IN SITU CONIFEROUS (TAXODIACEOUS) TREE REMAINS IN THE UPPER EOCENE OF SOUTHERN ENGLAND

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ABSTRACT. Coniferous tree stumps and roots attributable on evidence of wood anatomy to the form-genus *Glyptostroboxylon* Conwentz occur in Upper Bartonian (Upper Eocene) strata at two localities in the Hampshire Basin, southern England. They are the first trees found in growth position in the English Lower Tertiary. Evidence that they grew in a flooded or waterlogged habitat is given by the mode of fossilization and characteristics of the associated flora. The fossil root morphology and wood anatomy resembles that of certain living Taxodiaceae, especially *Glyptostrobus* and *Taxodium*, themselves inhabitants of waterlogged and flooded terrain. *Taxodium* type pollen occurs with the roots, but associated foliage and cones are attributable to *Sequoia couttsiae* Heer. These taxodiaceous macrofossil remains may represent a single species with the characters of more than one living genus. Similar instances are known from Tertiary deposits elsewhere.

CONIFEROUS tree stumps and roots have been recognized at two localities in Upper Bartonian (Upper Eocene) strata of the Hampshire Basin (text-fig. 1A). At the eastern end of Beacon Cliff (Grid reference SZ 261923), Hampshire, the tree remains occur in the Lower Headon Beds, spaced at irregular intervals along about 400 m of the outcrop of the Leaf Bed (text-fig. 1B). In the south-eastern corner of Totland Bay (SZ 321866), Isle of Wight, similar fossils occur in strata correlated on palynological evidence with Bed L of the Barton Sands of Beacon Cliff (Fowler 1971) (text-fig. 1C), now nearly obscured by new sea defences.

The Leaf Bed at Hordle and Beacon Cliffs has yielded a rich macrofossil flora (Chandler 1925, 1926, 1961, 1964) and a rich microfossil flora (Fowler, unpublished data). Although stems and rootlets in growth position have been observed in the Leaf Bed (Hastings 1853, Tawney and Keeping 1883), tree roots were not recorded until recently (Edwards 1967). No plant macrofossils had been recorded from the Totland Bay locality prior to discovery of the tree roots.

The occurrence of *in situ* tree roots in these deposits proves that at least one element in the large contemporaneous flora grew at the fossil localities. The purpose of this paper is to establish the identity of the tree remains and the nature of their habitat, chiefly by a detailed account of the Beacon Cliff occurrence.

