A review of the platanaceous woods from the Eocene paratropical rainforest of south-east England

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Small diameter pyritized axes, commonly referred to as ‘twigs’, of fossil platanaceous wood are described from the Lower Eocene London Clay Formation of south-east England. These twigs are characterized by solitary vessels with scalariform perforation plates, opposite intervessel pits, and tall, multiseriate rays that dilate in the phloem region. The wood anatomy supports close relationship to members of extant Platanaceae and the material is placed in the organ genus *Plataninium* Unger erected for fossil woods with close anatomical similarity to *Platanus* L. This material supplements the fossil record of platanaceous type wood from the Eocene London Clay and documents the first record of *Plataninium decipiens* Brett in the twig flora. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, **139**, 181–191.

ADDITIONAL KEYWORDS: fossil – London Clay – Platanaceae – Tertiary.

INTRODUCTION

Fossil floras often comprise a number of different components such as leaves, wood, flowers, fruits, seeds and pollen. These yield important information about past environments in that they are a source of data that supplement and complement that provided by the geological record. The pyritized flora from the Eocene (Ypresian) London Clay Formation in both the London and Hampshire Basins of south-east England is one such flora. Here, the wealth of information provided over the last three centuries has enabled us to understand one of the world’s most varied fossil floras. Moreover, it is the only diverse flora from the Lower Eocene strata in Europe and affords detailed insights into the ecology of south-east England during the early Eocene, some 52–49 Mya. Close similarities have been shown to exist between the London Clay fossil flora and extant Indo-Malaysian rainforests (Reid & Chandler, 1933; Poole, 1993) suggesting that a relatively warm, paratropical climate prevailed over south-east

England during the Eocene. Even though this assemblage has been intensively studied, new and old localities in both the London and Hampshire Basins continue to yield interesting material and this, coupled with improved techniques, has contributed significantly to our understanding of the preservation and composition of the flora. Unfortunately, pyritized material rapidly succumbs to oxidation and although a number of techniques (e.g. Cornish, 1987 and references therein) are known to retard the process, hitherto, it has not been possible to prevent decay completely. The small diameter woody pyritized axes that include twig material, stems, small roots, fern axes and splinters of larger diameter axes such as branches or trunks, are traditionally referred to as ‘twigs’. These twigs form one important component of the London Clay flora. They, together with fruits, seeds and remains of animals are washed out of the clay by wave action and are deposited on foreshores in the London and Hampshire Basins. The twigs, when compared with the fruits, seeds and pollen, have received comparatively little attention. Nevertheless, they are often well-preserved anatomically and can

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be used in systematic studies, thus furthering our understanding of a northerly (41°N) Lower Eocene paratropical ecosystem.

MATERIAL AND METHODS

The specimens discussed below are from a representative selection of over 100 specimens so far collected of this xylotype. They all originate from either the London Basin: Warden Point (NGR 021724; specimens V.64748–V.64757) and Hens Brook (NGR 996731 King, 1984; V.64758–V.64759) on the Isle of Sheppey, Herne Bay (NGR 177685 eastwards; V.64760–V.64761), or from the foreshore at Bognor Regis (NGR 9148–9398; V.64762) in the Hampshire Basin. The remaining material of this xylotype is less well preserved or lacks diagnostic anatomical characters and therefore has not been included in this study. Nevertheless, the relative abundance of platanaceous specimens indicates that they formed a significant percentage of the twig flora. The specimens were sectioned as described by Poole (1993), subjected to a fine polishing technique (Kenrick & Edwards, 1988) and studied using a reflected light, mineralogical microscope. Fractured surfaces and surface-etched (for 24 h in fuming nitric acid) material were studied using scanning electron microscopy. The specimens were deposited in the National History Museum (London).

Familial affinities were determined by consulting reference descriptions, such as those of Metcalfe & Chalk (1950, 1983), Miles (1978), Schweingruber (1990), Ilic (1991) and by searches of the computerized OPCN (Wheeler *et al.*, 1986; LaPasha & Wheeler, 1987) and CSIRO Family Key (Ilic, 1987) wood databases. Such aids are useful in identification to family level even though they are primarily designed to help in the identification of mature wood samples. Subsequently, specimens were compared with extant wood samples, regardless of their geographical origin, housed in the Jodrell Laboratory, RBG, Kew and the National Herbarium of the Netherlands, Utrecht Branch. Wherever possible, the wood is described and measurements undertaken in accordance with the recommendations outlined by the International Association of Wood Anatomists (IAWA Committee,

1989) except in the case of fibre and vessel element length. These measurements, for both fossil and modern wood, were taken from thin sections (to ensure consistency) as macerations of fossil material were not possible. For the purpose of this study the term ‘twig’ refers to the fossil material and ‘stem’ refers to extant material of small diameter used in the comparative studies. Plant authorities are in accordance with those listed in Brummitt & Powell (1992).

