnolia kobus* D. C. Furthermore, although Manchester (1994) indicated that Reid and Chandler had applied 'fine splitting' in their treatment of *Magnolia*, he still recognized three distinct species in the Clarno flora of Oregon.

Possible evidence of a temperate component in the Sheppey flora is provided by pyritized twigs, which show a much higher proportion of conifer remains than that represented in the seed assemblage (Scott and de Klerk, 1974; Collinson, 1983b; Poole, 1992, 1993a). Pollen of *Nothofagus* was reported from the London Clay (Sein, 1961) but Northern Hemisphere records are not generally accepted for *Nothofagus* (Tanai, 1986).

The bulk of the Sheppey flora was originally compared with tropical rain forest vegetation growing in Indo-Malaysia (Reid and Chandler, 1933) and the presence of what are today exclusively tropical elements suggests a more or less frost-free climate (Collinson, 1983b). The presence of apparently 'cooler elements' was originally explained in terms of the Sheppey assemblage representing both lowland and upland vegetation (Chandler, 1964; Montford, 1970). This agreed with the observation that the temperate elements (i.e. from the upland vegetation that had drifted down on rivers) were much less abundant than the tropical elements (i.e. from the lowland vegetation nearer the place of deposition). As pointed out by Daley (1972), however, there is no evidence of any significantly elevated land surrounding the London Clay basin, where the 'upland' elements could have been growing. According to Collinson (1983b), the presence of temperate elements in the London Clay flora may have been due to climate seasonality induced by variation in insolation through the year in relatively high latitudes.

Collinson (1983b, 2000b, in press b) and Collinson and Hooker (1987) have instead interpreted the Sheppey flora as being more comparable with today's paratropical rain forests, found in coastal lowlands in Asia (e.g. Burma, northern Vietnam) at more northerly latitudes than true tropical rain forests. Paratropical rain forests contain many of the same taxa as true tropical rain forests, but also have some elements normally regarded as temperate in character, especially growing alongside streams and in more open parts of the forest. Collinson (1983b, 2000b, in press b) pointed out that there were a number of differences between the Sheppey flora and the classic paratropical rain forests, presumably induced partly by the higher latitudes of the former, such as the rarity of the dipterocarps and the apparent absence of epiphytes. Poole (1993b) reported a single dipterocarp twig at Sheppey, but no fruits are known and the family cannot have been as abundant as it is in the modern paratropical forests of Asia. However, the coastal forests of places such as Burma and north Vietnam still seem to offer the nearest modern analogue of what we see at Sheppey.

Over 300 plant species have been described to date from here, mainly by Reid and Chandler (1933) and Chandler (1961a, 1978); no other site has yielded so many species from the London Clay. However, it is not just the shear number of the described species that makes Sheppey so important. For 39 genera and 12 families this is the only site where they occur as fossils in the London Clay, and 23 of these genera occur nowhere else as fossils. Sheppey is the type locality for over 225 fossil species and over 50 fossil genera. Similar *Nypa*-dominated seed and fruit floras are also known from the lower Eocene deposits of continental Europe and North America. The Brussels Sands of Belgium has yielded abundant *Nypa* together with a small assemblage of other fruit and seeds, and some ferns, similar to the Sheppey flora (Stockmans, 1936; Collinson, 1993, in press a). The Gieseltal fruit and seed flora from near Halle, central Germany, also shares many taxa with the Sheppey flora, including palms, icacinaceans, anacardiaceans, magnolias, sabiaceans and euphorbiaceans (Mai, 1976). The fruit and seed flora from the Messel flora from near Darmstadt in Germany again shares many taxa with Sheppey (Collinson, 1988), although does not have the mangrove elements (*Nypa*, *Ceriops*) as it represents the vegetation surrounding a freshwater lake.

The best comparison with the Sheppey flora is the middle Eocene Clarno Nut Beds of Oregon, USA (Manchester, 1981, 1994). Like Sheppey, the fruits and seeds are permineralized and thus allow a direct comparison of their anatomy. The Clarno Nut Bed was formed in a lake within an area of volcanic activity (hence the silica permineralization of the Clarno fossils) and so, as with Messel, there are not the mangrove elements there. Nevertheless, Manchester (1994) reported that there were 30 genera and 15 species in common between the floras (20% and 10%, respectively, of the Clarno flora). It is strongly suggestive that there was a land-bridge between Europe and North America during the early to middle Eocene times, perhaps via Greenland (Tiffney, 1985), which would provide further support for this being a time of significantly warmer climate than today. Manchester (1999) gives further palaeobiogeographical comparisons between Europe, North America and China, and the Sheppey flora (as well as those of Herne Bay and Bognor) is vital to these studies.

None of these other floras are, however, as diverse as that found at Sheppey. This may be partly because of the long history of research here compared with most of these other areas. It nevertheless makes the Sheppey flora the standard against which all other Eocene fruit and seed floras from the Northern Hemisphere need to be compared. The importance of the Sheppey flora is amplified by the fact that many of the fruits and seeds are anatomically preserved.

Sheppey has also proved to be the best site for the study of fossil wood and twigs in the London Clay (Figure 8.7; Brett, 1972; Collinson, 1983b, 2000b, in press a; Wilkinson, 1984, 1988; Crawley, 1989; Poole, 1992, 1993a,b, 1996, 2000; Poole and Wilkinson, 1992, 1999, 2000; Poole and Page, 2000). They provide additional insight into the Ypresian vegetation of southern Britain, yielding families that are often rare or in some cases absent from the fruit and seed flora, including dipterocarps and ferns. The presence of growth rings in some of the twigs is also an important palaeoclimatic indicator.

Sheppey has been central to the development of Tertiary palaeobotany, not only in Britain, but also throughout the world. Prior to the work of Reid and Chandler (1933) on the Sheppey fruits and seeds, angiosperm palaeobotany had been almost entirely devoted to the study of leaves, which are at best difficult to use for taxonomic work. As pointed out by Andrews (1980), the advances made by Reid and Chandler provided the impetus for other major studies in Europe, such as by Kircheimer (1936) on the Miocene German Bown Coal. Today, the study of fruits and seeds (palaeocarpology) is seen as part of the mainstream of Tertiary palaeobotany, but this only came about through the developments at Sheppey during the early 20th century.

Conclusions

Sheppey has yielded the most diverse seed and fruit flora representing the early Eocene paratropical broadleaf forests of the Northern Hemisphere, and includes over 300 species of angiosperms. It provides the best insight into the diversity of this lush vegetation, especially of the forests fringing the coastlines of Europe about 50 Ma years ago, and represents an international 'standard' with which other floras of this age must be compared. The flora includes abundant fossils of mangrove palms (*Nypa*), but also contains the remains of tropical forest trees, such as members of the laurel, sumac, palm, custard apple, sabia, dogwood and frankincense families. Also present are numerous fruits and seeds of lianas that presumably grew amongst these trees, including members of the icacina, moonseed and grape families. The fruit and seed fossils here are particularly important as many yield details of their anatomy, which can be essential in establishing the group of plants to which they belong. Also important are the abundant wood and twig fossils, which include representatives of some plant families not preserved in the fruit and seed record, such as the dipterocarps and ferns.

HERNE BAY (TR 185 685–TR 224 693)

Introduction

Herne Bay has yielded one of the most diverse fruit and seed floras from the Eocene London Clay. More than 130 species have been reported to date, and include six genera that are unique to here.

The palaeobotany of the Palaeocene and Palaeocene–Eocene transition strata at Herne Bay is discussed in Chapter 7. However, the site is also of considerable interest for early Eocene palaeobotany. Plant fossils are known from the A2 division of the London Clay Formation and were first described in detail by Reid and Chandler (1933), with further records provided by Chandler (1961a, 1964). Most of the species are listed by Cooper (1977) and Collinson (1983b), the latter including illustrations of some of the characteristic taxa. Brett (1972) described petrified wood from here.

Description

Stratigraphy

The fossil-bearing beds dealt with here are in the

Figure 8.13 Locule cast of *Nyssidium arcticum* (= *Jenkinsella apocynoides*) preserved in pyrite, × 7.5 (see Collinson, 1983b), from the Herne Bay GCR site. (Photo: M.E. Collinson.)

A2 division of the London Clay (*sensu* King, 1981) and are thus from a different stratigraphical level than Sheppey (divisions D and E) and Bognor (divisions B1 and B2). Further details of the stratigraphy here can be found in the previous chapter.