OCCURRENCE AND MORPHOLOGY OF THE STUMPS AND ROOTS

The morphological features of the stumps and roots are shown in Pl. 19, fig. 1. The illustrated specimens, from the Leaf Bed at Beacon Cliff, may be matched by similar specimens from the Isle of Wight locality. The partially crushed stumps, approximately 1·00 m in length by 0·25 m in diameter, are embedded chiefly in the sandy upper unit of the Leaf Bed (text-fig. 1B). The stumps are hollow and filled with the sandy matrix; the wood is black, humified, and soft. At the base of each stump, just above the point of origin of the roots, are buttress-like flanges. The laterally spreading roots appear to fork only occasionally. The basal part of the stumps and associated roots are embedded in the clayey-silt lower unit of the bed. In this lower
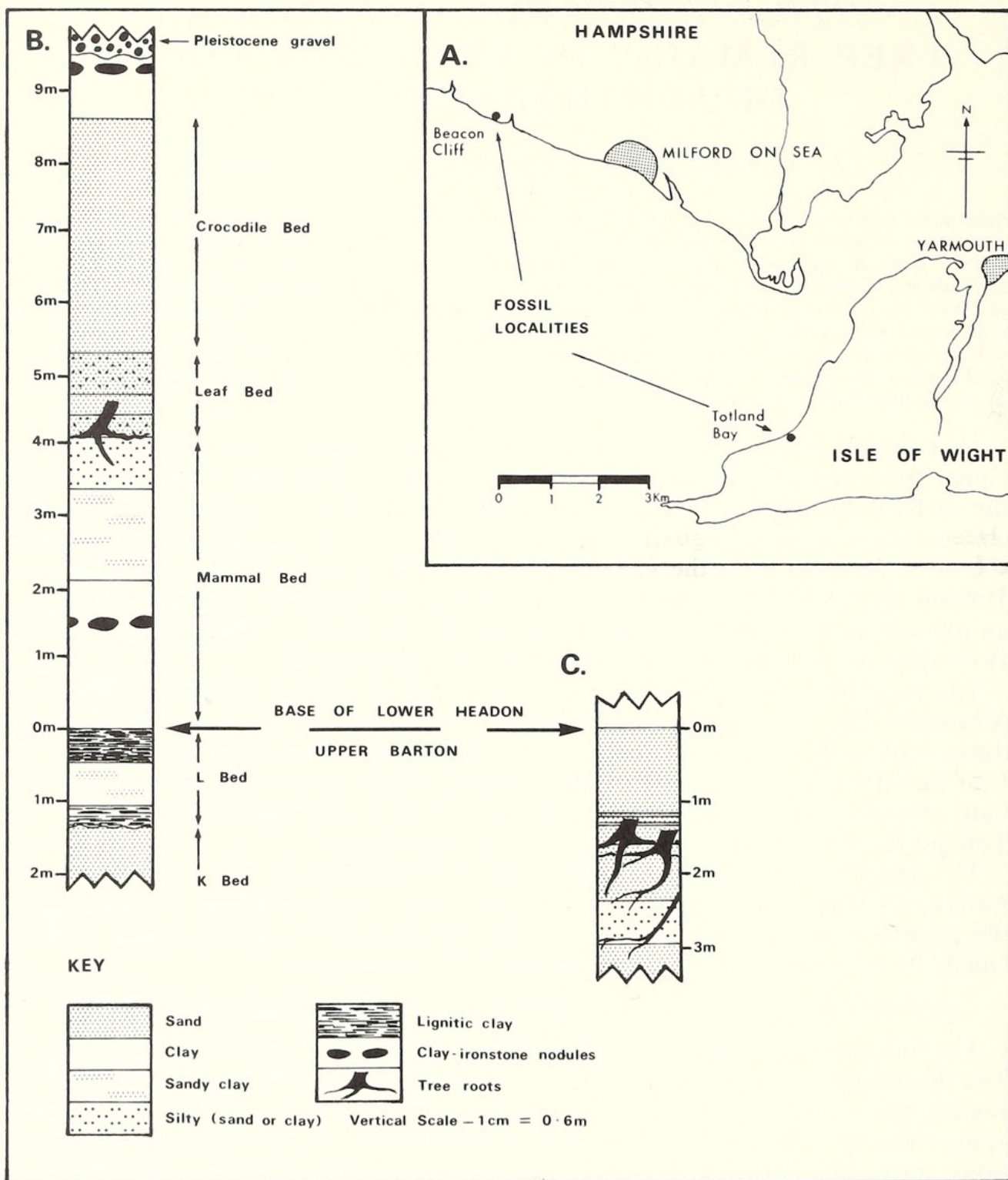
TEXT-FIG. 1. Geographical and stratigraphical location of the Eocene tree roots. A, location map; B, section at eastern end of Beacon Cliff; C, section at south-eastern end of Totland Bay.

unit, which is water-saturated, the wood is similar in appearance but better preserved than that above and slightly flexible, although partially pyritized. The roots have a flattened lens-shaped cross-section and are spread out over or slightly above the undulating upper surface of the underlying Mammal Bed. The roots are very long; one lying parallel to the cliff face was uncovered for a distance of about 3·00 m without its distal end being found. Some roots penetrate downward into the silty-clay upper unit of the Mammal Bed to a depth of 1·00 m. In this the wood is often heavily pyritized and sometimes thickly coated with pyrite.

The stumps and roots examined at Totland Bay occurred at two levels, each marked by a thin lignitic clay of local extent. Here, the laterally spreading parts of the root systems form interwoven mats and, as at Beacon Cliff, the wood preservation varies according to matrix.

The extent and continuity of branching of the fossil root systems, and their penetration of more than one stratum at both localities, seems good evidence that they are in growth position.

ANATOMY OF THE ROOT WOOD

Description. Pieces of root wood from both localities and driftwood from a pene-contemporaneous channel-fill deposit at Beacon Cliff were examined. As a result of compression, no useful transverse sections were possible. The following anatomical description is based on fractured surfaces and longitudinal sections. Much of the wood is badly degraded, especially near heavily pyritized areas, and fungal hyphae and rhizomorphs are frequent elsewhere. Preservation of the wood varies, only some parts being sufficiently well preserved to allow adequate examination of the finer features.

The wood is coniferous, consisting mainly of tracheids and ray parenchyma. Axial parenchyma is present but not abundant. There are no vessels or resin ducts.

The tracheids (Pl. 19, fig. 2) have circular bordered pits on the radial and tangential wall. Occasionally pitting is biseriate, but single pits usually are arranged along the tracheid, often irregularly, and never crowded. Where opposite pitting occurs, crassulae are present. The pits are approximately 10 μm in diameter, with inner apertures of 3–5 μm.

