The First Record of Fossil Wood of Winteraceae from the Upper Cretaceous of Antarctica

IMOGEN POOLE* and JANE E. FRANCIS

School of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

Fossil wood of the Winteraceae from the Upper Cretaceous sediments of James Ross Island, Antarctic Peninsula, is described here for the first time. The specimen is characterized by the absence of vessels, rays of two distinct sizes and tracheids with one–three rows of circular bordered pits, mainly on the radial walls, grading to horizontally elongate and scalariform. Despite anatomical conformity to the family Winteraceae, the fossil wood is not identical to any one extant genus and therefore has been assigned to the fossil organ genus *Winteroxylon* Gottwald with which the fossil shows greatest similarity.   © 2000 Annals of Botany Company

Key words: Antarctica, Cretaceous, angiosperm, wood, anatomy, Winteraceae, *Winteroxylon*, fossil, palaeoclimate.

INTRODUCTION

Today the Winteraceae are a family of trees and shrubs which range from the tropics to cool temperate and alpine zones on low latitude mountains (Carlquist, 1988*a*; Mabberley, 1997). Winteraceous taxa are represented in New Zealand, Australia, the Pacific Islands, Madagascar, southern Mexico and South America (Patel, 1974; Rancusi, Nishida and Nishida, 1987; Mabberley, 1997). There is some debate as to the number of genera within the family (Smith, 1943, 1966; Bailey and Nast, 1945; Mabberley, 1997). Metcalfe (1987) refers to nine genera in his reappraisal of the wood anatomy. Vink (1985) made a case for grouping *Bubbia* van Tiegh., *Exospermum* van Teigh. and *Zygogynum* Baill. into *Zygogynum sensu lato* and including *Belliolum* van Teigh. within *Bubbia* and thus reducing the number of genera to four. Carlquist (1989) advocates the recognition of eight genera based on macromorphological, pollen and leaf anatomical evidence. Although the wood anatomical evidence does not seem to enhance generic definitions (Carlquist, 1989), anatomical differences between the genera have been observed (e.g. Patel, 1974; Carlquist, 1981, 1982, 1983*a*,*b*, 1988*a*, 1989; Rancusi *et al*., 1987; this study). Therefore, for the purpose of this paper, we consider there to be eight genera (*Exospermum* Teigh., *Zygogynum* Baill., *Belliolum* Teigh., *Bubbia* van Teigh., *Drimys* Forst. & Forst., *Tasmannia* DC., *Pseudowintera* Dandy and *Takhtajania* Baranova & Leroy) within the Winteraceae.

Fossil records of the Winteraceae have been geographically relatively widespread in both the Northern and Southern Hemispheres since the Cretaceous (Doyle, 2000 and references therein). In Antarctica, Winteraceae pollen (Cranwell, 1959) and leaves (Dusén, 1908) have been reported from lower Tertiary sediments. The leaves, which were found on Seymour Island in the northern Peninsula region (Dusén, 1908), resemble those of extant *Drimys winteri* Forst. Winteraceae pollen is also known from Upper Cretaceous sediments of southeastern Australia and New Zealand in floras very similar to the palaeofloras found in Antarctica (Dettmann, 1989; Dettman and Jarzen, 1990). Torres and Lemoigne (1989) record homoxylous wood from the Upper Cretaceous at Williams Point on Livingston Island but this wood is probably bennettitalean. Therefore the specimen described here extends the macrofossil record of this family in Antarctica back into the Late Cretaceous.

MATERIALS AND METHODS

The wood was collected from James Ross Island, Antarctic Peninsula region, during the British Antarctic Survey's James Ross Island expedition in 1989.

The Antarctic Peninsula is an eroded volcanic arc which was formed during the Mesozoic (Pankhurst, 1982; Leat, Scarrow and Miller, 1995). James Ross Island is situated within the sedimentary back-arc basin that formed behind (to the east of) the volcanic arc. Palaeocurrent data and provenance studies of the sedimentary grains indicate that the main source of sediments was from the eroding arc to the west (Dingle and Lavelle, 1998 and references therein) and it is most likely that the plant material was also derived from the vegetation growing on the arc during the Cretaceous.

Fossil wood is common in the Cretaceous sediments on James Ross Island (Francis, 1986) and represents trunk and branches of large trees which floated out into the basin as driftwood. Much of the wood was subject to boring by marine bivalves and, once waterlogged, the wood sank and became buried within the basin sediments. Subsequently, the wood was petrified by carbonate minerals which have preserved its 3-dimensional structure.

* For correspondence. Fax +44 (0) 113 2335259, e-mail i.poole@earth.leeds.ac.uk

The specimen described below comes from the eastern side of Lachman Crags on the north east of James Ross Island (63°51′30″S, 57°48′00″W). The geological sequence here consists of Cretaceous marine siltstones, sandstones and conglomerates that belong to the Lachman Crags Member of the Santa Marta Formation, Marambio Group (Crame *et al.*, 1991). This unit has been dated, using invertebrate macrofossils and palynofloras, as mid–late Santonian to early Campanian in age (Crame *et al.*, 1991; Keating, 1992). The palaeolatitude for James Ross Island is considered to have been approx. 65°S (Lawver, Gahagan and Coffin, 1992) at this time.