Palaeobotany

The most abundant fossil plants at Herne Bay come from the London Clay Formation. Collinson (1983b) states that over 130 species of angiosperm fruits and seeds have been found here (see Table 8.1). In addition, rare conifer fragments occur: ***Cupressinites curtus*** Bowerbank (cypress family) and ***?Pinus macrocephalus*** (Lindley and Hutton) Gardner (pine family).

Interpretation

Herne Bay has yielded one of the best London Clay floras in Britain (Table 8.1; see also Figures 8.13 and 8.14), equal in diversity to that at Bognor and only being significantly bettered by the classic Sheppey flora. It adds considerably to our understanding of the biodiversity of the paratropical rain forests growing in Britain during early Eocene times, with 37 species, five genera and two families having only been found in Britain in the London Clay at Herne Bay (Collinson, 1983b). It is furthermore the type locality for 38 species and for the genera *Palmospermum*, *Shrubsolea*, *Sapindospermum*, *Citrispermum* and *Palaeobruguiera* (also for *Jenkinsella*, which is now included within *Nyssidium*; Figure 8.13).

Of the two unique families mentioned by Collinson (1983b), the alangias are represented by a single fruit described and figured by Chandler (1961a, pl. 27, figs 4 and 5). Although extremely rare, the one known example from here was almost identical to that of the living *Alangium*, a genus of mainly trees and shrubs found throughout most of the tropics. The determination to *Alangium* was accepted by Mai (1970) in his revision of the group. Although not known from any other British flora, *Alangium* has been described from the Eocene Clarno Beds of Oregon (Manchester, 1994) and Geiseltal flora of eastern Germany (Mai, 1976), and the Oligocene Brandon Lignite of Vermont (Eyde *et al.*, 1969).

The second unique family at Herne Bay according to Collinson (1983b) is that of the posidonias, which contains rare aquatic angiosperms that today are only found around the Mediterranean and the southern coast of Australia. Such a disjointed distribution suggests that it was more widely occurring in the past but according to Collinson *et al.* (1993b), its fossil record is very poor. The Herne Bay fossils consist of putative rhizomes with helically arranged ridges and pits (Chandler, 1961a), which are very similar to fossils from the Eocene strata of France that Fritel (1909) claimed to be indistinguishable from the rhizomes of living *Posidonia*.

Figure 8.14 Compound fruit of ***Platycarya richardsonii*** preserved in pyrite, × 3.5, from Herne Bay (see Collinson, 1983b). (Photo: M.E. Collinson.)

Of the other genera that are unique as London Clay fossils to Herne Bay, two are living genera: *Calycocarpum* (moonseed family) and

Talauma (magnolia family). The former genus is known today from just one species, a deciduous liana from south-western North America (*C. lyonii* Nutt). The one specimen tentatively assigned to the genus by Chandler (1961a) was indisputably a distinctive member of the Tinosporeae section of the moonseeds, but the preservation was not sufficiently good for an unequivocal generic assignment and Manchester (1994) has suggested that it might belong to a different genus.

Talauma is a genus that was used for a group of tropical lowlands plants, which are very similar to *Magnolia*. Chandler (1964) described a single seed from Herne Bay that was very similar in form and structure to that of *Talauma angatensis* (Blanco) F.-Vill. Later (Chandler, 1978) she referred to it as a 'convincing specimen of the lowland *Talauma*'. It has been argued that the living *Talauma* is insufficiently different from *Magnolia* to justify a generic separation (Nooteboom, 1985) and the taxonomic position of the Herne Bay fossil may have to be reconsidered in the light of this. Nevertheless, it will almost certainly remain distinctive at the specific or subgeneric level.

Shrubsolea was based on a single specimen of a large seed with clear characteristics of the rue family (Reid and Chandler, 1933). It is much larger than the seeds of most living plants of this family and was placed in its own form-genus. Knobloch and Mai (1986, 1991) recognized *Shrubsolea* in the Upper Cretaceous Series of the Czech Republic.

Chandler (1961a) described two species of what she intepreted as embryos of a red mangrove (Rhizophoraceae). They are broadly similar to those of the living *Bruguiera*, one of the mangoves growing today in Asia and Africa, but there are sufficient differences to justify placing the fossil embryos in a separate form-genus, *Palaeobruguiera*. Wilkinson (1983, fig. 2a,b) figured starch grains in the cortical tissue of the hypocotyls of *Palaeobruguiera*. *Palaeobruguieria* was among the genera listed by Collinson (1983b) as unique in the London Clay to Herne Bay, although Wilkinson (1983) has since recorded examples from Sheppey.

Herne Bay has yielded the most abundant examples of the fruit originally described as *Jenkinsella apocynoides* Reid and Chandler (Figure 8.13), which Crane (1984) has re-assigned to *Nyssidium arcticum* (katsura-tree family). Although more complete material is known from other localities such as Cold Ash (see Cold Ash GCR site report, this volume), the Herne Bay pyritized petrifactions provide additional details of the fruits of this important Palaeocene–Eocene plant.

Conclusions

Herne Bay has yielded an internationally important fruit and seed flora of early Eocene age. Among the London Clay floras, it is second in diversity only to the classic Sheppey flora, having yielded over 130 species, 32 of which are unknown from Sheppey. The flora has been particularly important for the study of the alangia, posidonia, mangrove and katsura-tree families in these floras. It provides important insights into the paratropical rain forests that covered much of southern Britain about 51 Ma ago.

WRABNESS (TM 172 323)

Introduction

Wrabness is the best site for London Clay fruits and seeds preserved in concretions. This mode of preservation complements the pyrite petrifactions such as found at Sheppey and the carbonaceous fossils of Walton-on-the-Naze.

Wrabness is a relatively recently discovered site for fossilized fruits and seeds of the London Clay. Daniels (1971) described the site in a field guide and Collinson (1983b) briefly mentioned the plant fossils from here.

Description

Stratigraphy

The cliffs and foreshore at Wrabness expose mudstones and siltstones of the London Clay, belonging to the upper A1 and lower A2 divisions of King (1981). The exact stratigraphical position of the plant bed(s) is unknown. However, the flora has been included here because it seems most likely some may be Ypresian in age (if derived from the London Clay division A2).

Palaeobotany

Collinson (1983b) states that five species are known from this site but she only specifically mentions *Iodes multireticulata* Reid and Chandler (icacina family), *Nyssidium arcticum* (Heer) Iljinskaja (katsura-tree family) and *Platycarya richardsonii* (Bowerbank) Chandler (walnut family). Daniels (1971) also mentions *Cinnamomum* sp. and *Mastixia* sp..

Interpretation

This is a relatively newly discovered site, whose potential has not been developed. Its importance lies in the preservation of the plant fossils. Although many of the fruits and seeds are preserved as pyrite petrifactions, similar to those at Sheppey, some occur in calcareous concretions. These give a totally new insight into the anatomy of the Thames Group fruits and seeds compared to both the pyrite petrifactions and the carbonaceous fossils such as found at Walton-on-the-Naze. This is particularly important for the smaller fruits and seeds, where pyritization can often obscure the detailed structure. Nodule preservation also retains the original size of the fruits and seeds, albeit in its external mould. Carbonaceous specimens have usually suffered some shrinkage, which can result in serious difficulties when making comparisons at the level of species.

Conclusions

The London Clay at Wrabness has yielded fruits and seeds preserved in concretions. This is a different mode of preservation to that normally associated with the London Clay and provides a significantly different insight into the structure of the fruits and seeds of the 'tropical' vegetation growing in Britain some 50 Ma ago.