The rays (Pl. 19, fig. 3) range from 1–5 cells in height, but are usually low, being only 2 cells high. They are exclusively uniseriate, the cells more or less isodiametric, rounded in cross section (tangential view), somewhat bulbous, and slightly taller at the margins. The horizontal walls of the ray cells are not obviously pitted, though a few pit-like irregularities can be seen. Vertical and horizontal walls are of similar thickness and indentures were not apparent in the few entire end walls adequately observed. In the driftwood, rays of up to 7 cells in height were observed.

Cross-field pitting is taxodioid (Pl. 19, fig. 4), that is, with large, almost circular or ovoid pits having a narrow border, most commonly 1–3 pits (occasionally more) per field and typically arranged rather irregularly in 2 or 3 tiers. A few pit-pairs with a common border were seen to occur. No ray tracheids were observed.

The ray and axial parenchyma cells are often partially or completely filled with a dense material.

Identification. Wood of modern coniferous genera was compared with that of the fossil. The fossil wood resembles that of living genera of the Taxodiaceae and *Thuja* of the Cupressaceae. It is closely comparable to the wood of *Glyptostrobus pensilis* Koch and *Metasequoia glyptostroboides* Hu and Cheng. The arrangement of the large taxodioid cross-field pits seen in the fossil wood (Pl. 19, fig. 4) is characteristic of *Glyptostrobus*, whilst it only occasionally occurs (usually in the marginal ray cells) in other members of the Taxodiaceae.

Comparison with descriptions of wood from other Tertiary deposits suggests that the wood described above closely resembles in all important respects the wood *Glyptostroboxylon tenerum* (Kraus) Conwentz, an important element in some European brown-coals (Zalewska 1953, 1955; Grabowska 1957; Kilpper 1967). In anatomical detail the root wood differs from that of the trunk in having very low rays (Zalewska 1953). The somewhat taller rays of the driftwood from the English locality, already noted, may be thus explained.

It is proposed to use the name *Glyptostroboxylon* sp. for the fossil wood here described. Representative material has been deposited in the British Museum (Natural History), London (Catalogue numbers V57010–57014).

PALAEOENVIRONMENTAL INTERPRETATION

Evidence from mode of fossilization of plant remains. There is good evidence that the root wood at both localities has been in a waterlogged medium since death, and indeed may have lived in such an environment.
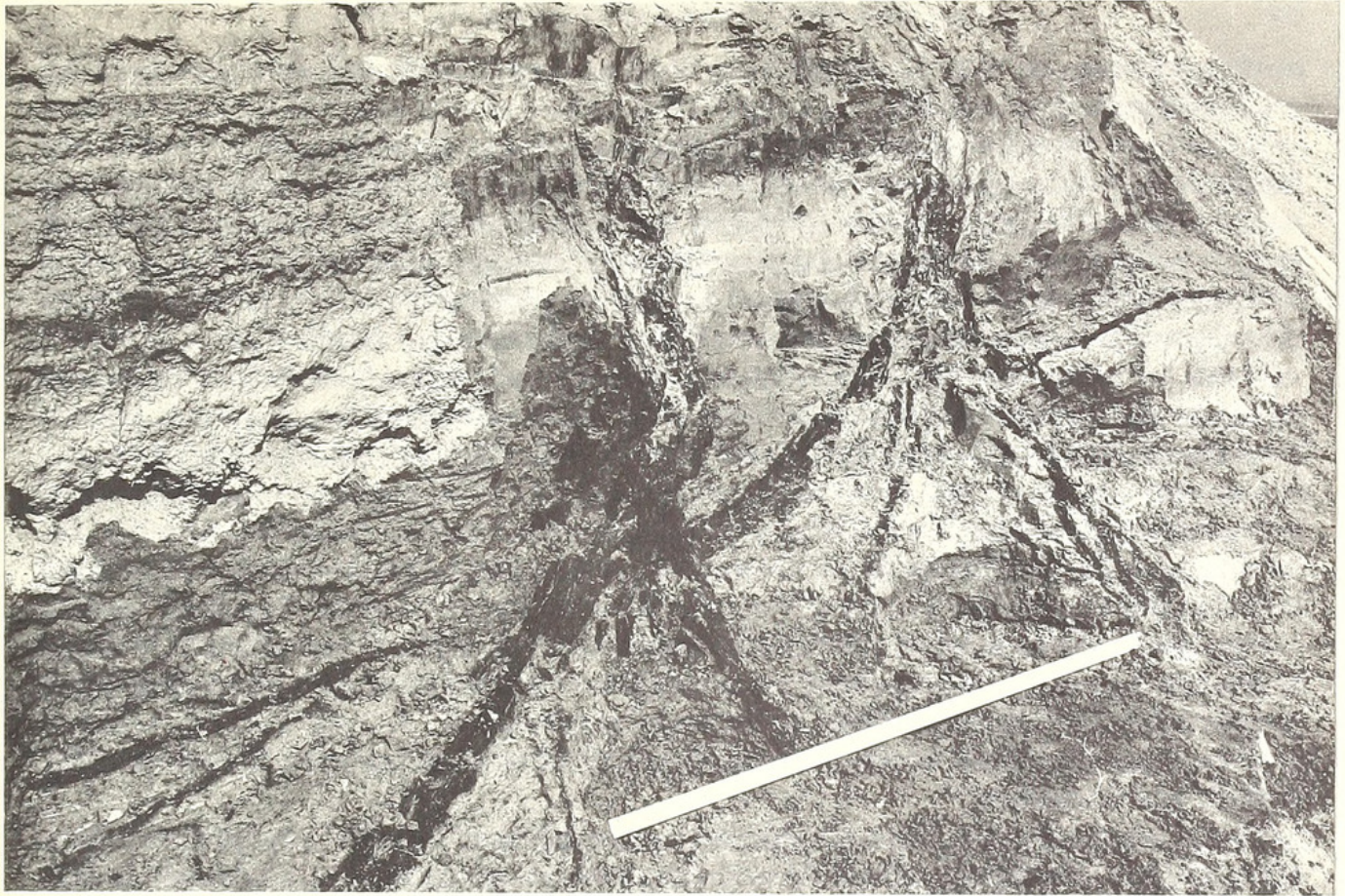
The high rate of organic accumulation in swamp environments, where woody vegetation is common, leads to arrest of decomposition at very shallow depths due to the toxic accumulation of humic derivatives (Coleman 1966b). In well-drained or aerated sediments wood is often destroyed by bacterial action and oxidation. The occurrence of well-preserved fossil wood suggests that it has remained under waterlogged conditions since its incorporation in these deposits. In waterlogged sediments, such wood becomes partially decayed and humified after death, ultimately collapsing during compaction of the matrix (Coleman 1966a) to give the lens-shaped cross-section seen in the fossil material. Corroborative evidence for these conditions is provided by the presence of abundant well-preserved macrofloral and microfloral remains in association with the fossil roots.