The fossil wood was thin-sectioned using techniques employed for rock specimens (see Haas and Rowe, 1999) and the extant woods were sectioned in the usual manner for living botanical specimens (see Jane, 1970). Familial affinities were determined by consulting reference works such as Cutler and Gregory (1998), Metcalfe and Chalk (1950, 1989), Metcalfe (1987), Ilic (1991) and searching computerized wood databases (Wheeler *et al.*, 1986; LaPasha and Wheeler, 1987) and the CSIRO (Australia) family key for hardwood identification (Ilic, 1987). Comparisons were made with the wood slide collections housed in the Jodrell Laboratory, Royal Botanic Gardens, Kew, UK and the Herbarium, Utrecht University, The Netherlands, and with thin sections of extant wood samples of *Tasmannia* collected from Tasmania, Australia, now deposited in the wood collection of the Wood Anatomy Section, Utrecht University, The Netherlands. The wood was described and measurements undertaken in accordance with the International Association of Wood Anatomists' recommendations wherever possible (Wheeler, Baas and Gasson, 1989) except in the case of tracheid length. Since macerations were not possible for the fossil wood, these measurements were taken from thin sections of both fossil and modern wood. The specimen is now sectioned and deposited at the British Antarctic Survey, Cambridge, UK.

RESULTS

Class: Magnoliopsida
Order: Magnoliales
Family: Winteraceae Lindley
Organ genus: *Winteroxylon* Gottwald

Emended generic diagnosis

Dicotyledonous wood without vessels (homoxylic) with indistinct growth rings. Secondary xylem with ground mass of tracheids rectangular in cross-section and an inner tangential diameter of 25–40 µm; pitting more abundant on the radial walls, circular, one to occasionally three rows and sporadically scalariform. Rays of two different types, heterocellular and very tall; uniseriate and multiseriate (three–15 cells wide); cells in tangential section irregularly rounded with sheath cells frequently present. Parenchyma difficult to distinguish from groundmass, apotracheal or in short uniseriate bands. Idioblast oil cells and occasional

sclerotic cells can be present in the secondary xylem and pith.

Type species: *Winteroxylon mundlosi* Gottwald
Locality: Germany
Age: late Eocene
  Winteroxylon jamesrossi Poole et Francis n. sp.
Holotype: DJ. 141.2
Repository: British Antarctic Survey, Cambridge, UK
Type locality: east side of Lachman Crags, James Ross Island, Antarctica (63°51·5′S, 57°48′W)
*Stratigraphic unit*: Santa Marta Formation, mid–late Santonian to early Campanian
Etymology: after James Ross Island

Diagnosis

Indistinct growth rings marked only by a decrease in radial tracheid diameter and cell wall thickness. Axial parenchyma predominantly diffuse. Tracheids thin-walled with circular bordered pits, radially elongate pits and scalariform-type pits mainly on overlapping areas. Rays predominantly multiseriate up to 13 cells wide, uniseriate, heterocellular and non-storied.

Description

This description is based on a piece of mature wood which probably originated from a large branch or small trunk with an estimated diameter of approx. 10 cm. The most diagnostic feature of this fossil is the multiseriate rays in conjunction with the groundmass composed exclusively of tracheids (Figs 1 and 2). In regions where crushing has not taken place, the fluctuation in the tracheid radial diameter is sufficient to describe 16 indistinct growth rings. Axial parenchyma is present as rare diffuse cells or in radial pairs and forms short axial strands of up to approx. four cells. The tracheids have a mean tangential diameter of 35 µm (range: 30–50 µm) and a mean radial diameter of 28 µm (range: 15–40 µm). The combined radial wall thickness ranges from 2·5 µm in the earlywood to 10 µm in the latewood. The length of the tracheids was difficult to measure because of the slight obliquity of the longitudinal section; even so, the tracheids seem to be greater than 1000 µm in length and generally approx. 1600 µm. Tracheid-to-tracheid pitting is relatively more abundant on radial walls compared with tangential walls. On some tracheids pitting is circular and bordered with elliptical pit apertures which seem to extend beyond the border. The circular pits (pit diameter 2·5–5 µm) are mainly in uniseriate (Figs 3–5) rows, although biseriate and triseriate rows are not uncommon in which case they are mainly oppositely (Figs 4 and 5), or very occasionally alternately, arranged. On other tracheids, or spatially separated along the same tracheid, radially elongated pits (pit diameter approx. 7·5 µm) can be observed which grade into a scalariform-type pitting (pit diameter approx. 22 µm) especially in the overlap areas between tracheids (Fig. 5). On one tracheid only, a more reticulate type of pitting was detected. No definite spiral thickenings were observed although
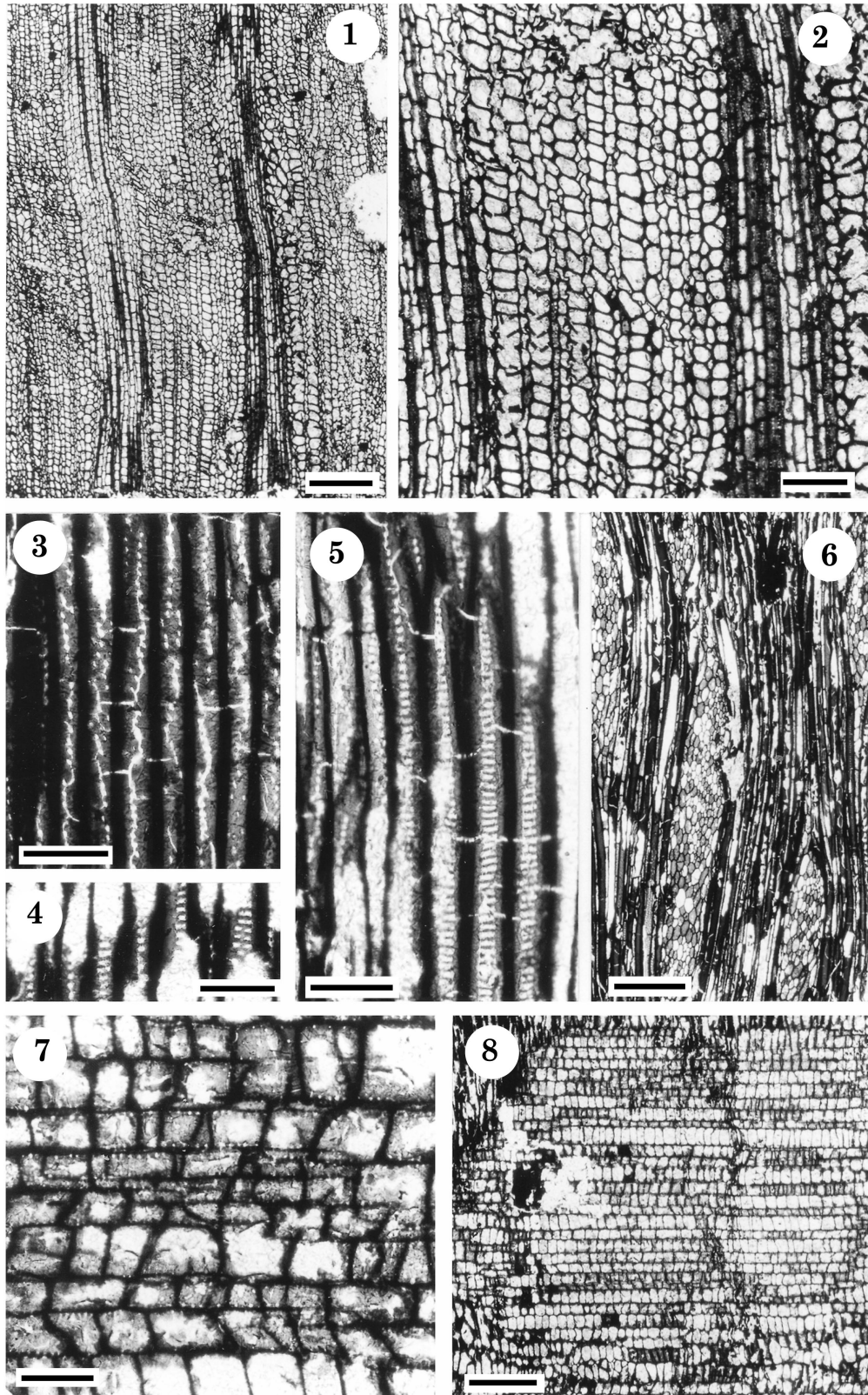
FIGS 1–8. Light micrographs of the winteraceous fossil wood. Figs 1 and 2, Transverse sections; Figs 3–5, 7 and 8, radial longitudinal sections; Fig. 6, tangential longitudinal section. Fig. 1. Multiseriate, uniseriate rays and tracheids; bar = 250 µm. Fig. 2. Multiseriate rays and tracheids; bar = 100 µm. Fig. 3. Uniseriate and biseriate tracheid pitting; bar = 50 µm. Fig. 4. Biseriate and tangentially elongate tracheid pitting; bar = 50 µm. Fig. 5. Scalariform tracheid pitting; bar = 50 µm. Fig. 6. Rays; bar = 50 µm. Fig. 7. Ray cell pitting; bar = 50 µm. Fig. 8. Ray cell composition; bar = 100 µm.