BOGNOR REGIS (SZ 889 970–SZ 934 987)

Introduction

The coastal exposures of London Clay at Bognor Regis (Figures 8.15 and 8.16) have yielded one of the most diverse early Eocene fruit and seed floras in Britain, second only to the classic flora at Sheppey. This is the only site in the Hampshire Basin to yield abundant fossilized fruits and seeds of the London Clay, and the only rich flora to have come from Division B of the London Clay anywhere in England. It has yielded some 130 species, of which 40 are only known from here. It is also the only known London Clay site to yield seeds of the arum family. The palaeobotany of this site thus provides valuable additions to our understanding of the

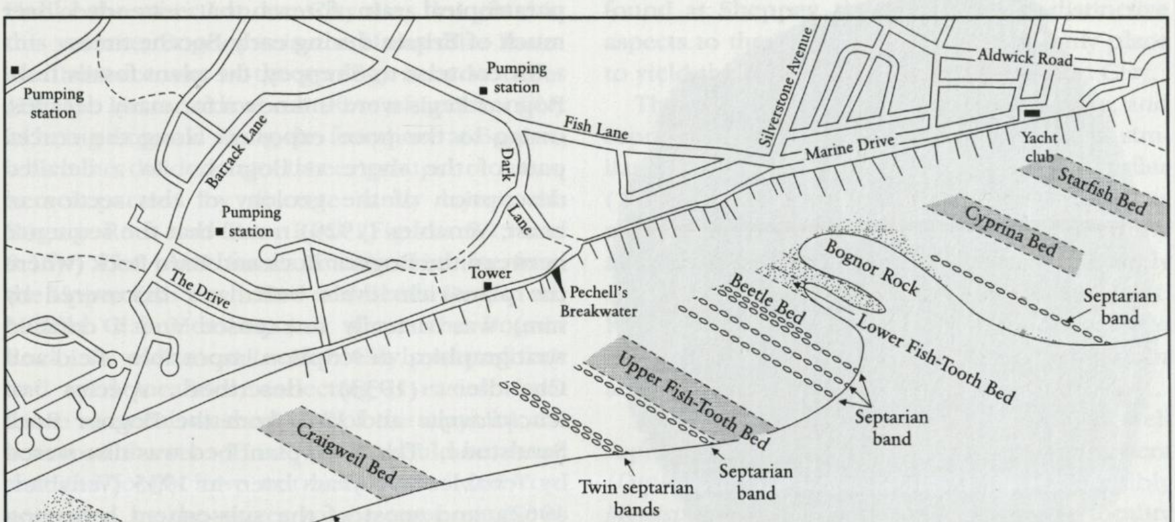

Figure 8.15 Foreshore exposure of Division A3 and Division B (King, 1981) of the London Clay at Bognor Regis. (After Venables, 1962.)

Figure 8.16 Collecting on the foreshore at Bognor Regis, Summer 1990. (Photo: M.E. Collinson.)

Figure 8.17 Endocarp of *Natsiatum eocenicum* (see footnotes to Tables 8.1 and 8.2), partially pyritized preservation, × 7.5 (see Collinson, 1983b). Bognor Regis GCR site. (Photo: M.E. Collinson.)

paratropical rain forests that extended over much of Britain during early Eocene times.

In contrast to Sheppey, the plant fossils from Bognor Regis were unknown for many decades, owing to the poor exposure along the crucial part of the shore at Bognor. In a detailed description of the geology of this section of coast, Venables (1929) noted that the sequence between the Bognor Rock and Barn Rock (where the plant-rich levels were later discovered by him) was virtually unexposed and a detailed stratigraphical description impossible. Reid and Chandler (1933) described species of *Icacinicarya* and *Vitis* from the Bognor Rock Sandstone. The main plant bed was discovered by Venables two years later, in 1935 (Venables, 1962), and most of the subsequent collecting was done by Venables. The first detailed account of the fossil fruits and seeds here was in Chandler (1961a), whose species list was essentially repeated by Venables (1962). Chandler (1964, 1978) described further material, and a summary of the assemblage was provided by Collinson (1983b).

Figure 8.18 Fruit of ***Leucopogon quadrilocularis*** showing locule casts, partly preserved in pyrite, × 15.5 (see Collinson, 1983b) from the Bognor Regis GCR site. (Photo: M.E. Collinson.)

Description

Stratigraphy

Unlike the other London Clay sites described in this volume, Bognor is in the Hampshire Basin. The best account of the geology is by Venables (1962). He records about 90 m of London Clay as being exposed along the foreshore at Bognor, which he divided into three 'groups' or members separated by discrete sandy layers, the Bognor Rock and Barn Rock (Figures 8.15 and 8.16). The plant fossils mainly originate from the Upper Fish Tooth Bed and Beetle Bed, in the Middle Clay Member, just above the Bognor Rock. As with most London Clay pyritized fruit and seed localities, collecting is easiest from loose material washed out of the clays by the action of the sea. However, it should be noted that the fossils have not been sorted and concentrated by the waves to the same extent as they have at Sheppey. Daley (in Daley and Balson, 1999) provides a more recent review of the geology here.

In the current classification of the London Clay (King, 1981), the Bognor plant beds are in the B1 and lowest B2 divisions, and are early Eocene (Ypresian) in age.

Palaeobotany

Fruits and seeds are preserved here mainly as pyrite petrifactions (Figures 8.17 and 8.18). It is, in theory, possible to collect them directly from the strata, but the poor exposure makes this for the most part impractical, and material is better collected loose from the foreshore. Although it is not as easy to collect large numbers of specimens compared to Sheppey, Collinson (1983b) has reported that nearly 130 species have been found in the Bognor London Clay. Of these the angiosperms are by far the most common and diverse (see Table 8.1). There are also rachides of a ?dennstaedtioid fern, which occurs elsewhere in the London Clay (Collinson, 1996a, in press a). The conifer ?*Libocedrus* sp. (cypress family) is unique to this site.

Interpretation

The compositional balance of the Bognor flora seems to be broadly compatible with that seen at the other London Clay sites, with abundant examples from the frankincense, grape vine, icacina, laurel, moonseed, palm and sumac families, all suggesting a paratropical vegetation of the shoreline and adjacent land areas.

While the assemblage has many taxa in common with other London Clay floras, such as that found at Sheppey, there are several distinctive aspects to the Bognor flora. It is the only place to yield the arum family from the London Clay.

The genus *Bognoria* is unique to this site, and represents an enigmatic type of fruit that is similar to the sabiacean genus *Meliosma*. Chandler (1961a) expressed some reservations as to its affinities with that family, due to the uncertainty as to whether or not the endocarp completely surrounded the basal aperture of the fruit. Records of ?*Trachycarpus* and *Palaeobursera* (Chandler, 1961a, 1978) are unique to Bognor among the London Clay sites.

As at Sheppey, the moonseed family is well represented at Bognor. For three of the genera (*Diploclisia*, *Parabaena* and possibly *Menispermum*) Bognor was the only locality where they were known as fossils (Collinson, 1983b), though a single specimen of *Diploclisia* has now been recorded at Sheppey. *Diploclisia* was subsequently reported from the Clarno Formation of Oregon (Manchester, 1994) and is one of 30 genera showing common occurrence and hence biogeographical similarity between the early and middle Eocene deposits of North America and Europe (Manchester, 1994, 1999). *Parabaena* has now been recognized in the much younger lower Miocene deposits of continental Europe (Mai and Walther, 1991).

Bognor is also the only known locality for fossils of the living dilleniacean genus *Hibbertia*. All of these genera, except the widely distributed *Menispermum*, are restricted today to south-eastern Asia or northern Australasia and provide added confirmation of the similarities between the Eocene London Clay flora and the Indo-Malaya vegetation of today.

Bognor is particularly important for the smaller fruits and seeds (Chandler, 1978), which probably explains the large number of seeds of the grape family described from here. The seeds of *Vitis* can be difficult to differentiate one from another when separated from the parent plant and it is far from certain that all the morphotypes described by Chandler (1961a) are natural species. They nevertheless give an impression of the diversity of this group of plants in the Eocene vegetation of southern Britain.

Bognor is the only known British site yielding fruits and seeds from the B2 division of King (1981). It also complements the other London Clay plant sites in being the only known locality in the Hampshire Basin to have yielded a diverse fruit and seed flora. These factors, together with the distinctive balance of its flora, make Bognor a key British site for Tertiary palaeobotany.

Conclusions

Bognor is one of the best sites in Britain for yielding fruits and seeds of Ypresian age, *c.* 50 Ma old. Only Sheppey has yielded significantly more species, but Bognor has many species not so far known from there. Bognor is also much further west and of a different age than the other London Clay plant sites, demonstrating the wide distribution of the paratropical rain forest from which its fruits and seeds originally came.

LAKE (SY 978 908)

Introduction

This is one of only two sites still yielding fossil plants from lower Eocene beds traditionally called the 'Dorset Pipe Clays'. These deposits are of about the same age as the London Clay, but are fluvial rather than marine deposits and thus largely lack the mangrove-palm-dominated vegetation seen in the London Clay. Lake yields the most diverse of the Dorset Pipe Clay floras, containing 69 species of mainly angiosperms and ferns, 30 of which (and 3 genera) are unique to the site.

Figure 8.19 Low cliff exposure at Lake, beneath the caravan site, on the eastern side of Poole Harbour, as seen in the mid 1970s. The section is now largely obscured by sea defence work. (Photo: M.E. Collinson.)