Further evidence for such an environment is presented by the occurrence of pyrite within, and forming encrustations on, the fossil roots. In modern freshwater environments, pyrite is most abundant in organic-rich, waterlogged sediments, often occurring as encrustations on dead plant rootlets (Coleman 1966b). It is regarded as being of early syngenetic formation under such conditions. The formation of pyrite is associated with the decay of protoplasm, and occurs commonly within plant cells (Love and Murray 1963). Crystals of pyrite in the parenchyma cells of the fossil root wood probably indicates that death of the parenchyma cells took place in the pyrite-producing medium (Brett and Edwards 1970).

Palaeobotanical evidence from taxodiaceous remains. The habitat requirements of modern taxa found to be closely related to the fossil taxa of the Leaf Bed provide
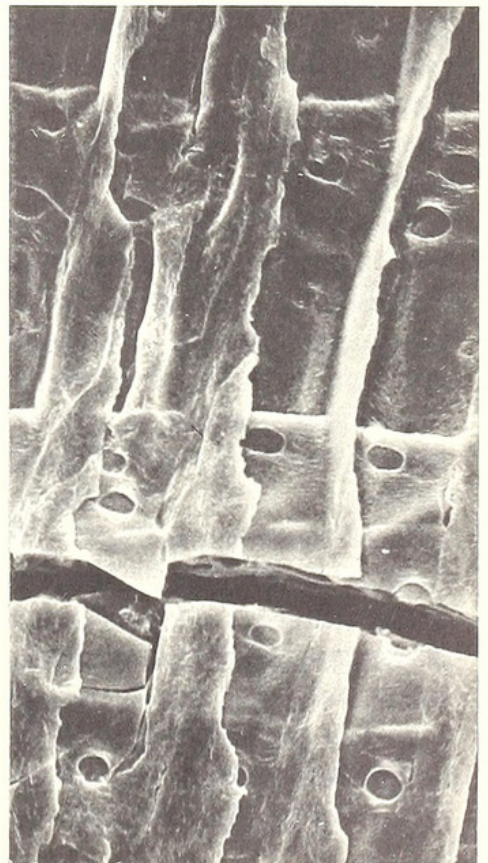
PLATE 19

FOWLER, EDWARDS, and BRETT, Eocene conifer

evidence to suggest that the fossil trees were not only entombed, but once grew, in a waterlogged environment.