occasionally there seemed to be a hint of such thickening, but this is more likely to be an artefact of preservation. The internal walls of the tracheids seem smooth with no indication of vestures. The rays (Fig. 6) are of two distinct types, either heterocellular and multiseriate ranging typically from four–13 cells wide with short uniseriate wings, or (rarely) biseriate and uniseriate. Uniseriate rays are composed of upright and square cells, whereas the bodies of the multiseriate rays are composed of procumbent, square and upright cells (Figs 7 and 8) mixed throughout the ray with upright cells forming short (two–three celled) uniseriate margins. Sheath cells are present. The uniseriate and multiseriate rays range from 200–1636 μm and 500–4300 μm in height, respectively. The ray-tracheid pitting (pit diameter approx. 2·5 μm) is bordered, although the borders are not always easy to observe. Small, simple ray parenchyma pitting is generally arranged in rows along the tangential margin of the ray cells (Fig. 7). Occasionally a small number of pits are found away from the margins of the squarer ray cells. There are on average between one and two multiseriate rays and one–two (sometimes three–four) uni- and biseriate rays per tangential mm.

DISCUSSION

Comparisons with extant taxa

Complete lack of vessels is recorded in the genera of five dicotyledonous families: Winteraceae, Trochodendraceae, Tetracentraceae (Metcalfe and Chalk, 1950), Amborellaceae (Bailey and Swamy, 1948; Money *et al*., 1950) and in the stem wood of *Sarcandra* Gard., one of the five genera of the Chloranthaceae (Swamy and Bailey, 1950; Carlquist, 1987). As a consequence the identification of the fossil material concentrated on these taxa. *Sarcandra* was eliminated from further comparisons because its stem has a xylem cylinder no greater than 3 mm in diameter and the tracheids of the secondary xylem do not have scalariform pitting/end walls (Carlquist, 1987; Metcalfe, 1987). The woods of the monogeneric families Trochodendraceae and Tetracentraceae have xylem similar to each other. They characteristically possess multiseriate heterocellular rays, and scalariform and circular pits which are in accordance with the fossil. However, the ray structures of each of these two families are sufficiently different to warrant exclusion: *Tetracentron* Oliv. has uniseriate and narrow (three–four cells wide) multiseriate rays with uniseriate extensions. In addition it is unique in having 'unusual tracheids', i.e. sporadic radial files of broad tracheids with the tangential walls supporting crowded alternate pitting and radial walls devoid of pits except in the cross fields (Suzuki *et al*., 1991*a*). *Trochodendron* Sieb. & Zucc. has characteristically much taller uniseriate extensions to the wider multiseriate (six–seven seriate) rays (Gupta, 1934; Scott and Wheeler, 1982) which distinguish it from the fossil. The wood anatomy of *Amborella* Baill., in the monogeneric family Amborellaceae, is distinct from the fossil in that these shrubs produce a limited amount of secondary xylem with rays generally narrow (i.e. 1–2 cells wide, rarely five), 15 rays per tangential mm, with long uniseriate tails composed of very tall upright and square cells (Bailey and Swamy, 1948; den Outer and van Veenendaal, 1982; Metcalfe, 1987). In addition, the bordered pits are mainly circular, sporadically transitional and scalariform, and restricted to the thinner parts of the fibre-tracheid (as opposed to tracheid) walls which make up the groundmass of the wood (Lemesle and Pichard, 1954).