SYSTEMATIC PALAEOBOTANY

FAMILY ?PLATANACEAE DUMORT.

ORGAN GENUS *PLATANINIUM* UNGER

PLATANINIUM DECIPIENS BRETT

Other records: *Plataninium* sp. (Wilkinson, 1984)

Additional material: V.64748–V.64762

Emended species diagnosis. Secondary xylem; growth rings indistinct. Vessels solitary (>70%), tangential diameter <200 µm, intervacular pitting opposite to scalariform. Perforation plates totally scalariform or with very rare simple perforation plates. Rays mainly multiseriate up to 35 cells wide and 8 mm in height; rarely uniseriate. Ray cells mostly procumbent except at ray margins, crystals sometimes present. Wood parenchyma apotracheal diffuse and scanty, or as strings of cells, paratracheal.

Description. This description is based upon 15 pyritized small diameter axes measuring less than 24 mm in diameter and 60 mm in length. Cortex eroded. Phloem region preserved in nine specimens (V.64748–V.64750, V.64752–V.64757). Triangular distal ends of rays separate phloem region into discrete triangular phloem ‘wedges’ (Figs 2, 6 and 22) where fibres and parenchyma and/or sieve elements can be distinguished (Fig. 22). The cambium in juxtaposition to rays intrudes deeply into the secondary xylem giving a ‘corrugated’ appearance at the junction between secondary xylem and phloem rays (Figs 2 and 22). Xylem diffuse porous. Growth rings absent. Vessels are small, solitary or occasionally paired due to overlapping end walls (Figs 1, 3, 6 and 9). There are ≈

Figures 1–9. Anatomy of fossil *Plataninium decipiens* twigs. Fig. 1. Fractured transverse section (TS) of V.61671. Scale bar = 1 mm. Fig. 2. TS V.64748 showing dilating rays in the phloem region. Scale bar = 100 µm. Fig. 3. TS V.64761 showing pith and xylem. Scale bar = 250 µm. Fig. 4. SEM V.64762 showing ?sheath cells (arrowed). Scale bar = 50 µm. Fig. 5. SEM scalariform perforation plate in 1/2/14 (personal collection; specimen now disintegrated). Scale bar = 15 µm. Fig. 6. Polished TS specimen V.64757. Scale bar = 500 µm. Fig. 7. Longitudinal section (LS) V.64762 showing some relatively thick-walled pith parenchyma cells. Scale bar = 300 µm. Fig. 8. LS thin-walled pith parenchyma cells in V.64761. Scale bar = 150 µm. Fig. 9. TS V.64761 showing uniseriate- and multiseriate rays and solitary, relatively angular vessels. Scale bar = 50 µm.

65 vessels mm^{-2} (range: 19–54 mm^{-2} , rarely up to 200), with mean tangential diameter of $\approx 81\mu\text{m}$ (range: 30–290 μm), mean radial diameter of $\approx 107\mu\text{m}$ (range: 20–340 μm) and mean vessel element length of $\approx 792\mu\text{m}$ (range: 150–2500 μm). Intervessel pitting opposite, circular to scalariform with bordered pits measuring up to 22 μm in diameter, very rarely more alternate. Tyloses occasionally present (Fig. 13). Perforation plates are scalariform (Figs 5, 10 and 13) with up to 22 bars per perforation plate. Rare simple perforation plates observed in specimens V.64759 and V.64760. Fibres are thin- to thick-walled with a mean diameter of $\approx 14.5\mu\text{m}$ (range: 8–30 μm) and mean length of $\approx 455\mu\text{m}$ (range: 150–600 μm). Fibre pitting is bordered and uniseriate (Figs 11 and 17) and 2–3 μm in diameter. Wood parenchyma could not easily be distinguished from the ground mass. Rays are mainly multiseriate (Figs 1 and 12), seldom uniseriate. Multiseriate rays range from (3-) 5–20 cells wide (mode is ≈ 9 cells) and up to 8 mm in height. The constituent cells are mainly square, occasionally upright or procumbent (Fig. 14). Less than five rows of square marginal cells occur when a ray is composed mainly of procumbent cells. Two specimens (V.64760, V.64762) have possible sheath cells or simply a wood parenchyma strand in juxtaposition to the ray (Fig. 4). Ray-vessel pitting is opposite to gash-like and scalariform (Fig. 10), rarely more alternate. There are ≈ 1 –6 rays mm^{-1} . No crystals in the ray cells were observed. The pith is absent from three of the specimens (V.64750, V.64759, V.64760). When present, the pith is composed mainly of thin-walled, homogeneous, isodiametric parenchyma cells (Figs 3 and 8), the majority of which have undergone degradation. Occasionally pith cells appear to have thickened walls (Fig. 7) and gash-like pitting (Fig. 21).