It has been shown that the fossil root wood anatomy resembles that of the modern monotypic Asiatic genus *Glyptostrobus*. Remains of this genus have been found repeatedly in Tertiary deposits of North America, Europe, and Asia, but the living species is confined to Kiangsi and Kwantung provinces, south-eastern China (Miki 1950). Its survival, at only two coastal localities, appears to be the result of cultivation since it is unknown as a wild tree (Henry and McIntyre 1926).

It has been suggested by some authors (Chaney and Axelrod 1959, Dallimore and Jackson 1966) that *Glyptostrobus* favours damp rather than swampy conditions. However, according to Henry and McIntyre (1926), *Glyptostrobus* is typically found in habitats not exceeding a few feet above sea-level, often growing near river banks in swampy soil subject to inundation. Morphological similarities between *Glyptostrobus pensilis* and *Taxodium distichum* (L.) Rich., an inhabitant of waterlogged and flooded terrain in the south-eastern United States, suggest that both genera occupy a similar ecological niche. *Metasequoia*, which also has wood similar to that of the fossil, is essentially a member of a stream bank community, preferring damp rather than waterlogged habitats (Chu and Cooper 1950).

Although considered ecologically equivalent, *Glyptostrobus* and *Taxodium* differ in their wood anatomy.

Morphologically, the fossil remains resemble the basal part of the trunk of *G. pensilis*, *M. glyptostroboides*, and *T. distichum*, species in which the bole and root systems exhibit special adaptations to waterlogged and flooded habitats (Henry and McIntyre 1926, Hu and Cheng 1948, Harrar and Harrar 1962). In such habitats, the bole becomes strongly buttressed and is often hollow, while the extensive lateral root system gives rise to downward-penetrating roots and upward-growing pneumatophores. Unlike the pneumatophore of *Taxodium* which is conical, that of *Glyptostrobus* is geniculate, a feature well illustrated by Henry and McIntyre (1926, pl. II). Buttressing of the fossil remains is apparent (Pl. 19, fig. 1), but it was not possible to confirm the presence of pneumatophores. Certain structures identified as smaller boles could have been pneumatophores, but it could not be shown that these 'boles' were in organic connection with major root systems. According to Kurz and Demaree (1934) pneumatophores of *T. distichum* do not develop in deep water or when flooding is only of short duration. Chu and Cooper (1950) suggest that the pneumatophores of *Metasequoia* develop only in deep-water swamps or during long periods of inundation. The absence of pneumatophores on *Glyptostrobus* trees up to 25 years old, growing in waterlogged habitats, may be due to their immaturity (Henry and McIntyre 1926). Therefore, the absence of pneumatophores on the fossil roots could be accounted for by the environmental conditions and age of the trees at the time of death. To the best of our knowledge no trace of pneumatophores in the fossil state has been found in Europe. This seems remarkable in view of the common occurrence in Tertiary deposits of remains of those taxodiaceous genera capable of producing such structures at the present time.

Fossil pollen attributable to the Taxodiaceae is also common in the Leaf Bed. This taxodiaceous pollen may represent more than one species, since the form-species *Inaperturopollenites hiatus* and *I. dubius*, described by Thomson and Pflug (1953),

are both recorded. Some authors, for example Zagwijn (1960), have decided fossil taxodiaceous pollen into two broad morphological groups, the *Sequoia* type (showing affinity with modern *Sequoia*, *Sequoiadendron*, *Metasequoia*, and *Cryptomeria*) and the *Taxodium* type (showing affinity with modern *Taxodium* and *Glyptostrobus*). The latter type has a smaller papilla and probably thinner exine than the former. Dispersed fossil taxodiaceous pollen which gape open, or in which the papillae cannot be readily seen, is therefore likely to belong to the *Taxodium* type. Although it is generally accepted that separation of fossil taxodiaceous pollen at modern generic level is far from reliable, comparison of pollen of modern genera has led to the conclusion that the taxodiaceous pollen found in the Leaf Bed resembles that of living *Taxodium* and *Glyptostrobus* species rather than that of *Sequoia*, *Sequoiadendron*, or *Metasequoia*.

On the basis of anatomical and morphological considerations it is evident that the fossil roots are closely comparable with modern *Glyptostrobus* and, to a lesser extent, *Metasequoia* and *Taxodium*. Although *G. pensilis* and *T. distichum* show anatomical differences, they are otherwise considered to have much in common (Dallimore and Jackson 1966). Palynological evidence suggests that *Glyptostrobus* or *Taxodium*, rather than *Metasequoia*, is represented in the Leaf Bed. Of greater significance is the fact that both *G. pensilis* and *T. distichum* inhabit waterlogged terrain.