The anatomical characters shared, in general, by the extant members of the Winteraceae and the fossil specimen are: vessels absent; growth rings present to varying degrees (in temperate species only; Carlquist, 1989); latewood tracheids radially-narrower and generally thicker-walled than earlywood tracheids; intertracheary pitting more frequent on the radial walls; axial parenchyma mainly diffuse; presence of multiseriate and uniseriate rays; and non-storied wood. The discrepancies are fewer uniseriate rays, more abundant scalariform tracheid pitting and to a lesser extent the greater abundance of procumbent ray cells in the fossil material. The characteristic scalariform pitting exhibited by the fossil is present only in the mature wood of *Zygogynum*, *Belliolum* and *Bubbia* (Carlquist, 1988*a*) although it is present in the metaxylem tracheids of all Winteraceae (Carlquist, 1988*a*, 1989; pers. obs.). *Belliolum*, however, has long (17–24 cells) axial parenchyma strands and unbordered ray pitting (Carlquist, 1983*a*) and *Zygogynum* has lignified ray cells and ethereal oil cells within the rays. Therefore, on close examination of the wood of the Winteraceae, the closest similarity seems to lie with the species of extant *Bubbia* which are found today distributed across New Guinea and Lord Howe Island (Mabberley, 1997).

The anatomical characters of the genus *Bubbia* compare closely with those exhibited in *Winteroxylon jamesrossi* (Figs 9, 11–14; Table 1) although differences can still be determined. For example, *Bubbia* has parenchyma present as diffuse cells or tangential bands, one–three cells thick, the uniseriate rays are more conspicuous and the multiseriate rays narrower in *Bubbia* than in the fossil (Fig. 9). The greater width and close axial proximity, verging on 'aggregations', of the rays seen in the fossil tend to be most similar to the arrangement seen in species of *Drimys* (Fig. 10) and *Tasmannia*, as opposed to the more discrete rays exhibited by *Bubbia*. However, Carlquist (1983*b*) notes that the width of the multiseriate rays of *Bubbia* varies depending on the age of the sample (i.e. the older the sample, the wider the rays) although no mention is made of whether there is any change in the height or frequency of the uniseriate rays with age. In addition to ray width, ray histology and dimensions also differ with more procumbent ray cells occurring towards the periphery of larger wood samples in *Bubbia*. The scalariform pitting in the tracheids of the fossil seems to be more abundant when compared with those in *Bubbia* (Fig. 14) although exceptionally abundant scalariform pitting is noted (Carlquist, 1983*b*) for *B. balansae* (=*Drimys balansae* Baill., material not seen). However, *B. balansae* has ethereal oil cells in the rays, a character which is not seen in *W. jamesrossi*. Even though the anatomical similarity between this genus and the fossil is greatest, the discrepancies outlined above are such that the fossil cannot, and in view of its age should not, be
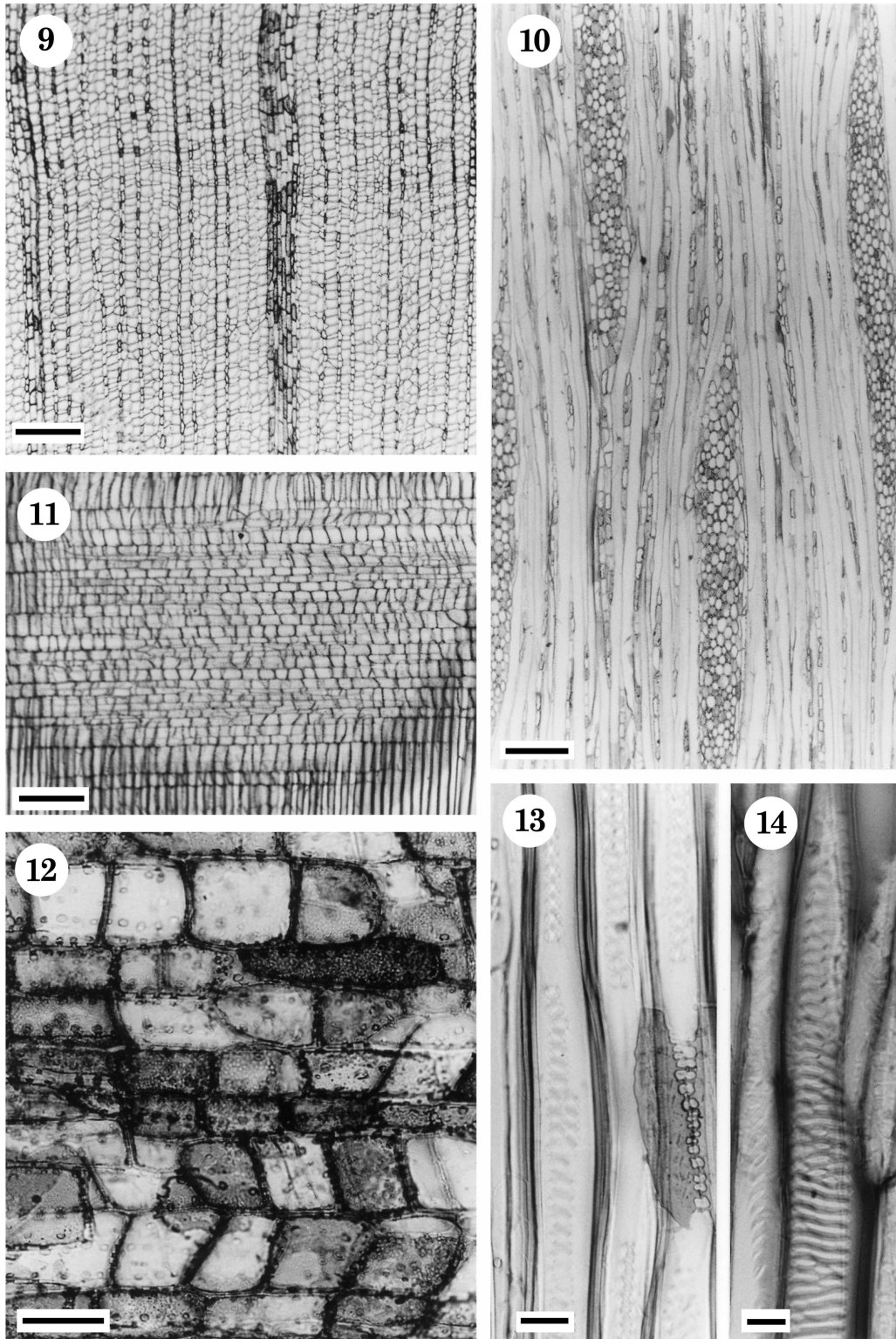
FIGS 9–14. Light micrographs of extant *Drimys winteri* (Fig. 10) and *Bubbia* sp. (Figs 9, 11–14) for comparison with the fossil. Fig. 9, Transverse section; Fig. 10, tangential longitudinal section; Figs 11–14, radial sections. Fig. 9. Multiseriate and uniseriate rays and tracheid distribution; bar = 250 μm. Fig. 10. Multiseriate and uniseriate rays; bar = 250 μm. Fig. 11. Ray cell composition; bar = 400 μm. Fig. 12. Ray cell pitting; bar = 50 μm. Fig. 13. Uniseriate and biseriate tracheid pitting; bar = 25 μm. Fig. 14. Scalariform tracheid pitting; bar = 25 μm.