IDENTIFICATION OF MATERIAL

COMPARISONS WITH EXTANT TAXA

The combination of exclusively solitary vessels, opposite pits, fibres with distinctly bordered pits and

rays, commonly over ten cells wide, occurs in Chloranthaceae, Dilleniaceae, Eupteleaceae, Ericaceae, Epacridaceae, Platanaceae and Icacinaceae. The Chloranthaceae have scalariform perforation plates with numerous fine bars, numerous uniseriate rays and multiseriate rays composed of upright cells; Eupteleaceae stem woods have scalariform perforation plates with numerous bars, heterogeneous rays and small (i.e. $<30\mu\text{m}$), abundant vessels in radial rows and parenchyma in terminal bands; Epacridaceae have spiral thickenings in the stem wood along with numerous and narrow (uniseriate and biseriate) rays and small diameter vessels. Predominantly scalariform perforation plates occur together with few simple perforation plates found in the Dilleniaceae, Ericaceae and Platanaceae. The Dilleniaceae have larger diameter vessels (i.e. $>100\mu\text{m}$) with numerous (i.e. >100) bars per scalariform perforation plate and rays of two distinct sizes. Ericaceae stem woods have abundant uniseriate rays and small (i.e. typically $<50\mu\text{m}$, typically $<25\mu\text{m}$) diameter vessels. Thus, the Icacinaceae and the Platanaceae most closely resemble our fossil material. Icacinaceae stem woods have no dilating rays in the phloem region; mature wood exhibits a range of unspecialized to specialized forms (Metcalfe & Chalk, 1950) with small vessels often in radial multiples. This family also has sheath cells associated with the multiseriate rays. Members of the Platanaceae (Figs 15, 16, 18–21) are very similar to the Icacinaceae but have homogeneous rays that dilate in the phloem region. Where the phloem region is still present, fossil material most closely resembles Platanaceae, but this is not so obvious when the phloem has been eroded. Süss & Müller-Stoll (1977) state that these two families can be distinguished by the longer length of their vessel elements (seen in some of the fossils described here), distinctly heterogeneous rays and in that the constituent ray cells of the Icacinaceae are greater in height. However, these observations were based on mature wood and thus the distinction becomes less clear when dealing with immature 'twig'/stem and root wood especially when it is ≈ 50

Figures 10–21. Anatomy of fossil *Plataninium decipiens* twigs and extant *Platanus* stems. Fig. 10. SEM RLS V.64757 showing gash-like and opposite vessel-ray pitting and scalariform perforation plate. Scale bar = 25 μm . Fig. 11. SEM V.64757 in LS showing intervessel pitting and uniseriate, bordered fibre pits to the right of scalariform perforation plate. Scale bar = 50 μm . Fig. 12. TLS polished face V.64760 showing multiseriate ray. Scale bar = 150 μm . Fig. 13. TLS polished face V.64760 showing vessels with tyloses and scalariform perforation plates with relatively few bars (arrowed). Scale bar = 150 μm . Fig. 14. RLS polished face of V.64760 showing ray cells. Scale bar = 150 μm . Fig. 15. RLS *Platanus* $\times$ *hispanica* (Kew HK) showing ray vessel pits. Scale bar = 15 μm . Fig. 16. TS *Platanus occidentalis* L. (Kew). Scale bar = 500 μm . Fig. 17. TLS V.64757 showing the fibre pitting. Scale bar = 10 μm . Fig. 18. TLS *Platanus kerrii* (Kew Wheeler E no. 8745) showing multiseriate rays. Scale bar = 500 μm . Fig. 19. RLS *Platanus* $\times$ *hispanica* (Kew HK) showing procumbent- and relatively square ray cells with pits. Scale bar = 15 μm . Fig. 20. SEM the pith cells of *Platanus* $\times$ *hispanica* showing elongate and circular vessel ray pits scale bar = 10 μm . Fig. 21. SEM of the pith cell pitting in V.64757. Scale bar = 25 μm .

