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 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; 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 (Figure 8.7), (Figure 8.8), (Figure 8.9), (Figure 8.10), (Figure 8.11), (Figure 8.12), although some partly carbonaceous fossils also occur (Figure 8.11). The pyrite fossils yield anatomical detail (Figure 8.10), (Figure 8.11), (Figure 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 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).

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 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.

(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	×		

	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			×
Anacardiaceae	*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	*Catyotispermum 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			×
	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		×	
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.		×
	Steinhauera subglobosa Presl (see Mai and Walther, 1985)[6]	×	×

Icacinaceae Iechinata Chandler	*Faboidea crassicutis* Bowerbank	×		×
	Icacinicarya amygdaloidea Chandler	×		
	I. bognorensis Reid and Chandler		×	
	I. echinata Chandler			×
	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			×

	Juglandicarya cantia Reid and Chandler			×
	J. cooperi Chandler	×		
	J. crassa (Bowerbank) Reid and Chandler			×
	J. depressa Reid and Chandler	×	×	×
Juglandaceae	*J. lubbockii* Reid and Chandler	?		×
	J. minuta Chandler	×		×
	Platycarya richardsonii (Bowerbank) Chandler, 1964	×	×	×
	Pterocaryopsis bognorensis Chandler[8]		×	
	P. elliptica Chandler, 1978		×	×
	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			×
Lauraceae	*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		×	×
	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			×
	Cranmeria trilocularis Reid and Chandler			×
	Minsterocarpurn alatum Reid and Chandler			×
Lythraceae	*Pachyspermum quinqueloculare* Reid and Chandler			×
	Tamesicarpum polyspermum Reid and Chandler	×	×	×

	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	×	×	×
Magnoliaceae	*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		×	×
	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]		×	
	Eohypsetpa 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	×	×	×
	Menispermaxylon sp. (see Poole and Wilkinson, 2000)			×
Moraceae	*?Mores* sp. (see Collinson, 1989)			×
Myrsinaceae	*Ardisia(?) eocenica* Reid and Chandler			×

	Aldwickia venablesii Chandler	×	×	×
?Myrtaceae /Theaceae	*Palaeorbodomyrtus subangulata* (Bowerbank) Reid and Chandler			×
Nymphaeaceae	*Protobarclaya eocenica* Reid and Chandler			×
Nyssaceae	*Nyssa oviformis* Reid[10]	×		×
	N. cooper 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)	×		
Rhizophoraceae	*Ceriops cantiensis* Chandler			×
	Palaeobruguieria elongata Chandler	×		
	P. alata Chandler	×		
	P. sp. nov. (Wilkinson, 1983)			×
Rosaceae	*Rubus* sp.		×	

Rutaceae	*Canticatya 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		×	
	Sbrubsolea 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. Tatum 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			×

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	×		×
Styracaceae	*Sterculia subovoidea* (Reid and Chandler) Mai in Mai and Walther 1985[12]	×		×
	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 ellzptica* Bowerbank	×	×	×
	H. turgida Bowerbank	×		×
Thymelaeaceae	*Aquilaria bilocularis* (Reid and Chandler) Mai[l']	×		×
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 ramunculifornzis Poole and Wilkinson, 2000			×

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] Kva■ek and Bužek (1995) recombined *Natsiatum eocenicum* from the London Clay as *Palaeobosiea marchiaca* (Mai) Kva■ek 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; 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).

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 southeastern 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 dipte-rocarp 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.