TABLE 1. *Tabulated summary of the wood characters of the taxa most closely resembling* Winteroxylon jamesrossi

Character	*Winteroxylon jamesrossi*	*Winteroxylon mundlosi*	*Bubbia*[1,2]
Growth rings	Indistinct	Indistinct	Absent
Tracheid			
Tangential diameter (μm)	15–40	24–36	23–51
Radial wall thickness (μm)	2·5–10	5–9	4–7
Pitting	2·5–15 μm diameter, circular to more elongate	7–9 μm diameter, circular	7–14 μm diameter, circular
Overlap areas	Uniseriate, biseriate, elongate to scalariform	Uniseriate, biseriate, sometimes scalariform	Two–three rows of circular pits, sometimes opposite, occasionally elongated and scalariform
Axial parenchyma	Diffuse	Uniseriate bands or in tangential apotracheal uniseriate bands	Diffuse or in bands one–three cells thick
Rays			
Structure	Heterogeneous Type I, ray body cells procumbent becoming more square towards the periphery, upright cells in the wings and uniseriate rays	Heterogeneous, ray body cells upright in uniseriate cells and the wings of the multiseriate cells	Heterogeneous Type I although uniseriate rays and uniseriate portions of multiseriate rays contain few procumbent cells
Total height	Uniseriates: 200–1636 μm Multiseriates: 500–4300 μm	All rays higher than 2000 μm	Uniseriates: multiseriates: all 600–>1500 μm
Width	Uniseriate and four–13 cells	Uniseriate and three–eight cells	Uniseriate and two–seven cells
Cell pitting	Circular, bordered	Circular	Circular, bordered
Contents	Occasional dark amorphous accumulations	Possible idioblastic oil cells present	Few small droplets of resin-like material; occasional ethereal oil cells in central portions of multiseriate rays

Data from personal observations and [1]Carlquist, 1983*b*, [2]specimen number U18312 (Utrecht University).

placed in the extant genus. In light of this, the fossil wood has been compared with organ genera erected for homoxylic fossil woods unassignable to an extant genus.

Comparisons with fossil taxa

Suzuki, Joshi and Shuichi (1991*b*) provide a revision of homoxylic fossil woods, from the Jurassic through to the Tertiary, that have been described since 1848. Homoxylic fossil wood has often been placed in the organ genus *Homoxylon* Hartig (Hartig, 1848) which is now considered to be coniferous based on the ray characteristics and tracheid pitting of the type species *H. blasii* Hartig (Bose and Sah, 1954). As a consequence, those fossils with angiosperm affinities have since been transferred to other organ genera. Torres and Lemoigne (1989) described a homoxylous fossil wood from the Cretaceous of Antarctica. The radial scalariform pitting, growth ring characters and homogeneous rays suggested that this wood originated from a bennettitalean as opposed to an angiosperm source and thus placed it in the organ genus *Sahnioxylon* Bose & Sah, erected for homoxylous woods with affinity with the Bennettitales, an order of extinct gymnosperms. The ray characters, ray and tracheid pitting of *Sahnioxylon antarcticum* Lemoigne and Torres are very different from those seen in the fossil wood described here, most notably in ray size, large bordered tracheid pitting, cross field pitting and characteristic tracheid zonation in cross-sections of *Sahnioxylon* species. Therefore *W. jamesrossi* is not considered to have bennettitalean affinities.