In the western part of the Hampshire Basin, the London Clay Formation *sensu stricto* is mostly missing, and is replaced by fluviatile sediments. These sediments have included a number of historically important palaeobotanical sites, including Alum Bay on the Isle of Wight (see La Harpe and Salter (in Bristow, 1862), Gardner (in Reid and Strahan, 1889) and Crane, 1977, 1978) and Corfe and Studland in Dorset (Brodie, 1853; Gardner, 1877, 1886a; Gardner and von Ettingshausen, 1879; Chandler, 1962). These leaf beds now yield very little material, but in recent years it has been discovered that there are also fruit and seed deposits, which are much more productive. The site at Lake, on the shore of Poole Harbour, was discovered in 1938 by E. St J. Burton and most of what we know about the flora here is based on his collection (now stored at the Natural History Museum, London). Chandler (1955, 1962) has described the fossils from here, and some were briefly mentioned by Collinson (1980a), who also illustrated a *Ficus* fruit (Collinson, 1989). Fruits of the dogwood family from here were also used in a chemical investigation of fossil resins (van Aarssen *et al.*, 1994).

Description

Stratigraphy

The low cliffs here (Figure 8.19) show fluviatile sands and muds of the Lower Eocene (Ypresian) (Plint, 1988). For recent correlations see Hooker and Collinson in Collinson (1996b). They were originally assigned to the Lower Bagshot Beds, but were renamed as they are older than the true Bagshot Formation in the Thames Valley (Curry *et al.*, 1978). Most of the section consists of poorly consolidated sands with bands of red and white mottled clay, traditionally known as the Dorset Pipe Clay 'Series'. These are sometimes now referred to as the 'Corfe Member' of the Poole Formation, but we have here continued to refer to them as the 'Dorset Pipe Clays'. In the sands are numerous lenses and thin bands of carbonaceous material, mainly consisting of woody tissue but also containing fruits and seeds.

Palaeobotany

Lake has yielded nearly 70 species of plant fossil, the full assemblage being shown in Table 8.2. The enigmatic '*Scirpus*' *lakensis* (see Figure 8.20), together with an extinct member of the caper family (*Palaecleome*) and pyrenes of *Ehretia* dominate the flora. There are also numerous seeds of lianas, especially of the icacina, moonseed and grape families. Most species are represented as carbonaceous fossils that have probably suffered significant shrinkage. They reveal no internal anatomical detail, although details of the sclerotic tissue are often preserved. Lake is the type locality for 44 species and 3 genera.

Interpretation

Lake has produced by far the most diverse and well-preserved fossil flora from the Dorset Pipe Clays. The only comparable site is Arne, but that has yielded only just over half the number of species. The Arne fossils also often suffer from the coarse overgrowth of pyrite crystals, which can mask the morphology of the fruits and seeds.

The dominant plant fossils at Lake are what Chandler (1962) identified as isolated fruits of *Scirpus*. However, essentially identical specimens in the Eocene strata at Messel occur within receptacular fruiting heads, showing that they are seeds and thus totally unlike *Scirpus* but more similar to modern Cyclanthaceae (Panama hat family) (Collinson, 1982b, 1988, 1996b). Collinson (1996b) showed that these fossils came from plants that grew along rivers and lakeshores. Further evidence of aquatic conditions is the presence of the water lily, *Palaeonymphaea* (Collinson, 1980a). The relatively high proportion of icacina, moonseed and grape family members probably reflects a dense swathe of lianas, growing on trees surrounding the rivers and lakes, whose fruits dropped directly into the water.

The Dorset Pipe Clay flora at Lake is important because it complements the more diverse London Clay flora, such as found at Sheppey, Bognor Regis and Herne Bay. Whereas the *Nypa–Ceriops* mangrove vegetation that fringed the coast dominates the London Clay flora, the Dorset Pipe Clay flora represents more inland vegetation. Only one example of a *Nypa* fruit has been recorded from the Dorset Pipe Clays, from a temporary exposure near Stoborough, Dorset (Collinson, 1993, 1996b). There are nevertheless many similarities between the floras, especially at the family level. Putting the

Table 8.2 Composition of floras from the Dorset Pipe Clays, Hampshire Basin. Species descriptions, or references to them, can be found in Chandler (1962), unless otherwise referenced. Discussions on some of these species can also be found in Manchester (1994), Mai and Walther (1978, 1985), Mai (2000) and Collinson (1996b, in press a). The family classification used here is summarized in Chapter 1 of the present volume

Family	Species	Lake	Arne	Studland
Pteridaceae	*Acrostichum lanzaeanum* (Visiani) Chandler		×	×
Schizaeaceae	*Lygodium kaulfussii* Heer *emend.* Gardner and Ettingshausen			×
	L. poolensis Chandler	×		
	Anemia poolensis Chandler	×	×	
	Ruffordia subcretacea (Saporta) Barthel, 1976[1]		×	
Taxodiaceae	*Taxodium lakensis* Chandler	×	×	
	Sequoia couttsiae Heer[2]			×
Actinidiaceae	*Saurauia crassisperma* (Chandler) Mai[3]	×		
	S. poolensis (Chandler) Mai, 1970[4]	×		
Anacardiaceae	*Dracontocarya glandulosa* Chandler	×		
	?*Lannea* sp.	×		
	Rhus lakensis Chandler	×		
	R. spp.	×		
Apocynaceae	*Apocynospermum acutiforme* Chandler[5]	×		
	A. lakense Chandler[5]	×		
Arecaceae	*Calamus daemonorops* (Unger) Chandler	×		
	?Sabal sp.		×	
Boraginaceae	*Ehretia lakensis* Chandler	×		
Burseraceae	*Palaeobursera lakensis* Chandler	×		
Capparaceae	*Burtonella emarginata* Chandler	×	×	×
	Palaeocleome lakensis Chandler	×		
	Capparidispermum eocenicum Chandler	×		
Caprifoliaceae	*Sambucus parvula* Chandler	×		
Cornaceae (including Mastixiaceae)	*Dunstania lakensis* Chandler[6]	×		
	Eomastixia rugosa (Zenker) Chandler (see Mai, 1993)	×	×	
	E. urceolata Chandler	×		
	?*Mastixia cantiensis* Reid and Chandler[7]		×	
	Mastixicarpum crassum Chandler (see Mai, 1993)	×		
	Swida quadrilocularis (Chandler) Mai, 1999[8]	×		
Cucurbitaceae	*Cucurbitospermum lakense* Chandler	×		
	C. obliquum Chandler	×		
Cyperaceae	'*Scirpus*' *lakensis* Chandler	×	×	
	?*Scirpus* sp.	×		
	Caricoidea arnei Chandler		×	
	C. obscura Chandler	×		
	?*Caricoidea* sp.	×		
	Cladiocarya minima (Chandler) Mai in Mai and Walther, 1978[9]		×	
Ebenaceae	*Diospyros headonensis* Chandler	×		
Euphorbiaceae	*Euphorbiotheca lakensis* Chandler	×		
	E. platysperma Chandler	×		
	E. tuberculata Chandler	×		
	E. digitata Chandler	×		
	Euphorbiospermum punctatum Chandler	×		
	Wetherellia variabilis Bowerbank		×	
Flacourtiaceae	*Oncoba rugosa* Chandler		×	
Hamamelidaceae	*Steinhauera subglobosa* Presl[10]	×		