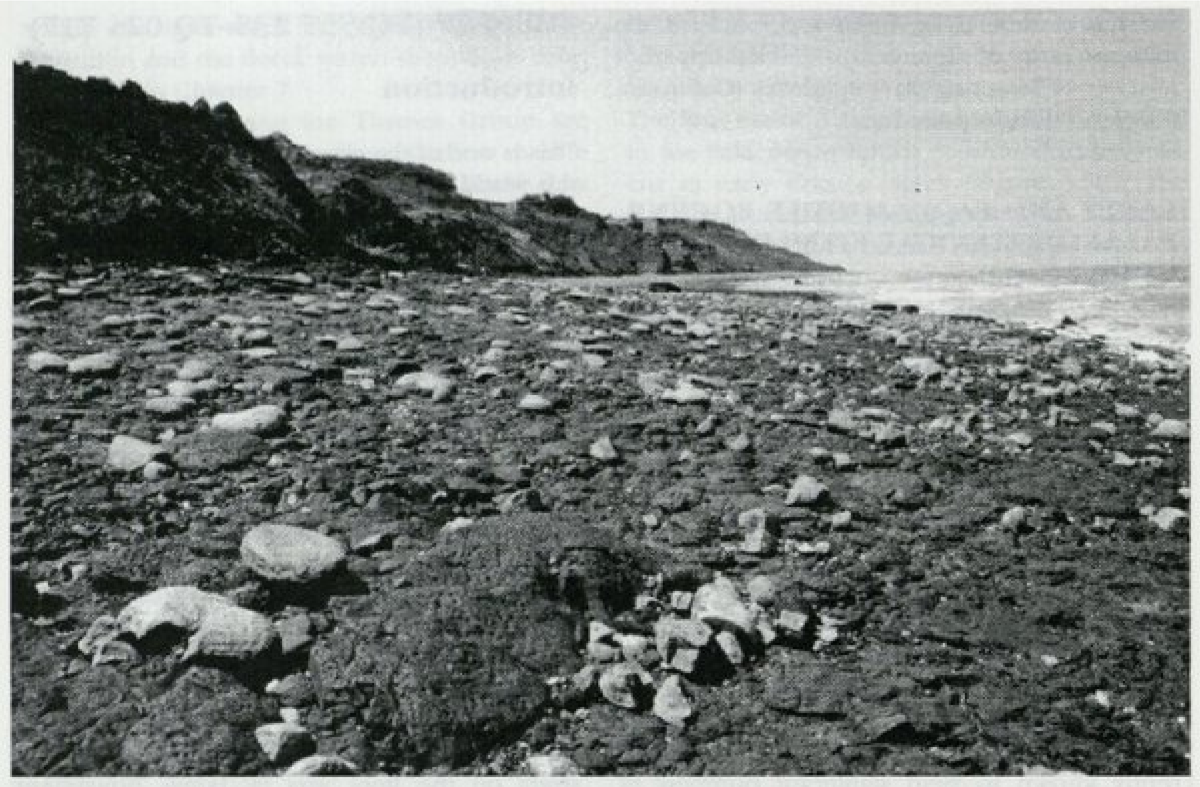
Sheppey has also proved to be the best site for the study of fossil wood and twigs in the London Clay (Figure 8.7; Brett, 1972; Collinson, 1983b, 2000b, in press a; Wilkinson, 1984, 1988; Crawley, 1989; Poole, 1992, 1993a,b, 1996, 2000; Poole and Wilkinson, 1992, 1999, 2000; Poole and Page, 2000). They 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.