There are three fossil wood taxa which have close anatomical similarity to extant genera of angiospermous homoxylous woods: (1) *Trochodendron beckii* (Hergert & Phinney) Scott & Wheeler *comb. nov.* from the Tertiary of North America (Hergert and Phinney, 1954; Scott and Wheeler, 1982); (2) *Tetracentron japonoxylon* Suzuki, Joshi & Noshiro from the Tertiary of Japan (Suzuki *et al.*, 1991*b*); and (3) *Tetracentronites panochetris* Page from the Upper Cretaceous of North America (Page, 1968, 1979, 1981). The main distinguishing features between the fossil wood described here and *Trochodendron beckii* are that *T. beckii* has distinct growth rings, tracheids with a smaller diameter but up to 3600 μm in length, no pit pairs on the tangential walls and generally narrower rays with high, well-defined uniseriate wings. *Tetracentron japonoxylon* has the characteristic 'unusual' tracheids outlined above (Suzuki *et al.*, 1991*b*). *Tetracentronites panochetris* is considered by Page (1968) to be most similar to extant *Tetracentron* and *Trochodendron* and differs from *Winteroxylon jamesrossi* in tracheid wall thickness, ray size and composition. Although the general description of *T. panochetris* does seem similar to the Antarctic material, the lack of photographic illustrations of the detailed microscopic anatomy coupled with Page's conclusion of greater anatomical similarity seen in *Tetracentron* and *Trochodendron* strongly suggests that her vesselless angiosperm belongs to a different taxon. Other genera of 'angiospermous' homoxylic woods have somewhat more uncertain affinities and are probably not angiosperm in origin and, since they are less similar to

the Antarctic fossil described here, they are not considered further.

Gottwald (1992) erected the organ genus *Winteroxylon* for fossil wood with anatomical similarities to the genera of the Winteraceae for a piece of Upper Eocene phosphatized wood from Germany. The generic diagnosis fits the fossil wood from Antarctica except for the lower limit for tracheid tangential diameter (i.e. 15 μm in the Antarctic fossil as opposed to 24 μm) and the presence of idioblast oil cells. Therefore the specimen under study here could be included within this organ genus. There is only one species described, *W. mundlosi*, which can be compared with the Antarctic wood (Table 1). Differences between *W. mundlosi* and *W. jamesrossi* include the presence of a central pith with stone cells in *W. mundlosi* along with rays greater than 2 mm in height and only up to eight cells wide, sclerotized uniseriate rays and idioblastic oil cells which are present in the multiseriate rays. Gottwald (1992) states that the closest similarity lies with the extant genera *Drimys* and *Bubbia*. Although the fossil material described here shows close resemblance to *W. mundlosi*, in light of the anatomical discrepancies, the difference in geological age and hemispheres from which these fossils have been found, it is felt that the erection of a new species of *Winteroxylon* for the Antarctic wood is warranted.

Ecological considerations

The present day ecological range of the Winteraceae is from the tropics to cool temperate regions, including alpine zones, covering Malaysia to Australasia, the South Pacific and south and central America. This distribution range is, to a certain extent, reflected in anatomy. Tracheid length and diameter within species of the Winteraceae tend to correlate with age and ecological setting. Older material and plants in warmer environments have longer, wider tracheids than plants from relatively colder conditions (Carlquist, 1988a,b, 1989). From the growth ring curvature it can be assumed that the fossil wood is mature xylem that probably originated from a relatively large branch or a small trunk, rather than small stem or twig. Although the tracheid length quoted here for the fossil material is an estimate, the majority of the tracheids are approx. 1600 μm in length and, on average, 35 μm in tangential diameter which is 17% greater in diameter and double the average length of the tracheid dimensions exhibited by *Drimys winteri* 'winteri' Forst. This might suggest that the parent plant was growing in an environment that was somewhat warmer than that experienced by *D. winteri* 'winteri' in Tierra del Fuego today, where frosts and probable freezing of the soil moisture occur (Carlquist, 1988a), and more similar to the seasonally-flooded habitat of *Bubbia* sp. in New Caledonia (although for completeness it should be noted that other species of *Bubbia* with longer, wider tracheids occur in New Caledonia at altitudes above 1000 m; Carlquist, 1983b).

The degree of scalariform pitting is suggested to be related to transpiration rate with an increase in scalariform pitting with enhanced transpiration (Carlquist, 1988a). Therefore, as the fossil exhibits a high degree of scalariform

pitting this may suggest that the parent plant grew in a relatively warm environment not lacking in water. However, because scalariform end wall and lateral wall pitting is present in the metaxylem tracheids of all the Winteraceae this has also been considered (Carlquist, 1988a) to be a juvenile and thus a primitive feature. Therefore, perhaps it is not surprising that there is a greater degree of scalariform pitting in the fossil wood compared with the modern material.

According to the observations made by Carlquist (1988a,b) the presence of growth rings and the proportion of each growth ring devoted to narrower latewood tracheids in the Winteraceae reflect the degree of extremity within the environment. The relatively narrow, indistinct latewood zones which were observed in *W. jamesrossi* may also suggest that the parent plant grew in a relatively seasonless environment.

In addition to the indications seen in the anatomy outlined above, the presence of winteraceous material in the Late Cretaceous sediments of James Ross Island helps to confirm ideas put forward in support of a temperate climate (e.g. Crame, 1992; Hill and Scriven, 1995; Francis, 1996; Dingle and Lavelle, 1998 and references therein) prevailing over the Antarctic Peninsula at a palaeolatitude of 60–65°S. Evidence for a temperate vegetation type is obtained from the present day ecological ranges of the nearest living relatives of fossil plant material such as the Podocarpaceae (Dettmann, 1989), Atherospermataceae (Poole and Francis, 1999), Nothofagaceae (e.g. Torres, 1984; Askin, 1992), Aquifoliaceae (Dettmann, 1989) and Myrtaceae (Dettmann and Thomson, 1987) from the Cretaceous of Antarctica.