Table 8.2 - *contd.*

Family	Species	Lake	Arne	Studland
Icacinaceae	*Iodes acutiformis* Chandler	×	×	
	Natsiatum eocenicum Chandler[11]	×		
	?*Palaeophytocrene foveolata* Reid and Chandler	×		
	Icacinicarya inornata Chandler	×	×	
Lauraceae	*Laurocarpum* spp.	×		
Lythraceae	*Ammannia lakensis* Chandler	×		
	Alatospermum lakense Chandler	×		
Menispermaceae	*Tinospora arnensis* Chandler	×	×	
	Palaeococculus lakensis Chandler	×	×	
	Wardensheppeya poolensis (Chandler) Eyde, 1970	×	×	
Moraceae	*Ficus lucidus* Chandler (see Collinson, 1989)	×		
	F. sp.			×
?Moraceae	*Ovicarpum reticulatum* Chandler (see Collinson, 1989)		×	
Nymphaeaceae	*Palaeonymphaea eocenica* Chandler (see Collinson 1980a)	×		
Nyssaceae	*Nyssoidea eocenicum* Chandler	×	×	
Rosaceae	*Rubus acutiformis* Chandler	×		×
Rutaceae	*Phellodendron costatum* Chandler		×	
	Rutaspermum excavatum Chandler		×	
	R. glabrum Chandler	×		
	R. magnificum Chandler	×	×	
	R. striatum Chandler	×		
Sabiaceae	?*Meliosma sheppeyensis* Reid and Chandler	×		
Sapotaceae	?*Sapoticarpum* sp.		×	
Solanaceae	*Solanum arnense* Chandler		×	
	Solanispermum reniforme Chandler		×	
Styracaceae	*Styrax elegans* Chandler	×		
Symplocaceae	*Symplocos headonensis* Chandler		×	
	S. lakensis Chandler	×	×	
Theaceae	*Cleyera*? *obliqua* Chandler	×	×	
	?*Gordonia* sp.	×		
Thymelaeaceae	*Thymelaeaspermum lakense* Chandler	×	×	
	T.? *sulcatum* Chandler	×		
Vitaceae	*Vitis ambigua* Chandler	×		
	V. arnensis Chandler		×	
	V. cuneata Chandler	×		
	V. excavata Chandler	×	×	
	V. lakensis Chandler	×		
	V. lusatica Czeczott and Skirgiello[12]	×	×	
	V. platysperma Chandler	×	×	
	V. poolensis Chandler	×	×	
	V. pygmaea Chandler	×	×	
	V. goodhartii Chandler	×	×	
	V. symmetrica Chandler	×	×	
	V. triangularis Chandler		×	
	Tetrastigma acuminata Chandler		×	
	?*T. lobata* Chandler	×		
Zingiberaceae	*Alpinia arnense* (Chandler) Mai in Mai and Walther, 1985[13]		×	
Incertae sedis	*Rhamnospermum bilobatum* Chandler	×	×	
	Carpolithus arnense Chandler		×	

For footnotes to this table, see p. 218.

Footnotes to Table 8.2

1 *Ruffordia subcretacea* (Saporta) Barthel (1976) is the name in current use for *Anemia subcretacea* (Saporta) Gardner and Ettingshausen. However, the fossil, known as an almost complete plant, is very similar to *Anemia* and certainly belongs in the clade including *Anemia* (Collinson, in press a).

2 *Sequoia couttsiae* Heer = *Athrotaxis couttsiae* (Heer) Gardner, both Taxodiaceae. The former name has been applied to British material but the latter is used currently in continental Europe. However, as both these genera are modern genera, more than a mere nomenclatural decision is involved here. For the British material, Chandler (1925–1926 p.13) initially rejected Gardner's assignment to *Athrotaxis*. She reconfirmed and re-instated the affinity with *Sequoia* in full and made detailed studies of leaves, leafy shoots, twigs, cones and seeds (Chandler, 1962, 1963b, 1964), noting a marked similarity to *Sequoia sempervirens* (Chandler, 1964, 1978, p. 40, under discussion of *Sequoiadendron fordii*) and rejecting affinity with *Sequoiadendron* (Chandler, 1964, p. 104, 1978 pp. 40 and 41). Fowler *et al.* (1973) emphasized the difficulties of determining isolated foliage of Taxodiaceae, noting that Chandler (1964) had stated that the leaves of *S. couttsiae* were not identical with either *Sequoia* or *Sequoiadendron*. Rüffle (1976) also treated the species as a member of genus *Sequoia*. Subsequently workers in continental Europe (Mai and Walther, 1978, 1985, 1991; Mai, 1998; Knobloch *et al.*, 1996) have assigned the species to *Athrotaxis* citing the work of Dorofeev and Sveshnikova (1963) as the basis for this assignment. However, Dorofeev and Sveshnikova (1963) combined a range of material into their recombination *Athrotaxis taxiformis* (Unger) Dorofeev and Sveshnikova (including *S. couttsiae* and *A. couttsiae*). *Athrotaxis taxiformis* in their sense included material later assigned to an extinct genus of Taxodiaceae *Doliostrobus* Marion by Kvaček (1971). Mai (1998) expressed some reservations as to the use of the genus *Athrotaxis* for the remaining material. Furthermore, Dorofeev and Sveshnikova (1963) were apparently unaware of, and did not cite, the work of Chandler (1962, 1963, 1964) and, to the best of our knowledge, they had not been able to study the British material. There is considerable variation in Taxodiaceae leaves resulting in similarities between those of *Taxodium*, *Sequoia*, *Sequoiadendron* and *Glyptostrobus*. *S. couttsiae* is associated with tree stumps with wood of the *Glyptostroboxylon* type (Fowler *et al.*, 1973). It is therefore possible that, even though Chandler found a convincing affinity with *Sequoia* based on foliage, cones and seeds, a fully reconstructed plant bearing *S. couttsiae* foliage and cones might not resemble modern *Sequoia* in all features. Until such a plant can be reconstructed, ideally based on organic attachment, and included in a cladistic analysis of the Taxodiaceae, its relationships must remain slightly uncertain. Finally one must consider the relative unlikelihood of a relationship with modern *Athrotaxis*, which is endemic to Tasmania. There are numerous relationships between the Palaeogene floras of Europe, and those of the USA and Asia (Manchester, 1999). Numerous modern genera recorded in these Palaeogene floras now grow in south-eastern Asia and America (Manchester, 1999; Tiffney, 1994), some occur in Africa and South America (Tiffney, 1994) and a few occur in Australia (Tiffney, 1994). However, all those occurring in Australia also occur today in eastern Asia or in both eastern Asia and the New World; none are Australian endemics today. Some claims for records of Proteaceae and Cunoniaceae in the northern hemisphere Tertiary are all based on very old literature and all have been subsequently rejected (Mai, 1995). Thus, there is no evidence for floristic affinity between Australia and the European Palaeogene, and the occurrence of a modern Australian endemic in the European Palaeogene is judged to be extremely unlikely. For all these complex reasons we have retained the name in current use in Britain for British material i.e. *Sequoia couttsiae*. While this volume was in press, Kunzman (1999) reassessed the systematic affinity of *S. couttsiae* and judged that it represented an extinct member of the Taxodiaceae, which he assigned to the genus *Quasisequoia* as *Q. couttsiae* (Heer) Kunzman.

3 Formerly *Hordwellia crassisperma* (Chandler) Chandler and thought to belong to the Theaceae (see Mai and Walther, 1985).

4 Formerly *Actinidia poolensis* Chandler, 1963b.

5 According to Manchester (1999, p. 476), the genus *Echitonium* Unger has priority for apocynaceous seeds for which the generic affinity is unclear.

6 *Dunstania* has been assigned to *Cornus* by some authors (e.g. Eyde, 1988) (see discussion in Manchester, 1994, p. 42).

7 Mai (1993) synonymized this with *Mastixiopsis* (Kirchheimer).

8 Formerly *Cornus quadrilocularis* Chandler.

9 Formerly *Caricoidea minima* (Chandler) Chandler.

10 Includes *Protaltingia hantonensis* Chandler (see Mai and Walther, 1985).

11 See footnote 8 to Table 8.1. Kvaček and Bužek (1995) treated the Lake and Hordle *N. eocenicum* as *Palaeohosiea bilinica* (Ettingshausen) Kvaček and Bužek, whilst Mai and Walther (1978) used *Hosiea bilinica* (Ettingshausen) Holy.

12 Includes *Vitis glabra* Chandler (see Mai and Walther, 1991).

13 Formerly *Aracispermum arnense* Chandler, then included within the Araceae.

dominant diagnostic elements of this interval aside (*Nypa* in the London Clay and '*Scirpus*' for the Dorset Pipe Clays – Collinson, 2000a), both assemblages include species of the dillenia, dogbane, dogwood, flacourtia, grape, icacina, moonseed, sapodilla, spurge, sumac, sweetleaf and tea families. There are groups present at Lake and not in the London Clay, including the caper, elder, ebony and styrax families. Nevertheless, it seems that behind the effects of the 'local' mangrove versus lake or river margin vegetation, both floras are representing basically similar, paratropical forests.

As suggested by Collinson (1983b), a superficial appraisal of the London Clay and Dorset Pipe Clay fruit and seed assemblages (compare Tables 8.1 and 8.2) suggests marked differences at the rank of species. This may, however, be as much to do with the differences in preservation as with differences in the composition of the original vegetation (Collinson, 1983b). For instance, ***Dunstania glandulosa***, ***Iodes acutiformis***, ***Icacinicarya inornata*** and ***Palaeobursera lakensis*** from the Dorset Pipe Clay may well be the same as ***D. multilocularis***, ***I. corniculata***, ***I. platycarpa*** and ***P. bognorensis*** from the London Clay, respectively (Chandler, 1962). The classic London Clay palaeobotanical sites (e.g. Sheppey) produce pyrite petrifactions that often yield the type of anatomical detail not seen in the Lake fossils. Furthermore, they are less vulnerable to shrinkage during fossilization, which can produce apparently dramatic differences in size and morphology. Work on the sites that yield carbonaceous London Clay-type fruits and seeds (e.g. Walton-on-the-Naze) might help resolve this problem (Collinson, 1983b).