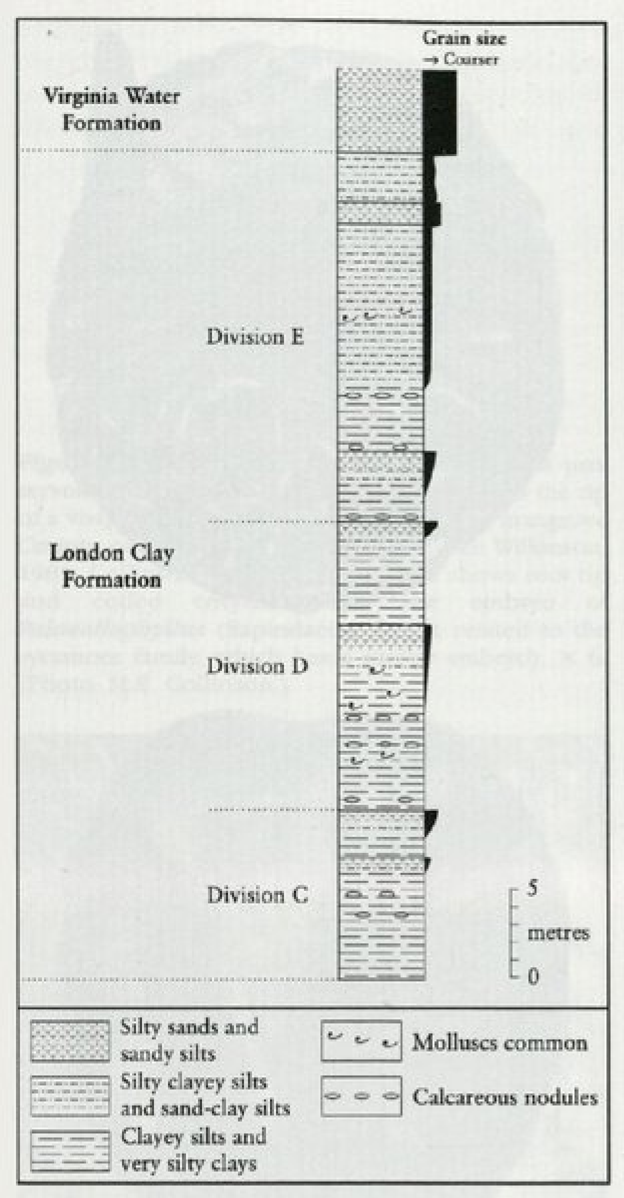
Conclusions

Sheppey has yielded the most diverse seed and fruit flora representing the early Eocene para-tropical 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.