Evidence from the associated macro- and microfossil assemblages. The combined plant macrofossil and microfossil assemblages of the Leaf Bed have yielded 76 families with 100 genera identifiable to modern taxa. The total fossil flora has an essentially woody aspect, with evergreen and deciduous trees and shrubs, and some climbers.

Fossil macrofloral and microfloral assemblages should complement one another in the interpretation of the whole flora. The macroflora is likely to be biased toward plants growing in swamps or close to rivers and delta distributaries, whereas many of the pollen and spores are likely to be derived from plants of more remote, and possibly very different, habitats (Chaloner 1968). However, the combined macro-microfossil floral assemblages of the Leaf Bed contain a number of taxa totalling about 40% of those identified, which, to judge from the habitats of their modern representatives, indicate very wet conditions (Table 1). Many of the other identified fossil taxa today inhabit moist lowland environments. Therefore, wet habitats seem to have occupied relatively large areas around the fossil locality. In such an environment, water transport may be more important than wind transport in carrying the plant material to the depositional site, thus increasing the likelihood of both types of fossil assemblage being derived from similar plant communities.

Palaeobotanical evidence suggests that the Leaf Bed is a freshwater deposit. The only real indication of brackish conditions is the occurrence of pinnules of *Acrostichum lanzaeanum* (Visiani) Chandler at the, now obscured, eastern end of the outcrop in Hordle Cliff (Chandler 1961). However, their association with the remains of such freshwater genera as *Salvinia*, *Brasenia*, and *Stratiotes*, together with the fact that living *Acrostichum* sp. grows in freshwater marshes (Small 1938), suggest freshwater conditions. There is no palynological evidence for the presence of *Acrostichum*. Although *Acrostichum* spores, because of their large size, are deposited in

abundance near the source areas (Tschudy 1969), the spores may go unrecognized as such (Frederiksen 1969). *Nipa*, another brackish water indicator, is also recorded from the Leaf Bed, but it is by no means certain that the macrofossil material, in an old collection, actually came from this bed (Chandler 1961). Macrofossils attributed to *Nipa* are not otherwise recorded in the Tertiary of southern England above the Auversian (Chandler 1964), and palynological work in progress (Fowler, unpublished) indicates that *Nipa* had disappeared from the Hampshire Basin before deposition of the Barton Beds had ended.

The flora contains abundant remains of the algae *Pediastrum* and *Botryococcus*, together with the aquatic genera *Salvinia*, *Azolla*, *Brasenia*, *Stratiotes*, and *Potamogeton*. Typically, these genera are inhabitants of freshwater ponds, lakes, and sluggish rivers, suggesting areas of open water on a lowland coastal plain situated away from the influence of the more saline water of tidal estuaries. Shallower water was probably occupied by the above-mentioned types together with plants such as *Scleria*, *Sparganium*, and *Typha*. The more exposed marshy areas around the open water may have been occupied by such plants as *Acrostichum*, *Osmunda*, *Aldrovanda*, *Sphagnum*, *Jussiaea*, and members of the Cyperaceae. Many of the remaining recorded genera are characteristic of well-wooded swampy habitats, and it is possible that much of the surface of the coastal plain, including river banks, was occupied by plant communities of this habitat type.

The presence of *Pinus* in the microfossil assemblage need not suggest remote source areas of drier upland communities. Modern pine species can grow at low

TABLE 1. Modern representatives of the macro- and microfossil plant assemblages from the Leaf Bed which are considered indicative of a wet palaeoenvironment. Habitat preferences in such an environment are given in columns 1–4: 1, Brackish marsh. 2, Freshwater habitats of open aspect. 3, Permanent swamp or seasonally waterlogged soil. 4, Drier areas in and around swamp, and wet woods. Ecological data from Harper (1911, 1914), Davies (1943), Saucier (1963), Monk (1965), and Machin (1971).