Another difference between the floras is the apparently greater abundance of smaller fossils at Lake, such as ***Ficus lucidus***, ***Ehretia lakensis***, ***Palaeocleome lakense***, ***Capparidispermum eocenicum*** and ***Alatospermum lakense***. However, this is probably mainly because of tidal winnowing of the seeds at Sheppey removing the smaller fraction rather than any significant difference in the original vegetation. Collinson (1983b, p. 16) noted a comparable difference between surface-picked larger fruits and smaller fruits in sieved concentrates at Sheppey.

Associated with the angiosperm fruits are very small fragments of fern foliage. They show extremely fine preservation of the reproductive structures, from which Chandler (1955) was able to establish that they all belong to the now mainly tropical family, the Schizaeaceae. They demonstrate that ***Lygodium***, ***Anemia*** and the ***Anemia***-like ***Ruffordia*** had a much wider geographical range during the Eocene Epoch than they have today (Collinson, 1996a, in press a), a situation similar to that which we observe in the angiosperms.

Conclusions

The coastal exposures at Lake have yielded the most diverse assemblages of fossil fruits and seeds from the Lower Eocene Dorset Pipe Clays, about 50 Ma old. It preserves evidence of vegetation probably surrounding lakes or rivers, together with paratropical forest trees and lianas. It complements the floras of the similar-aged London Clay, as it lacks evidence of the ***Nypa*** mangrove-palm vegetation fringing the coasts. In contrast, it is dominated by '***Scirpus***' ***lakensis*** from a river or lake marginal plant. ***Nypa*** and '***S.***' ***lakensis*** are together diagnostic for early and middle Eocene floras in Britain. It also includes remains of the fern family Schizaeaceae, far outside the geographical range of their living relatives.

ARNE (SY 970 892)

Introduction

This exposure on the shore of Wareham Channel is one of only two sites still yielding fossil plants from the Lower Eocene beds traditionally called the 'Dorset Pipe Clays'. It complements the more diverse Lake flora by containing a number of species not found there (see Table 8.2).

The site was not discovered to be of palaeobotanical interest until some time after the better-known site at Lake. The only account of the fossils from the Arne exposures is by Chandler (1962).

Description

Stratigraphy

The low cliff and foreshore at Arne exposes sands and clays of the Dorset Pipe Clays (Poole Formation), which is early Eocene (Ypresian) in age. Within the sands are thin seams of carbonaceous material, probably deposited near the limits of a flood channel, and which contain numerous fossil fruits and seeds. There was also

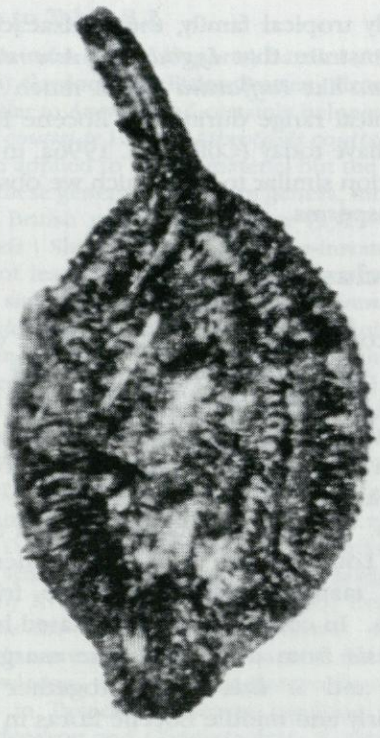

Figure 8.20 *Scirpus lakensis* in carbonaceous preservation (specimen number BMNH V.40396), found at Arne, × 50 (see Chandler, 1962; Collinson, 1996b). (Photo: M.E. Collinson.)

exposed (now apparently covered by silt) a band of densely packed fossil ferns.

Palaeobotany

Chandler (1962) has reported 39 species from Arne, which are listed in Table 8.2. Most are angiosperm fruits and seeds, but there are also schizaeacean and pteridacean ferns, and foliage of a redwood conifer. As at Lake, the dominant fossil is usually the fruit of the enigmatic plant '*Scirpus*' (Figure 8.20), although the pteridacean fern *Acrostichum* dominates at least one level. The fossils are mainly carbonaceous fragments. Coarse pyrite overgrowth sometimes occurs but unfortunately does not preserve the anatomy of the plants, as in the London Clay flora.

Interpretation

Arne is only the second site now known to yield fossil fruits and seeds from the Dorset Pipe Clays (the importance of the plant fossils from these deposits is discussed in the account of the Lake site). It is thus of national importance for understanding the paratropical forests that grew over much of southern Britain during early Palaeogene times. The Arne flora is neither as diverse nor as well preserved as the Lake flora. Arne is nevertheless of considerable interest as it yields taxa not found at Lake, including members of the pteridacean, arum, flacourtia, nightshade, moonseed and sapodilla families. Arne is the type locality for 11 species.

The presence here of the pteridacean fern *Acrostichum*, also recorded in a nearby borehole (Collinson, 1978b), is of considerable interest as it is far outside its current geographical distribution. It is also notable that these Eocene examples were growing in freshwater swamps, whereas today it is normally found in mangrove settings (Collinson, 1996a, in press a).

Conclusions

The exposures at Arne have yielded a nationally important assemblage of early Eocene fruits and seeds from the Dorset Pipe Clays, about 50 Ma old. It is not as diverse or well preserved as the flora from Lake, but includes a number of plant groups not found there, such as the pteridacean ferns, arums, flacourtia, sapodilla and nightshade families.

BRACKLESHAM (SZ 775 975–SZ 844 930)

Introduction

The foreshore between Chichester Harbour and Selsey Bill (Figure 8.21) is one of the classic sites for studying the geology of the Bracklesham Group, the interval of strata overlying the London Clay in the eastern Hampshire Basin, and it has been independently selected for the GCR for Tertiary stratigraphy (under the name 'Wittering to Selsey Foreshore'; see Daley in Daley and Balson, 1999). Palaeobotanically, this is the best site for studying the flora of the Eocene Bracklesham Group. Sixteen horizons through the upper Ypresian and Lutetian Stages have yielded plant fossils, providing a record of the vegetational changes taking place in Britain during the onset of the post-Ypresian climatic cooling.

The earliest record of plant fossils from here was by Dixon (1850), in his account of the geology of this stretch of coast, while a second edition of the work (Dixon, 1878) included a review of the fossils by Carruthers. Gardner (1884) figured conifer cones from here, and Rendle (1894) and Reid (1897) illustrated examples of *Nypa* fruits. More recent accounts of the palaeobotany of this site are by Chandler (1961b) and Collinson (1978a, 1996b).

Description

Stratigraphy

The classic account of the geology here was by Fisher (1862) and, although there are more modern accounts (e.g. Curry and Wisden, 1958; Curry *et al.*, 1977), these often still refer to Fisher's numerical classification of the beds. The most recent review is by Daley (in Daley and Balson, 1999). The foreshore sequence (Figure 8.21) consists of mainly arenaceous deposits, the lower few metres belonging to the London Clay Formation, and the rest to the Bracklesham Group (Figure 8.22). Daley (in Daley and Balson, 1999) points out the difficulty of establishing the true thickness of the succession, but it is probably somewhere between 90 m and 120 m.

The Bracklesham Group consists of shallow marine to brackish deposits formed along the coastal margin (Plint, 1983) and are in part coeval with the non-marine Poole and Branskome Sand Formation to the west. There has been some disagreement as to the subdivision of the Group but it is now normally divided into the Wittering, Earnley, Marsh Farm and Selsey Formations. The Wittering Formation belongs to the upper Ypresian Stage, the rest to the Lutetian Stage.