References

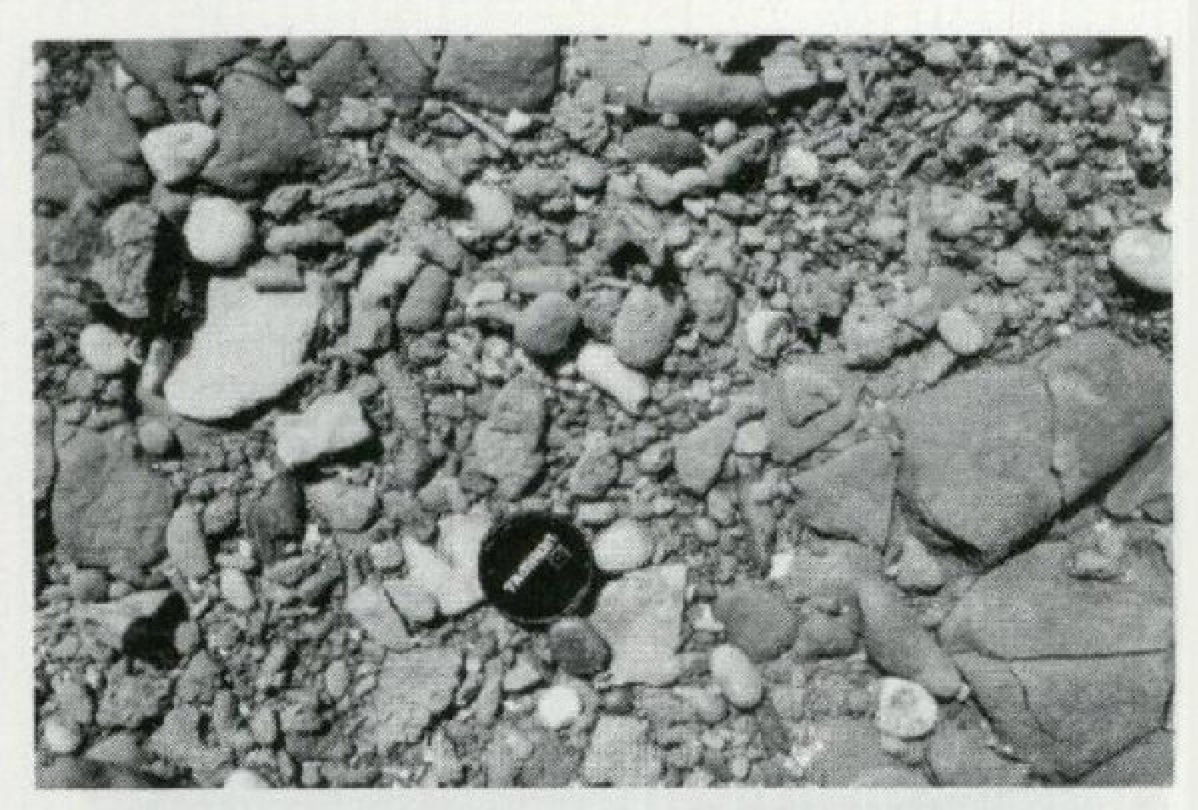


(Figure 8.5) Cliffs and foreshore at Sheppey, as seen looking west from Warden Point. (Photo: M.E. Collinson.)