	Macro-fossil	Micro-fossil	1	2	3	4
Nipa	+	+	+			
?Acanthus	+	+	+			
Acrostichum	+	+	+	+		
Salvinia	+			+		
Stratiotes	+			+		
Brasenia	+			+		
Scleria	+			+		
Aldrovanda	+			+		
Potamogeton	+	+		+		
Cyperaceae	+	+		+		
Botryococcus		+		+		
Pediastrum		+		+		
Sphagnum		+		+		
Azolla		+		+		
Sparganium		+		+		
Typha		+		+		
Jussiaea		+		+	+	
Osmunda		+		+	+	
Gordonia	+	+			+	
Myrica	+	+			+	
Parthenocissus	+	+			+	
Gleichenia		+			+	
Lygodium		+			+	
Nyssa		+			+	
Viburnum		+			+	
Cyrilla		+			+	
Clethra		+			+	
Ulmaceae		+			+	
Rhus		+			+	
Carya		+			+	+
Planera		+			+	+
Ericaceae	+	+			+	+
Liquidambar	+	+			+	+
Pinus	+	+			+	+
Glyptostrobus or Taxodium	+	+			+	+
Serenoa		+			+	+
Thrinax		+			+	+
Sabal		+			+	+
Alnus		+			+	+
Corylus		+			+	+
Quercus		+			+	+
Ilex		+			+	+
Acer		+			+	+

altitudes in subtropical climates (Mirov 1967), and this genus grows in lowland wet habitats in Florida today (Monk 1965), often occupying only slightly elevated, though poorly drained areas, within or on the landward side of swamps. The effect of slight variation in the level of the water table, resulting in distinct vegetational differences has been demonstrated in southern Florida by Spackman *et al.* (1964). According to Zak (1961), water absorption by roots in saturated soil is difficult, but pines can live under such conditions because of their drought resistance. Such a distribution of *Pinus* on slightly elevated and drier areas might account for the paucity of macrofossil remains of this genus in the Leaf Bed.

INTERRELATIONSHIPS AND TAXONOMIC SIGNIFICANCE OF THE TAXODIACEOUS REMAINS FROM THE LEAF BED

Evidence presented by anatomical and morphological features of the fossil roots, supported by pollen morphology and habitat requirements of modern members of the Taxodiaceae, indicates affinity between the fossil roots and modern *Glyptostrobus* and *Taxodium*. Being deciduous, both genera would contribute abundant foliage, as well as cones, to the contemporary sediments. Such dispersed structures, if found in association with the fossil roots, might therefore be expected to have once belonged to the same source trees.

Taxodiaceous shoots, twigs, and female cones are locally abundant in the Leaf Bed (Chandler 1961), suggesting that the trees grew near the depositional site. However, they are all recorded as *Sequoia couttsiae* Heer (Chandler 1964).

Whilst both the *Taxodium* type and *Sequoia* type of pollen have been recorded from the Lower Tertiary of southern England (Ma Khin Sein 1961, Machin 1971), only the former has been found in abundance, the *Sequoia* type occurring in relatively insignificant amounts. *S. couttsiae* is the only taxodiaceous macrofossil occurring in the same deposits and it is therefore interesting that the above authors refer the *Sequoia* type pollen to *Sequoiadendron* and *Metasequoia*, and not to *Sequoia*.

It would be tempting to consider that the foliage and cones of *S. couttsiae* and the fossil roots here described as *Glyptostroboxylon* sp. might all belong to the same parent plant which produced *Taxodium* type pollen. An analogous situation has been reported from the Oligocene Florissant Formation of North America. Here, male cones referred to the Tertiary species *Sequoia affinis* Lesq. were found to contain pollen, also found commonly in the dispersed state, resembling that of living *Taxodium* rather than *Sequoia* (E. Leopold, quoted by Penny 1969).

In view of the palaeoecological conclusions drawn from this work, it would seem necessary to consider briefly the extent to which *S. couttsiae* resembles modern *Sequoiadendron giganteum* (Lindl.) Buchholz and *Sequoia sempervirens* Endl. This is particularly significant considering that these modern genera live in a much drier habitat than that suggested for the fossil species. At the same time, it would seem pertinent to consider the modern generic affinities of taxodiaceous macrofossil remains found in association with *Glyptostroboxylon* in some European deposits.

The morphology of *S. couttsiae*, based on foliage and cones from the Lower Tertiary of southern England, has been described by Heer (1862) and Chandler (1922, 1957), with details of cuticular structure added later (Chandler 1962). Fossil