Figure 22. High magnification diagram illustrating the characteristic dilating rays and phloem wedges of 2/421 (personal collection, species now disintegrated). Scale bar = 50 µm.

million years old. As already mentioned, rare, simple perforation plates were only observed in two of the seven specimens described. Such rare occurrences of simple perforation plates have been noted in Platanaceae although these are not usually observed in fossil platanaceous woods. Furthermore, elongated sheath-like cells, a feature of some Icacinaceae, have been noted in two specimens (V.64760 and V.64762). Moreover, it may be that the two specimens (V.64759 and V.64760) which lack a definite pith may be roots rather than stems (cf. Süss & Müller-Stoll, 1977). Therefore, it is likely that there may be more than one group of platanoid wood present in the London Clay material. However, as the fossils are of immature 'twigs' and show only minor anatomical variation, we do not feel that we can subdivide these specimens further at this stage. When well-preserved mature specimens become available, this xylotype can be re-evaluated.

Baas (1969) described the anatomy of young twigs of *Platanus kerrii* Gagnep. This species exhibits the most primitive characters in the genus. Baas noted that 85% of the vessels have scalariform perforation plates and the vessel elements are longer than those in similar-aged stems of other *Platanus* species. Wheeler (1995) undertook a detailed study of mature wood of *Platanus kerrii* from Vietnam and found that the vessel elements are not significantly longer than those of other extant species of *Platanus* although the proportion of scalariform perforation plates was gen-

erally greater. The rays of *Platanus kerrii* are the widest in the genus comprising up to 30 cells. However, our twigs differ anatomically from *Platanus kerrii* in that upright cells within the body of the rays are absent. Interestingly though, 'sheath cells' similar to those seen in V.64762 (Fig. 4) were observed in one specimen of *Platanus kerrii* (NHN Utrecht Branch, specimen U35081).

COMPARISONS WITH FOSSIL TAXA

Fossil woods from the Cretaceous and Tertiary similar to the London Clay platanoid woods are among the earliest known dicotyledonous woods, occurring as far back as the Albian (Thayn *et al.* 1985; Herendeen, 1991) and are usually assigned to either *Plataninium*, *Platanoxylon* or *Icacinoxylon*. Geologically ancient platanoid woods have exclusively scalariform perforation plates and very wide rays, i.e. up to 25 cells (Wheeler, 1995). The type genus *Icacinoxylon* is used for woods with large, markedly heterocellular, multiseriate rays alongside numerous uniseriate rays and predominantly solitary vessels (Wheeler *et al.*, 1995). *Plataninium* is distinguished by the presence of large, multiseriate rays that are not markedly heterocellular and by the paucity or absence of uniseriate rays. However, as stated by Wheeler *et al.* (1995), there is a need to re-evaluate these organ genera as the boundaries between them and their species have become unclear.

Plataninium and *Platanoxylon* can be distinguished by the presence or absence of spiral thickenings – a feature not present in modern *Platanus* woods – such that fossil *Platanus*-like woods with spiral thickenings are placed in *Plataninium* (Süss & Müller-Stoll, 1977). In advocating this much narrower circumscription for *Plataninium*, Süss & Müller-Stoll (1977) undertook a review of the platanaceous fossil woods thus described and transferred many *Plataninium* species to *Platanoxylon*. Brett's *Plataninium decipiens* specimens, however, were retained in this organ genus because Süss and Müller-Stoll considered these specimens to be anatomically more similar to the Icacinaceae, based on their relatively long vessel members. Brett's *Platanus* sp. specimens were later assigned to *Platanoxylon* emend. Süss & Müller-Stoll (1977) by Süss (1980). Differences between species of *Plataninium* are often quantitative and this makes dealing with juvenile or twig wood problematical as it is known that quantitative features vary according to distance from pith and chronological age (Carlquist, 1988; Poole, 1994).