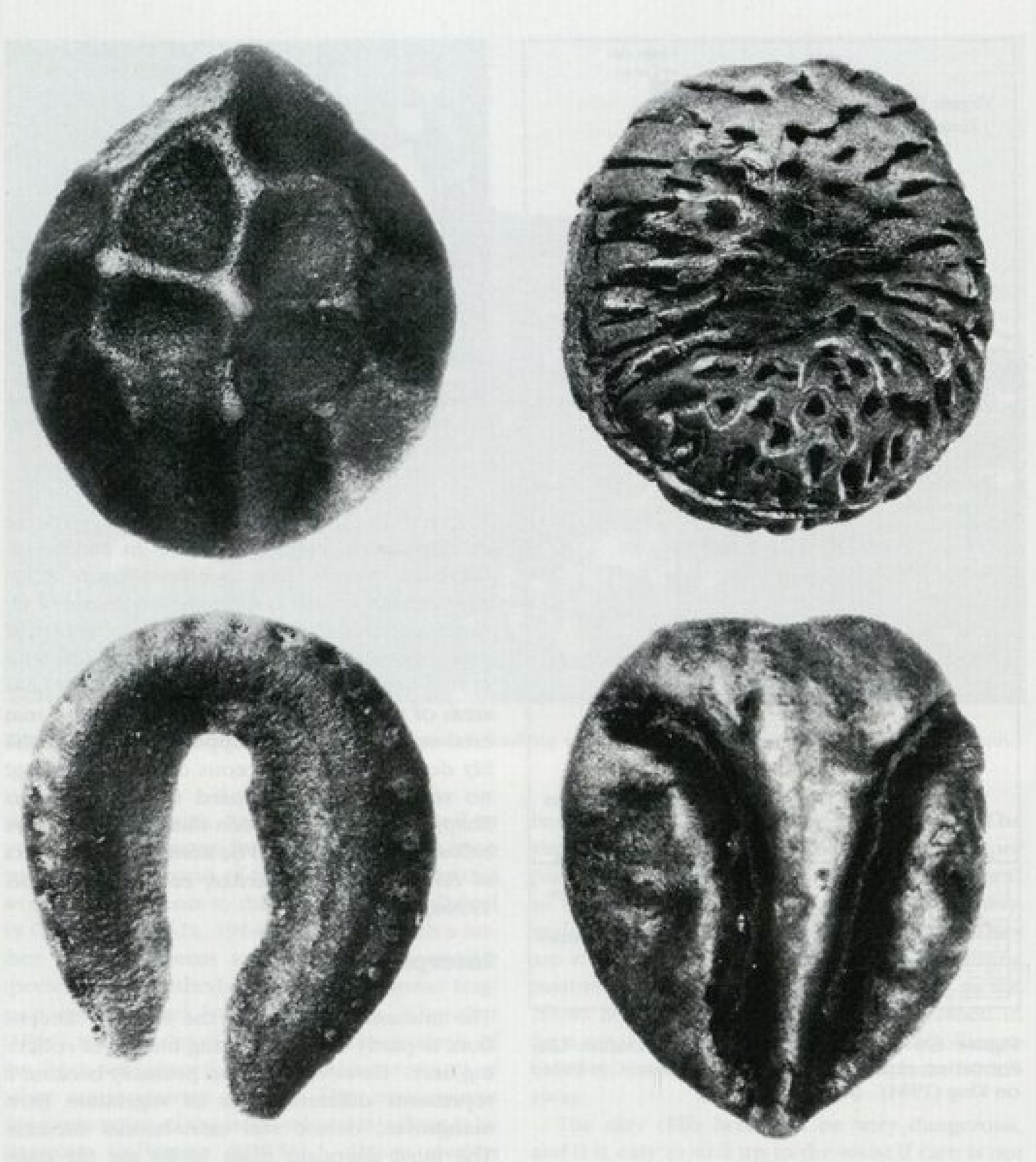


(Figure 8.6) Lithostratigraphy of the London Clay Formation exposed at Sheppey. Division C is based on King (1984). (After King, 1981)

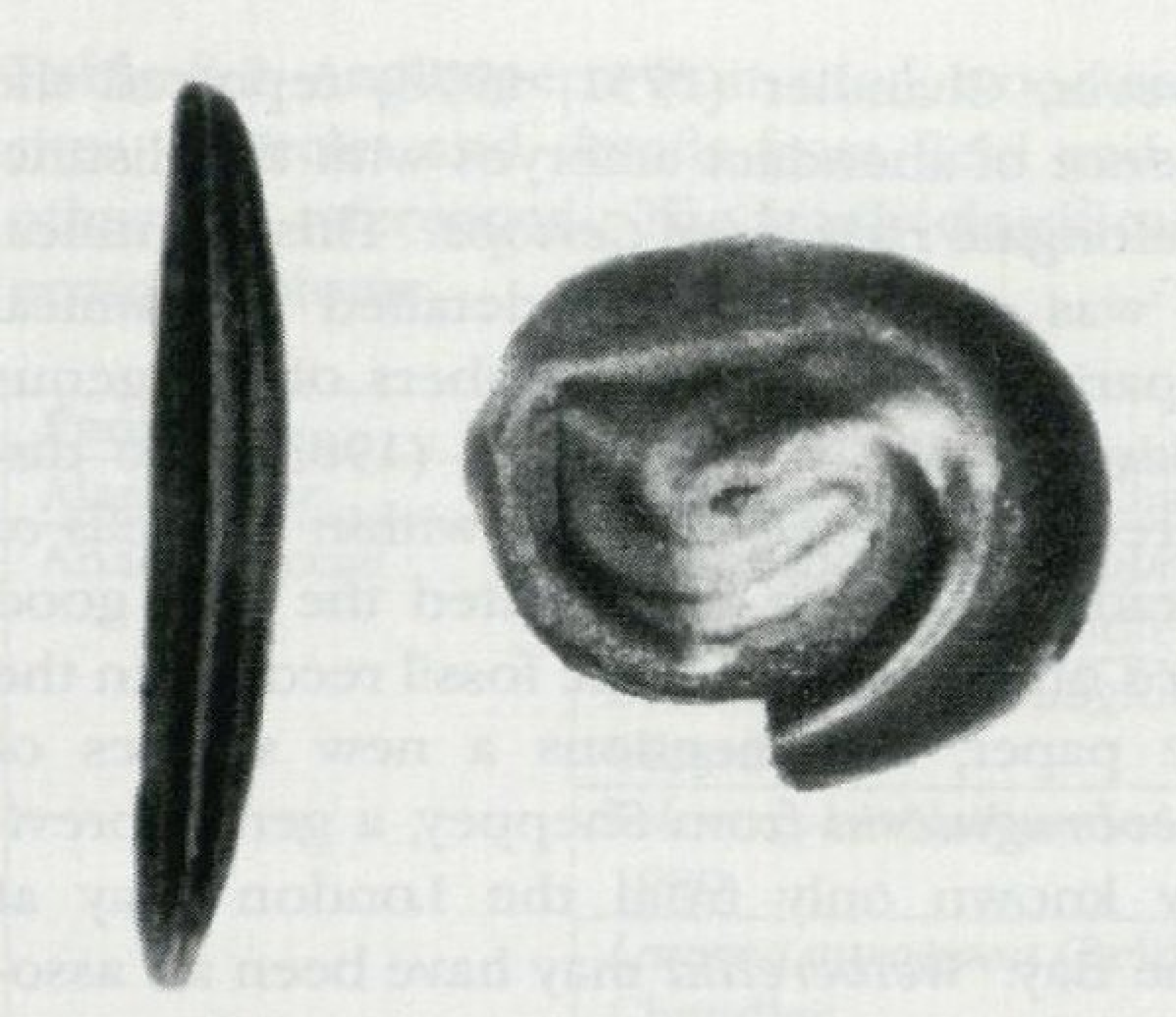
(Figure 8.11) Leafy shoot of the conifer Araucarites sp., × 3.7 (see Collinson, 1983b). This is a rare example of an in-situ fossil from the clay sediment at Sheppey. (Photo: M.E. Collinson.)