Palaeobotany

Plant fossils have been found here throughout the Bracklesham Group. The commonest are remains of the mangrove vegetation (fruits of *Nypa burtinii* (Brongniart) Ettingshausen (Figure 8.23) and a possible piece of *Nypa* bark, together with the enigmatic *Wetherellia dixonii* (Carruthers) Chandler), especially in the lower Wittering and upper Earnley Formations. Other levels have the remains of brackish aquatic plants (*Limnocarpus forbesii* (Heer) Chandler, *Selseycarpus enormis* (Chandler) Collinson) and freshwater plants (*'Scirpus' lakensis* Chandler (Figure 8.24), *Caricoidea obscura* Chandler). Sometimes the brackish and freshwater elements are associated with the

Figure 8.21 Foreshore exposure of parts of the *Nypa* Bed exposed at Bracklesham Bay. (Photo: M.E. Collinson.)

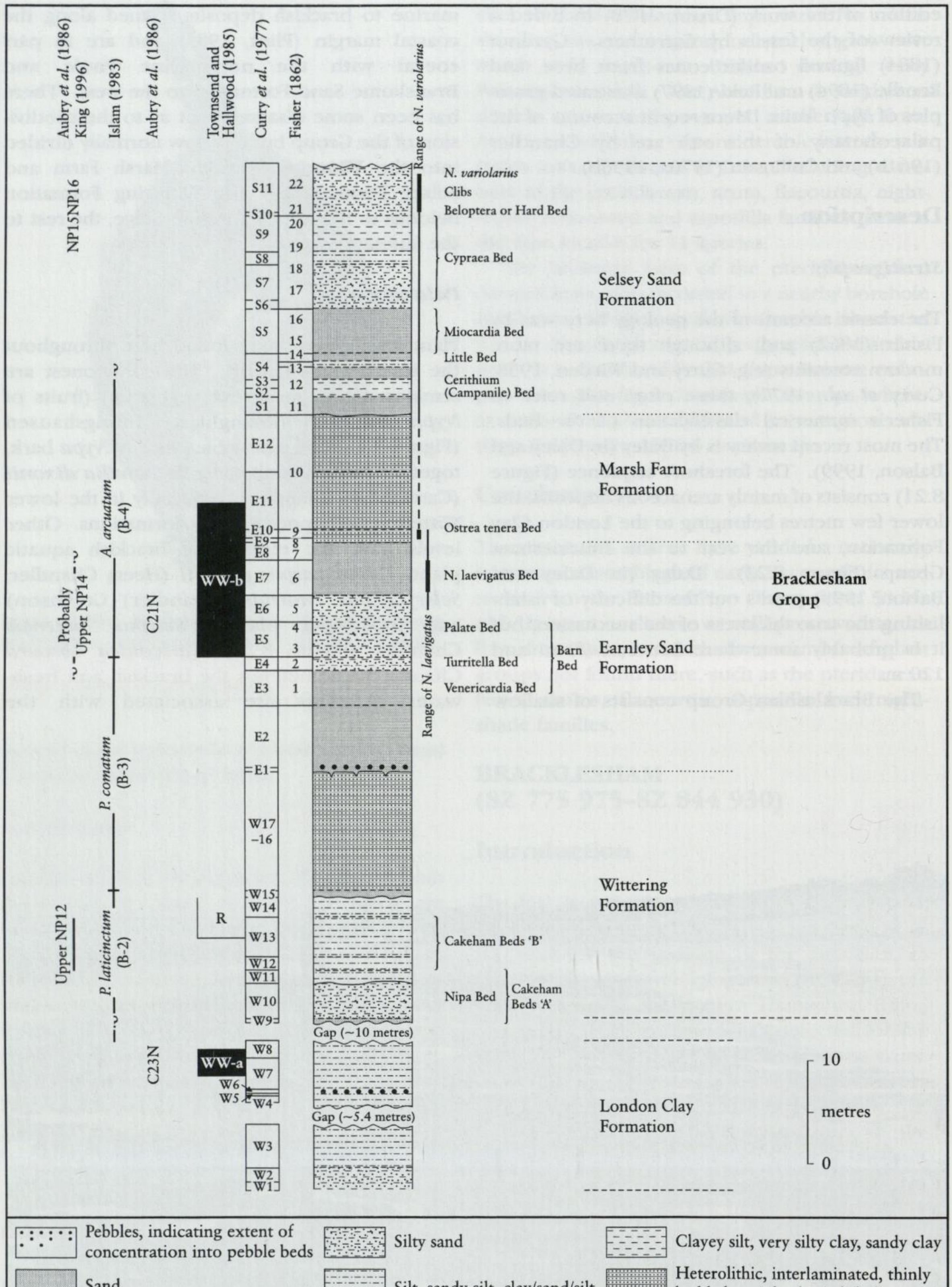

Figure 8.22 Stratigraphical succession at Bracklesham Bay. (After Daley and Balson, 1999, fig. 6.20)

Figure 8.23 Fruit of the mangrove palm *Nypa*, × 0.7. Bracklesham Bay. (Photo: Natural History Museum, London.)

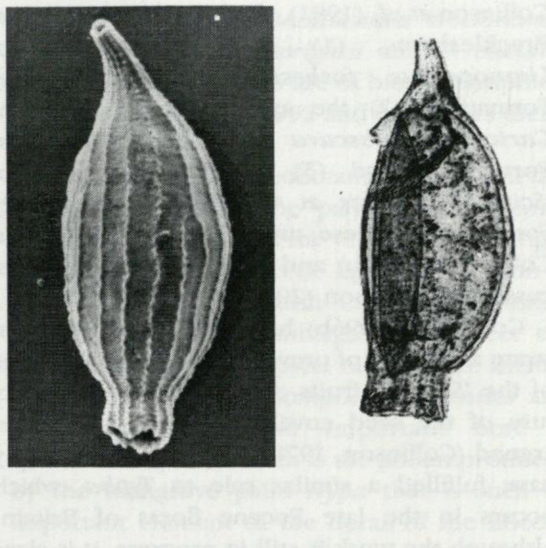

Figure 8.24 Seeds of *'Scirpus' lakensis*, viewed under Scanning Electron Microscope (left) and light microscopy (right); both × 38. See Collinson (1996b). Bracklesham Bay. (Photo: M.E. Collinson.)

mangroves, but they are, on the whole, commoner in the upper part of the section (Marsh Farm and Selsey Formations).

Chandler (1961b) described what she interpreted as a rhizome of a pondweed (Potamogetonaceae) from the topmost beds of the Selsey Formation. Collinson (1996b) has reinterpreted this fossil and together with additional material from the same bed, identifies it as a seagrass-like plant. Significantly, also from this bed, Murray and Wright (1974) described forminifera that are very similar to the faunas found today in seagrass communities.

In addition to these aquatic and marginal plants derived from the vegetation near to where these deposits were formed, there are the remains of trees presumably representing the vegetation of the surrounding forests. Most widely found are conifers, including *Pinus* cones, and leafy shoots known as '*Araucarites*' *selseyensis* Chandler. The latter might in fact have been from the extinct conifer genus *Doliostrobus* Marion, which belongs to either the redwood or monkey puzzle families (Mai, 1976; Collinson, 1996b). There are also various angiosperm fruits, seeds and foliage, including members of the sedge (*Carcoidea*), laurel (*Laurocalyx* sp.), moonseed (*Palaeococculus lakensis* Chandler, *Palaeosinomenium* cf. *venablesi* Chandler), mastic tree (cf. *Eomastixia rugosa* (Zenker) Chandler), rue and tea families. They occur at several levels within the sequence, but are most common in the upper Wittering Formation (Collinson, 1996b).

Interpretation

The Wittering Formation is contemporaneous with the upper London Clay and Dorset Pipe Clay. However, it complements the palaeobotany of both of these sites, by including both upstream riparian vegetation and mangroves, and is thus intermediate between the coastal mangroves preserved in the London Clay and the inland vegetation seen in the Dorset Pipe Clays.

Bracklesham is also important as the only British site with a good record of plant macrofossils through the late Ypresian–early Lutetian Bracklesham Group. This is a critical part of the palaeobotanical record in northern Europe, reflecting vegetational changes during the onset of global climatic cooling (Collinson *et al.*, 1981). This is especially evident in the record of the aquatic and marginal plants, which are especially well represented here. Of the events given as significant in this vegetational change by

Collinson *et al.* (1981), three can be identified at Bracklesham: (1) the appearance of ***Limnocarpus forbesii*** in the Wittering Formation; (2) the appearance of abundant ***Caricoidea obscura*** in the Marsh Farm Formation; and (3) the disappearance of ***'Scirpus' lakensis*** at the base of the Selsey Formation. These are fully documented in Collinson (1996b) and the latter is further discussed in Collinson (2000a).