Wilkinson (1984) described the first platanaceous/icacinaceous fossil twig wood from the Isle of Sheppey (London Clay, Eocene) and illustrated its anatomy

using scanning electron micrographs. She assigned her material to *Plataninium* sp. *Plataninium* had already been described from this and other localities around the south-east coast of England by Brett (1972) but Brett's material was calcified and originated from larger diameter trunk/branch material. The difference between the specimens described by Brett (1972), Wilkinson (1984) and those described herein are given in Table 1. From Table 1 it can be seen that these specimens differ in terms of quantitative features only (i.e. vessel diameter and abundance, ray width, ray abundance, vessel element length). However, qualitative features include rare, simple perforation plates in two of the specimens described here, and the obvious presence of crystals in the mature specimens of *Plataninium decipiens* (Brett, 1972). Because the twig material has some characters not fitting modern Platanaceae, is of the same geological age as those described by Brett (1972) and Wilkinson (1984) and because the anatomical distinctions are slight considering the relative maturity and diameter of the material, we believe that Wilkinson's material and the material described herein can be assigned to the same organ taxa as those described by Brett (1972).

DISCUSSION

The fossil record of Platanaceae extends back some 100 Myr since leaves and reproductive features are known from the Albian (Crane *et al.*, 1993). It seems likely that this family was more diverse during the Cretaceous and Tertiary than it is today (Manchester, 1986). Indeed, Wheeler & Lehman (2000) suggest that the narrow diameter axes that they describe from Big Bend National Park (USA) might represent Platanaceae with a vine-like habit. The fossil record of platanoid wood is extensive, occurring at almost all localities where Cretaceous and early Tertiary dicotyledonous woods have been found including North America (e.g. Page, 1968; Süss & Müller-Stoll, 1977; Scott & Wheeler, 1982; Wheeler & Lehman, 2000; Wheeler & Manchester, 2002), Europe (e.g. Andreánsky, 1951; Greguss, 1969; Prakash *et al.* 1971; Brett, 1972; Süss & Müller-Stoll, 1977; Wilkinson, 1984; Selmeier, 1996) and East Asia (Suzuki, 1976).

Today, the Platanaceae is a north temperate and subtropical family of trees comprising a single genus *Platanus* L. with two subgenera *Platanus* Leroy and *Castanephyllum* Leroy. Members of the subgenus *Platanus* are native to temperate and subtropical areas (of North America and Europe) whereas *Platanus kerrii*, the only member of the subgenus *Castanephyllum*, can be found in Indochina (Leroy,

1982). *Platanus kerrii* is morphologically distinct from subgenus *Platanus* in that it possesses elliptical to lanceolate leaves and long reproductive axes with 12 or more sessile heads (Leroy, 1982) rather than the familiar palmate leaves and reproductive axes that can range from solitary to several heads per peduncle. The current distribution of this species in Indochina is similar to other components of the paratropical rain-forest of south-east England. Reid & Chandler (1933) documented a >60 and 53% similarity between fossils identified from the London Clay and living taxa found in India and South China-Burma, respectively. In addition to platanaceous pollen reported for the London Clay (Sein, 1961), leaves with superficial similarity to *Platanus* have been described from the underlying Woolwich and Reading Beds (Chandler, 1961). These records help to confirm the presence of platanaceous plants in the Lower Tertiary of south-east England.

CONCLUSION

This paper documents the occurrence of platanaceous twig wood, from the Eocene London Clay outcropping in both the London and Hampshire Basins of south-east England. These twigs, that form an abundant component of the twig flora, have been assigned to the organ genus *Plataninium* in accordance with the conclusions of Süss & Müller-Stoll, (1977). The specimens described herein have been assigned to the species *Plataninium decipiens* erected by Brett (1972) and document for the first time the occurrence of this species in the London Clay twig flora. In undertaking this review, platanaceous twigs described by Wilkinson (1984) as an undefined species of *Plataninium* have also been assigned to the same species.

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Table 1. Summary of the anatomical features of the platanaceous material described from the Eocene of south-east England. V, vessel; Ø, diameter; t, tangential; r, radial, *, fibre-tracheids; – data not provided in original. Data from: ¹Wilkinson (1984); ²Brett (1972); ³Baas (1969) and Wheeler (1995); ⁴data from personal observations in addition to that cited in Metcalfe & Chalk (1950), Baas (1969) and Wheeler (1995). In the column headed ‘extant *Platanus*’ anatomical characters for immature small diameter stem (twig) wood of the two subgenera have been italicised when they differ from that of mature wood.