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

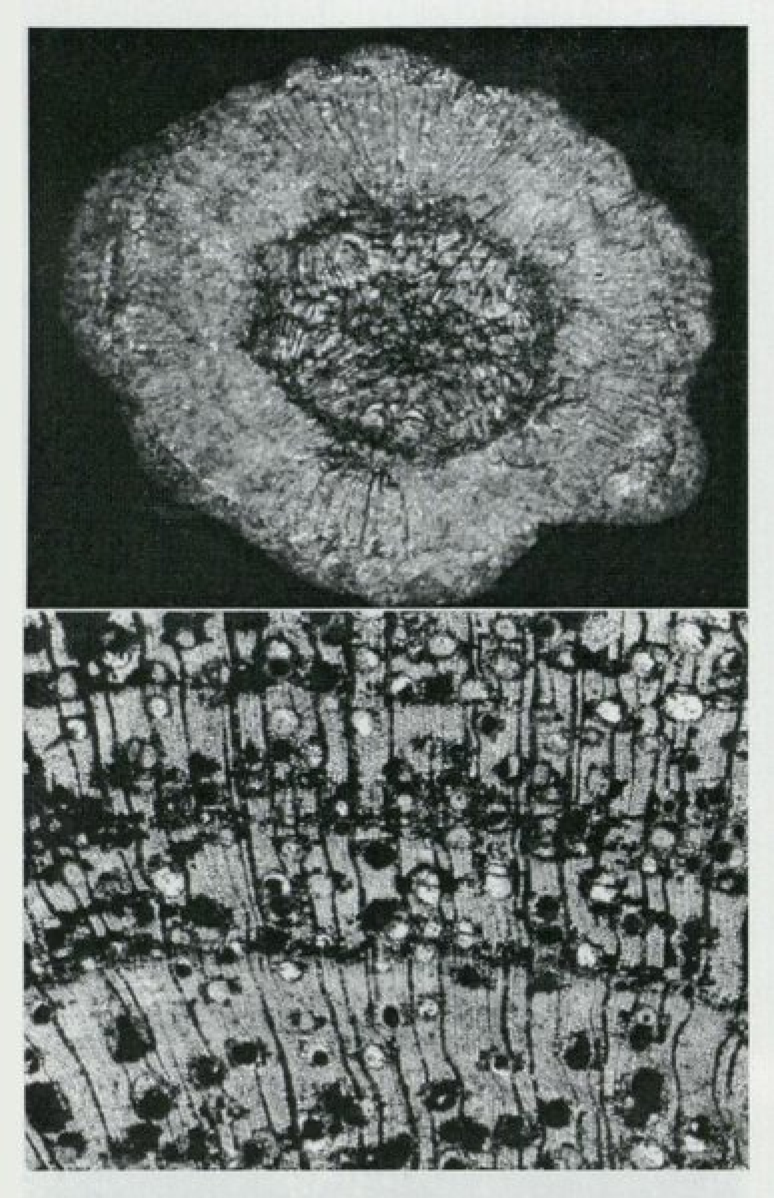


(Figure 8.8) Pyritized internal casts of fruits and seeds of families typical for the London Clay flora at Sheppey (see Collinson, 1983b). Upper left shows Iodescorniculata (icacina family), × 12. Upper right shows Anonaspermum cerebellatum (custard apple family), × 14. Lower left shows Diploclisia auriformis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