CONCLUSIONS

Palaeobotanical (and palynological) data from Antarctica are crucial to our understanding of the biodiversity, long-term vegetational changes and palaeoclimate of this unique high-latitude palaeoenvironment which has no modern analogue. The fossil wood, *Winteroxylon jamesrossi*, described here represents the first record of the Winteraceae in the wood flora of Antarctica. The differences in anatomical structure between *W. jamesrossi* and *Bubbia*, with which the fossil shows greatest anatomical similarity, may be attributed to one or more of the following: (1) differences in ecological tolerance which are reflected in the wood; (2) evolutionary processes over the last 80 million years; or (3) the relative ages of the specimens. From nearest living relative studies, this fossil helps confirm that during the Late Cretaceous the Antarctic Peninsula supported a vegetation-type similar to that seen in southern hemisphere temperate regions today.

LITERATURE CITED

Askin RA. 1992. Late Cretaceous-early Tertiary Antarctic outcrop evidence for past vegetation and climates. *Antarctic Research Series* **56**: 61–73.

Bailey IW, Nast CG. 1945. The comparative morphology of the Winteraceae VII. Summary and conclusions. *Journal of the Arnold Arboretum* **26**: 37–47.

Bailey IW, Swamy BGL. 1948. *Amborella trichopoda* Baill., a new morphological type of vesselless dicotyledon. *Journal of the Arnold Arboretum* **29**: 245–253.

Bose MN, Sah SCD. 1954. On *Sahnioxylon ramahalense*, a new name for *Homoxylon ramahalense* Sahni, and *S. andrewsii* a new species of *Sahnioxylon* from Amrapara in the Rajmahal Hills, Bihr. *Palaeobotanist* **3**: 1–8.

Carlquist S. 1981. Wood anatomy of *Zygogynum* (Winteraceae); field observations. *Adansonia* **3**: 281–292.

Carlquist S. 1982. *Exospermum stipitatum* (Winteraceae); observations on wood, leaves, flowers, pollen and fruit. *Aliso* **10**: 277–289.

Carlquist S. 1983a. Wood anatomy of *Belliolum* (Winteraceae) and a note on flowering. *Journal of the Arnold Arboretum* **64**: 161–169.

Carlquist S. 1983b. Wood anatomy of *Bubbia* (Winteraceae) with comments on origin of vessels in dicotyledons. *American Journal of Botany* **70**: 578–590.

Carlquist S. 1987. Presence of vessels in wood of *Sarcandra* (Chloranthaceae); comments on vessel origins in angiosperms. *American Journal of Botany* **74**: 1765–1771.

Carlquist S. 1988a. Wood anatomy of *Drimys* s.s. (Winteraceae). *Aliso* **12**: 81–95.

Carlquist S. 1988b. *Comparative wood anatomy, systematic, ecological and evolutionary aspects of dicotyledon wood.* Berlin: Springer-Verlag.

Carlquist S. 1989. Wood anatomy of *Tasmannia*; summary of wood anatomy of Winteraceae. *Aliso* **12**: 257–275.

Crame JA. 1992. Late Cretaceous palaeoenvironments and biotas—an Antarctic perspective. *Antarctic Science* **4**: 371–382.

Crame JA, Pirri D, Riding JB, Thompson MRA. 1991. Campanian Maastrichtian (Cretaceous) stratigraphy of the James Ross Island area, Antarctica. *Journal of the Geological Society* **148**: 1125–1140.

Cranwell LM. 1959. Fossil pollen from Seymour Island. *Nature* **184**: 1782–1785.

Cutler DF, Gregory M. 1998. *Anatomy of the dicotyledons. Volume IV. Saxifragales.* Oxford: Clarendon Press.

Dettmann ME. 1989. Antarctica: Cretaceous cradle of austral temperate rainforests? In: Crame JA, ed. *Origins and evolution of the Antarctic biota. Geological Society Special Publications* **47**: 89–105.

Dettmann ME, Jarzen DM. 1990. The Antarctic/Australian rift valley: Late Cretaceous cradle of northeastern Australasian relicts? *Review of Palaeobotany and Palynology* **65**: 131–144.

Dettmann ME, Thomson MRA. 1987. Cretaceous palynomorphs from the James Ross Island area, Antarctica—a pilot study. *British Antarctic Survey Bulletin* **77**: 13–59.

Dingle RV, Lavelle M. 1998. Late-Cretaceous-Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. *Palaeogeography, Palaeoclimatology and Palaeoecology* **141**: 215–232.

Doyle J. 2000. Paleobotany, relationships, and geographic history of Winteraceae. *Annals of the Missouri Botanical Garden* **87** (in press).

Dusén P. 1908. Über die tertiäre Flora der Seymour Insel. *Wissenschaftliche Ergebnisse der Schwedische Südpolar-Expedition 1901–1903* **3**: 1–27.

Francis JE. 1986. Growth rings in Cretaceous and Tertiary wood from Antarctica and their palaeoclimatic implications. *Palaeontology* **29**: 665–684.

Francis JE. 1996. Antarctic palaeobotany: clues to climate change. *Terra Antarctica* **3**: 135–140.

Gottwald H. 1992. Hölzer aus Marinen Sanden des Oberen Eozän von Helmstedt (Niedersachsen). *Palaeontographica B* **225**: 27–103.

Gupta KM. 1934. On the wood anatomy and theoretical significance of homoxylous angiosperms. *Journal of the Indian Botanical Society* **13**: 71–101.

Haas H, Rowe NP. 1999. Thin sections and wafering. In: Jones TP, Rowe NP, eds. *Fossil plants and spores: modern techniques.* London: Geological Society, 76–81.

Hartig T. 1848. Beiträge zur Geschichte der Pflanzen und zur Kenntniss der norddeutschen Braunkohlen-Flora. *Botanische Zeitung Jahrbuch* **6**: 185–190.

Hergert HL, Phinney HK. 1954. *Trochodendroxylon beckii* gen. et sp. nov. from the Tertiary of Oregon. *Bulletin of the Torrey Botanical Club* **81**: 118–190.