Feature	<i>Plataninium</i> twigs herein	<i>Plataninium</i> sp. ¹	<i>Plataninium decipiens</i> ²
Preservation	Pyritized	Pyritized	Silicified
Organ type	Twig (stem, root)	Twig (stem)	Branch/trunk
Growth rings	Absent	Absent	Indistinct
Vessels range and (mean)			
No. mm ⁻²	19–54 (65)	30–46	30–42
Range VØt (µm)	30–290 (81)	93–156 (122)	35–120 (84)
Range VØr (µm)	20–340 (107)	63–146 (111)	–
Element length (µm)	150–2500 (792)	–	–
Distribution	Solitary, occasionally paired due to overlapping end walls	Solitary, crowded, oblique, some tangential rows of ≈ 3 vessels	Mostly solitary except for overlapping end walls, occasionally in tangential rows of 2–4 vessels
Porosity	Diffuse	Diffuse	Diffuse/weakly diffuse
Perforation plates (No. bars)	Scalariform with up to 22 bars or scalariform and rare simple in two specimens	Scalariform with up to 18 + bars	Scalariform with 13–32 bars
intervessel pitting	Opposite, circular to scalariform	Opposite	Opposite, scalariform
Rays			
Width (average)	Rarely uniseriate, mainly multiseriate 5–20 cells wide	Secondary rays 2–5 cells; primary rays 9–11 cells	2–24 cells
Height (µm)	Up to 8000	≈ 8500	1000–6000, acutely tapered at margins
Ray vessel pitting	Circular, opposite to scalariform	Opposite and gash-like	–
Crystals	None observed	–	Present
Cellular composition	Procumbent, square, occasionally upright body cells; square marginal cells	Wide rays procumbent body cells; narrow rays with relatively square to upright body cells	Procumbent body cells with relatively squarer cells forming marginal rows
No. per mm	1–6	1–5	1–3
Parenchyma			
Distribution	Difficult to distinguish from fibres; ?scanty	Vasicentric paratracheal: narrow sheath	Diffuse in short wavy bands of cells, abundant
Fibres			
Range Øµm	8–30	–	–
Pits	Bordered	Bordered	–
Phloem	Separated by dilating rays	Absent	Absent

<i>Platanus</i> sp ²	Extant <i>Platanus</i> subgenus	
	<i>Platanus</i> ^{3,4}	<i>Castaneophyllum</i> ^{3,4}
Calcified		
Branch/trunk	Mature and twig wood	Mature and twig wood
Distinct marked by several rows of flattened fibres	Distinct	Indistinct marked by radially shortened cells and crystals in rays; present
150	≈ 70	30–56
20–72 (50)	50–100 (<100)	51–127 (94)
–	34–128 (69) 18–75 (43)	60–165 (117) 30–75 (49)
–	600–875 (500–800) 160–850 (466)	443–880 (648) 240–710 (560)
Crowded in multiples, irregular clusters; late wood more solitary and less numerous	Solitary and in radial pairs and threes; oblique and tangential pairs and groups	Mostly solitary (relatively angular in outline), also in oblique and tangential pairs
Diffuse	Diffuse	Diffuse
Scalariform with 8–16 bars	Simple and scalariform with up to c. 20 bars	Simple and scalariform 1–24 (53%, 82%) with 2–22 (–30), 1–24 (7) bars
Opposite	Opposite (horizontally elongate alternate)	Opposite (scalariform)
Uniseriate, rare part- Uniseriate, mostly broad up to 22 cells wide (7)	Few uniseriate rays if present; multiseriate 12–15 (–20) cells	Rarely uniseriate
2000–3000 (–6000 and dissected diagonally by fibres)	2000–3000, often dissected	449–2873, dissected
–	<i>Circular, opposite, elongate; circular- elongate, gash like</i>	Circular to elongate
Present	Present	Present
Procumbent body cells with relatively squarer cells forming marginal rows	Homocellular with procumbent body cells, sometimes more square	Upright/square in uniseriate rays; with procumbent (<i>with upright cells</i>) with square/upright marginals in multiseriate rays
3	0–2, 1–3	0–2, 2–3
Diffuse in short wavy bands of cells	Apotracheal, diffuse, sometimes in uniseriate bands	Apotracheal diffuse to diffuse in aggregate, very scanty, <i>plus scanty paratracheal</i>
15–20	18–21 (20)	9–32 (20), 4–12 (9)
Bordered	Bordered	*Bordered
Absent	<i>Separated by dilating rays</i>	<i>Separated by dilating rays</i>

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