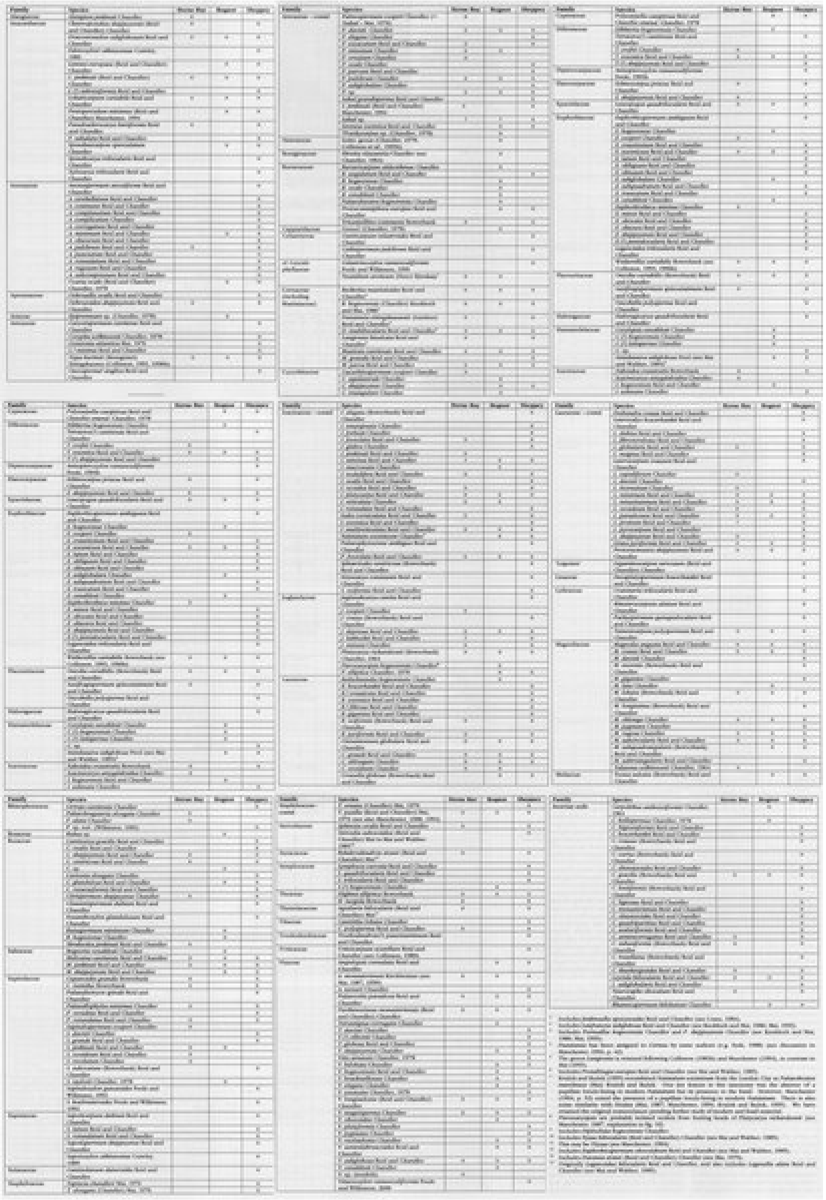


(Figure 8.9) Pyritized preservation of embryos preserved in the London Clay at Sheppey. Left is the tip of a viviparous embryo ('sea pencil') of the mangrove Ceriops cantiensis, about natural size (see Wilkinson, 1981; Collinson, 1983b, 1993). Right shows root tip and coiled cotyledons of the embryo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

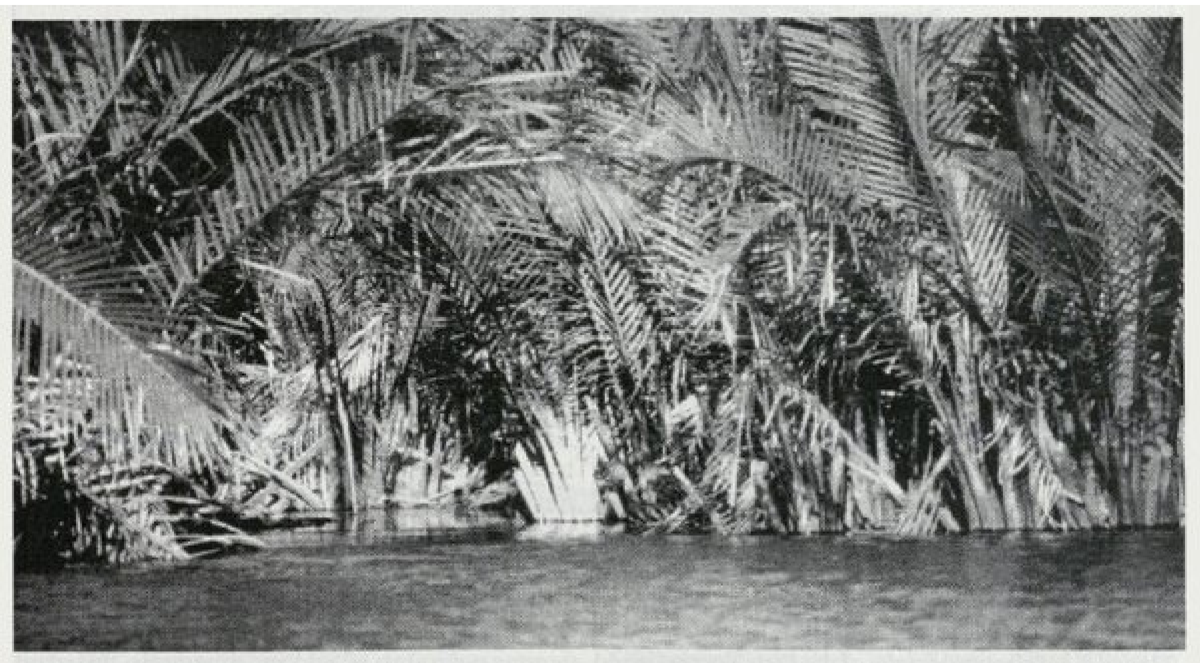
(Figure 8.10) Anatomical preservation by pyrite per-mineralization of the axis of a fern frond (a possible dennstaedtioid fern) (see Collinson, in press a). The uppermost picture is of a polished, transverse section of the axis, × 14. Below is a close-up showing cell detail, even in the delicate parenchyma 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.)



(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.



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