taxodiaceous leaves and shoots are difficult to identify. According to Ferguson (1967) it is particularly difficult to assign fossil material to modern *Sequoia*, only the cuticle in conjunction with other leaf features and the female cone being sufficiently diagnostic. *S. couttsiae* has been considered by many authors (Heer 1862, Zalewska 1953) as an intermediate type between the extant genera *Sequoiadendron* and *Sequoia*. Only the seeds and female cones of the fossil species are closely comparable with the modern monotypic *S. sempervirens*, the leaves being more reminiscent of *Sequoiadendron giganteum*. However, Chandler (1964) points out that *Sequoia couttsiae* has foliage which is characteristic of neither *Sequoia* nor *Sequoiadendron*. Schwartz and Weide (1962) regard the fossil species *Sequoia reichenbachi* (Geinitz) Heer and *S. langsdorfi* (Brongn.) Heer as identical respectively with *S. gigantea* and *S. sempervirens*, but no mention was made of *S. couttsiae*. Some authors have found cuticular structure useful in the identification of fossil Taxodiaceae (Kilpper 1968) and of *Sequoia* in particular (Bandulska 1923, Chandler 1962). However, Boulter (1970) has shown that certain features of the stomatal apparatus of fossil and modern taxodiaceous cuticles may be altered by the normal maceration process, and suggests that more refined maceration techniques together with the use of the scanning electron microscope may be necessary for separating the genera. Boulter also reported that cuticular material from the Lower Pliocene of Derbyshire, attributed to *Cryptomeria* by means of various types of evidence, could not, by means of the light microscope, be distinguished from cuticles of *S. couttsiae* described by Chandler (1962). Identification to *Sequoia* of fossil foliage found in the Leaf Bed would therefore seem to be hazardous. Equally hazardous would be the identification of these remains to other modern taxodiaceous genera, and to *Glyptostrobus* in particular. Living *Glyptostrobus* is heterophyllous, the foliage varying in character with the age of the tree so that up to three distinct leaf types may be found on an individual tree at the same time (Henry and McIntyre 1926). Usually a single branchlet bears only one leaf type, but the different leaf types produced by the tree simulate those of other taxodiaceous genera. If such morphological variation existed in fossil taxodiaceous types, misidentification of such material is understandable.

It is of interest to note that, in the original description of *S. couttsiae*, Heer (1862) states 'It is however questionable if all branches belong to the same parent, because young twigs closely resemble those of *Glyptostrobus europaeus*.'

In Poland, woody assemblages have been examined from Oligo-Miocene deposits at Turów (Zalewska 1953, 1955) and Konin (Grabowska 1957). At both localities, abundant root remains of *Glyptostroboxylon tenerum* and *Taxodioxylon sequoianum* Goth. (= *T. gypsaceum* Kräusel in Zalewska 1953 and Grabowska 1957) were found, in association with abundant foliage of *S. couttsiae* and *Glyptostrobus europaeus* Heer. These authors presumed that *G. tenerum* and *G. europaeus* belonged to the same parental type. Such an alliance is supported by anatomical and morphological features which suggest affinity with modern *Glyptostrobus*. At the same time, *T. sequoianum* was regarded as being closely related to *S. couttsiae*. Again this alliance is plausible, as both types show a relationship, though tenuous, to modern *Sequoia* and *Sequoiadendron*. However, it seems equally feasible due to lack of positive evidence, that *G. tenerum* produced foliage of the *S. couttsiae* type, a situation analogous to that found in the Leaf Bed.

CONCLUSIONS

The taxodiaceous fossil remains recovered from the Leaf Bed in the Lower Headon Beds exhibit features characteristic of a number of modern genera within the family. In general morphology and anatomy the root remains resemble *Metasequoia*, *Taxodium*, and particularly *Glyptostrobus*. In foliage and leaf cuticle features, however, there are certain similarities to modern *Sequoia*, whereas the fossil pollen is like that of modern *Glyptostrobus* and *Taxodium*. It is conceivable that more than one genus is represented here, but the association of these different plant structures in abundance suggests that only one genus is involved. Present evidence further suggests that this fossil genus had the attributes of more than one modern member of the Taxodiaceae.

The Leaf Bed plant assemblage corresponds, to some extent, with that of the deciduous and evergreen hardwood swamps of southern Florida, which characterizes wet, periodically flooded ground (Monk 1965). Previous workers on Tertiary material from Europe and North America have suggested such an analogy (Traverse 1955, Teichmüller 1958, Machin 1971).

It is suggested that the conifer trees which gave rise to the roots described as *Glyptostroboxylon* grew in a waterlogged habitat, as evidenced by their mode of fossilization, anatomical, and morphological features. It is possible that they occupied very wet, permanently flooded sites within the mixed deciduous hardwood swamp vegetation.

The occurrence of a rich terrestrial flora in the western part of the Hampshire Basin late in the Upper Bartonian accords with other evidence (Curry 1965) for the onset of extremely shallow, freshwater conditions in the area at this time. This palaeoenvironmental interpretation of the region renders unnecessary the hypothesis of long-distance river transportation of plant macrofossil remains from the west (Chandler 1963, 1964). The developing picture is of a coastal alluvial flood plain, with open water, marshes, and swamp forest.

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