Hill RA, Scriven LJ. 1995. The angiosperm dominated woody vegetation of Antarctica: a review. *Review of Palaeobotany and Palynology* **86**: 175–198.

Ilic J. 1987. *The CSIRO family key for hardwood identification.* Leiden: EJ Brill.

Ilic J. 1991. *CSIRO atlas of hardwoods.* Australia: Crawford House Press and CSIRO Publications.

Jane FW. 1970. *The structure of wood.* London: Black.

Keating JM. 1992. Palynology of the Lachman Crags Member, Santa-Marta Formation (Upper Cretaceous) of north-west James Ross Island. *Antarctic Science* **4**: 293–304.

LaPasha CA, Wheeler EA. 1987. A microcomputer based system for computer-aided wood identification. *International Association of Wood Anatomists Bulletin* **8**: 347–354.

Lawver LA, Gahagan LM, Coffin MF. 1992. The development of paleoseaways around Antarctica. The Antarctic Palaeoenvironment: a perspective on global change. In: Kennett JP, Warnke DA, eds. *American Geophysical Union Antarctic Research Series, Part One* **56**: 7–30.

Leat PT, Scarrow JH, Miller IC. 1995. On the Antarctic Peninsula batholith. *Geological Magazine* **132**: 399–412.

Lemesle R, Pichard Y. 1954. Les caractères histologiques du bois des Monimiacées. Difficultés d'application à la phylogénie. *Revue Génerale de Botanique* **61**: 69–95.

Mabberley DJ. 1997. *The plant book. A portable dictionary of the higher plants*, 2nd edn. Cambridge: Cambridge University Press.

Metcalfe CR. 1987. *Anatomy of the dicotyledons. Magnoliales, Illiciales and Laurales*, 2nd edn, volume III. Oxford: Clarendon Press.

Metcalfe CR, Chalk L. 1950. *Anatomy of the dicotyledons*, volumes I and II. Oxford: Clarendon Press.

Metcalfe CR, Chalk L. 1989. *Anatomy of the dicotyledons. Wood structure and conclusion of general introduction*, 2nd edn, volume II. Oxford: Clarendon Press.

Money L, Bailey IW, Swamy BGL. 1950. The morphology and relationships of the Monimiaceae. *Journal of the Arnold Arboretum* **31**: 372–404.

den Outer RW, van Veenendaal WLH. 1982. Wood anatomy of *Tambourissa* (Monimiaceae) from Madagascar. *Acta Botanica Neerlandica* **31**: 265–274.

Page VM. 1968. Angiosperm wood from the Upper Cretaceous of Central California: Part II. *American Journal of Botany* **55**: 168–172.

Page VM. 1979. Dicotyledonous wood from the Upper Cretaceous of central California. *Journal of the Arnold Arboretum* **60**: 323–346.

Page VM. 1981. Dicotyledonous wood from the Upper Cretaceous of central California. III. Conclusions. *Journal of the Arnold Arboretum* **62**: 437–455.

Pankhurst RJ. 1982. Rb-Sr geochronology of Graham Land, Antarctica. *Journal of the Geological Society of London* **139**: 701–711.

Patel RN. 1974. Wood anatomy of the dicotyledons indigenous to New Zealand 4. Winteraceae. *New Zealand Journal of Botany* **12**: 19–32.

Poole I, Francis JE. 1999. The first record of fossil atherospermataceous wood from the Upper Cretaceous of Antarctica. *Review of Palaeobotany and Palynology* **107**: 97–107.

Rancusi MH, Nishida M, Nishida H. 1987. Xylotomy of the important Chilean woods. In: Nishida M, ed. *Contribution to the botany of the Andes II*. Tokyo: Academia Science Books, 68–154.

Scott RA, Wheeler EA. 1982. Fossil woods from the Eocene Clarno Formation of Oregon. *International Association of Wood Anatomists Bulletin* **3**: 135–154.

Smith AC. 1943. Taxonomic notes on the Old World species of Winteraceae. *Journal of the Arnold Arboretum* **24**: 119–164.

Smith AC. 1966. A reconsideration of the genus *Tasmannia* (Winteraceae). *Taxon* **18**: 286–290.

Suzuki M, Joshi L, Fujii T, Noshiro S. 1991*a*. The anatomy of unusual tracheids in *Tetracentron* wood. *International Association of Wood Anatomists Bulletin* **12**: 23–33.

Suzuki M, Joshi L, Shuichi N. 1991*b*. *Tetracentron* wood from the Miocene of Noto Peninsula, Central Japan, with a short revision of homoxylic fossil woods. *Botanical Magazine of Tokyo* **104**: 37–48.

Swamy BGL, Bailey IW. 1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. *Journal of the Arnold Arboretum* **31**: 117–129.

Torres T. 1984. *Nothofagoxylon antarcticus* n. sp., madera fósile del Terciario de la isla Rey Jorge, islas Shetland del Sur, Antárctica. *Instituto Antarctico Chileno Serie Cientifica* **31**: 39–52.

Torres T, Lemoigne Y. 1989. Hallazagos de maderas fósiles de Angiospermas y Gimnospermas del Cretácico Superior en punta Williams, isla Livingston, islas Shetland del Sur, Antárctica. *Instituto Antarctico Chileno Serie Cientifica* **39**: 9–29.

Vink W. 1985. The Winteraceae of the Old World V. *Exospermum* links *Bubbia* to *Zygogynum*. *Blumea* **31**: 39–55.

Wheeler EA, Pearson RG, LaPasha CA, Zack T, Hatley W. 1986. *Computer-aided wood identification*. Raleigh: North Carolina Agricultural Research Service Bulletin 474.

Wheeler EA, Baas P, Gasson PE. 1989. IAWA list of microscopic features for hardwood identification. *International Association of Wood Anatomists Bulletin* **10**: 219–332.