Collinson (1996b) has been able to demonstrate a number of previously unknown features of the *'Scirpus'* fruits, including the ultrastructure of the seed envelopes. She had earlier argued (Collinson, 1978a) that these plants may have fulfilled a similar role to *Typha*, which occurs in the late Eocene floras of Britain. Although the work is still in progress, it is clear that the Bracklesham fossils will play a major role in understanding the affinities of this important Ypresian–lower Lutetian aquatic plant.

The ***Nypa burtinii*** from near the top of the Selsey Formation is one of the youngest authenticated examples of that genus known from the fossil record (Collinson, 1996b). The only younger example is a single specimen said to be from the Boscombe Sand Formation and lost since 1894 (Chandler, 1960; see also Collinson, 1996b). The examples of ***N. burtinii*** from the Wittering Formation are also of interest, as they were probably deposited nearer where the plant grew than the comparable fossils from the London Clay. They are sufficiently common at one level in the lower Wittering Formation for it to be known as the *Nypa* Bed and to have been interpreted as representing a strand-line (Collinson, 1996b). Also near this level, Collinson (1996b) reported the discovery of what may be a segment of bark of *Nypa*, the only such example known from the British Tertiary strata. This all offers one of the best opportunities to study the Eocene *Nypa* mangroves and to reconstruct this important ecosystem (Collinson, 1993, 1996b).

Bracklesham is the best site for the study of Eocene seagrass communities. Seagrasses are generally very rare in the fossil record and were for a long time only recognized through the presence of the characteristic foraminifera faunas (Brasier, 1975). While macrofossil remains of the plants themselves are known from Herne Bay and Belgium (Stockmans, 1936; Chandler, 1961a; Collinson, 1983b), Bracklesham has yielded the plants with their associated fauna (Collinson, 1996b).

It is evident that Bracklesham is a site of outstanding importance for Tertiary palaeobotany, in understanding both the vegetational changes occurring in the late Ypresian and early Lutetian, and some of the individual plants that made up that vegetation. This was a time of significant climatic and vegetational change (Collinson *et al.*, 1981; Collinson, 2000a,b) and Bracklesham is crucial for understanding them.

Conclusions

Bracklesham is an internationally important site for early and middle Eocene plant fossils, *c.* 45–50 Ma old. It helps significantly in understanding the changes in vegetation that were taking place at that time, changes that were being triggered by a cooling of the climate. It is one of the best sites for studying the mangrove palms (*Nypa*) and the ***'Scirpus' lakensis*** plant, both of which were diagnostic elements in the middle Eocene vegetation of Europe. It is also the best site for the study of seagrass communities of this age.

WHITECLIFF BAY (SZ 638 858– SZ 652 871)

Introduction

Whitecliff Bay is the best exposure in western Europe of a long sequence through part of the Eocene Series, with potential for studying the vegetational succession. It is particularly important for allowing other isolated floras to be placed in their superpositional context. This site has been independently selected as a Tertiary stratigraphy GCR site (Daley in Daley and Balson, 1999).

The plant macrofossils from here are rather few, the only specimens having been reported by Chandler (1961b, 1963a) and Collinson (1978a, 1996b). However, the exposure has revealed an unrivalled sequence of palynological data through the Eocene Series (Collinson *et al.*, 1981), which has provided important evidence as to the pattern of vegetational and climatic change occurring at that time. Charophytes have been found in the upper Eocene strata of this section (Feist-Castel, 1977) and there is a rooted lignite in the middle Eocene (Plint, 1983).

Description

Stratigraphy

Daley (in Daley and Balson, 1999) reviews the stratigraphy of this site. The full Tertiary sequence here is *c.* 550 m thick and lies unconformably on the Chalk. The Tertiary beds have been assigned to the Lambeth, Thames, Bracklesham, Barton and Solent groups, and range in age from late Palaeocene (Thanetian) to early Oligocene (Rupelian).

Palaeobotany

Two specimens of fan palm leaf from the Bembridge Marls at Whitecliff Bay were described and figured by Reid and Chandler (1926) as *Palaeothrinax mantellii* Reid and Chandler. Chandler (1963a) did not revise these specimens but recorded a seed of *Sabrenia chandlerae* Collinson from the Bembridge Marls. From the middle muds within Bembridge Limestone, Allan Lawson has recovered seeds of *Stratiotes* (Collinson, pers. obs.). Singer (1993) undertook a detailed palynological study of this unit.

Limnocarpus forbesii (Heer) Chandler was figured by Chandler (1961b) from the basal Wittering Formation and is one of the earliest records of the genus (Collinson, 1982a, 1996b). '*Scirpus*' *lakensis* was recorded from the Fisher Bed V in the upper Wittering Formation (Collinson, 1996b). Also in Fisher's Bed V is a rooted lignite (Plint, 1983) that preserves thick, long roots, suggesting a rooted woody vegetation (Collinson, pers. obs. in foreshore exposures). Fungal remains from here are described by Collinson (1978a) in her unpublished thesis. There are plant remains from the London Clay exposed here, in the collections of the Natural History Museum, London (e.g. *Nypa*) and *Platycarya* occurs here (Collinson, pers. obs.) but they have never been described in the literature.

Groves (1926) and Feist-Castel (1977) described charophytes from the upper part of the Whitecliff Bay section. From the Osborne Beds (Solent Formation), Feist-Castel (1977) described *Gyrogona wrightii* (Salter ex Reid and Groves) Pia, *Harrisichara* sp., *Chara* sp. and *Sphaerochara* sp.. From the Bembridge Beds, she reported *Harrisichara tuberculata* (Lyell) Grambast, *Sphaerochara subglobosa* (Groves) Horn af. Rantzien, *Rhabdochara stockmansii* Grambast, *Gyrogona wrightii* and *G. caelata*. Several of these species are of biostratigraphical value (see Collinson, 1992 and references therein).

Very significant palaeobotanical interest at this site is provided by the palynological record, which gives evidence of the vegetational changes taking place in the Eocene Epoch (Collinson *et al.*, 1981). The London Clay and Wittering Formations yield assemblages that reflect the mangrove and paratropical rain forests, including *Bombacacidites*, *Compositoipollenites* and *Anacolosidites*. Also important here is *Spinizonocolpites*, which is the pollen produced by the mangrove palm *Nypa* that is such an important element of the floras of the Eocene Thames and Bracklesham Groups. Most of these taxa disappear in the upper Wittering Formation, to be replaced by conifer pollen such as *Tsugaepollenites* and *Sciadopityspollenites*. A second change follows in the upper Selsey Formation and basal Barton Group, with an increased proportion of fern spores and of bisaccate and inaperturate pollen originating from conifers. Also seen here is the first appearance of *Aglaoreidia*, the pollen associated with the Potamogetoneae tribe of the pondweed family (Collinson, 1982a), although this tribe occurs as macrofossils rather lower in the sequence. Boulter and Hubbard (1982) expanded this palynological study, recognizing four palynologically based floras reflecting changing climate through the Cainozoic Era in Britain. Their work was based largely on borehole material but it shows the research potential of long sequences such as that at Whitecliff Bay.

Interpretation

Whitecliff Bay has yielded the best succession of Eocene palynofloras in an exposed sequence in western Europe. There are other known palynological sequences through strata of this age, but only in boreholes such as at Ramnor near Bracklesham (Anon., 1978, Boulter and Hubbard, 1982). Although currently sparse and scattered, the macropalaeobotanical records from the London Clay, Wittering Formation, Bembridge Marls and Bembridge Limestone indicate that there is also considerable research potential here.

Combined with the complementary macrofossil record from sites such as Bracklesham Bay, Whitecliff Bay gives an unrivalled insight into the vegetational changes taking place at that time as a response to climatic cooling. Of particular interest is the evidence that there was not a single vegetational change in Eocene times, but a change that occurred in at least two steps. This in turn has consequences for understanding Palaeogene climatic changes, which have to be balanced against palaeotemperature curves obtained through physical measurements, which indicate an ultimate sharp cooling event at the Eocene–Oligocene boundary, within an overall cooling trend during late Palaeogene times.

The biostratigraphical significance of the charophytes from Whitecliff Bay is discussed in the Tertiary stratigraphy GCR volume (Daley in Daley and Balson, 1999).

Conclusions

Whitecliff Bay has yielded the best sequence of pollen and spores through the Eocene strata of Western Europe. It has also yielded a sparse macrofossil record and stratigraphically important charophyte floras. It is the only place to show clearly the pattern of vegetational changes that were occurring through a 20 Ma interval (55–35 Ma ago) as the climate gradually cooled from the Eocene 'greenhouse' conditions towards the onset of 'icehouse' conditions.