

**EVIDENCE FOR GONDWANAN ORIGINS FOR
SASSAFRAS (LAURACEAE)?
LATE CRETACEOUS FOSSIL WOOD OF ANTARCTICA**

by

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SUMMARY

Sassafrasoxylon gottwaldii sp. nov. is a new taxon for fossil wood with a suite of features diagnostic of *Sassafras* Nees & Eberm. of the Lauraceae. The fossil wood described is from Late Cretaceous (Santonian-Maastrichtian) sediments of the northern Antarctica Peninsula region. This new species of *Sassafrasoxylon* Brezinová et Süß resembles the species of extant *Sassafras* in being distinctly ring-porous, having vessel elements with simple perforation plates and very occasional scalariform plates with relatively few bars in the narrowest latewood vessels, alternate intervacular pitting, marginal (initial) parenchyma bands and paratracheal vasicentric parenchyma in the latewood, multiseriate rays and oil and/or mucilage cells. The fossils were found as isolated pieces of wood and therefore it is not certain whether the parent plant was *Sassafras*-like in all characters. Consequently the fossils have been placed in an organ genus rather than in extant *Sassafras*. This is the oldest record of an organ with features closest to extant *Sassafras* and may suggest that *Sassafras* first appeared in Gondwana and later radiated into the Northern Hemisphere. The distribution of extant *Sassafras* in North America and East Asia may represent a relict of a geographically more widespread taxon in the past.

Key words: Lauraceae, *Sassafras*, Antarctica, Cretaceous, wood anatomy, fossil.

INTRODUCTION

The lack of palaeofloras from mid-Cretaceous rocks from the Southern Hemisphere accounts for the dearth of knowledge about Gondwanan floristic diversity, angiosperm radiation and diversification. Studies of Southern Hemisphere Cretaceous fossils are needed to provide a more complete picture of floral diversity and dynamics through a period of global greenhouse warmth. Such studies will provide information pertinent

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to the break-up of Gondwana and its influence on land plant evolution. The Antarctic Peninsula has probably the most complete Cretaceous sequence in the Southern Hemisphere but material from this sequence has not been studied extensively.

During the Late Cretaceous and Early Tertiary the Antarctic Peninsula was lying at a palaeolatitude of approximately 60–65° S. Such a high latitude would have experienced a polar climate with short days and long periods of darkness followed by summers with continuous low-angle sunlight, coupled with a relatively mild temperature and ample moisture (Truswell 1991; Askin 1992; Francis 1996). Plant material, including wood, originating from vegetation that grew on the Antarctic Peninsula was washed into a sedimentary basin (the James Ross Basin) to the east. Subsequently it became waterlogged and buried within sediments that gradually filled the basin (Francis 1986; Pirrie et al. 1991; Pirrie 1994). The wood was infiltrated by calcium-rich solutions and petrified. These woods can be found in marine clastic sediments such as those now exposed on James Ross Island and Seymour Island.

This paper describes two calcified wood samples similar to *Sassafras* (Lauraceae) from the Late Cretaceous of Antarctica and forms part of an ongoing investigation of the fossil angiosperm wood flora of the northern Antarctic Peninsula region. These studies aim to determine changes in vegetation and climate, and to record trends in the evolution and specialization of secondary xylem through the Late Cretaceous and Early Tertiary.

MATERIALS AND METHODS

The fossil material illustrated in this paper is from two Late Cretaceous localities in the northern Antarctic Peninsula region. The type specimen (DJ. 1051.5), with an estimated diameter of at least 6 cm, was found in the López de Bertodano Formation on Seymour Island. This Formation is dated as Maastrichtian based on ammonite zonation (Crame et al. 1991, 1999). The paratype (DJ. 451.6), with an estimated diameter of at least 12 cm, was collected from the Santa Marta Formation, James Ross Island. This Formation is dated as mid-late Santonian to early Campanian based on dinoflagellates, ammonites and bivalves (Crame et al. 1991; Keating 1992).

The calcified wood specimens were thin-sectioned (Haas & Rowe 1999). Systematic affinities of the fossils were initially determined by consulting references such as Cutler & Gregory (1998), Metcalfe & Chalk (1950, 1989), Metcalfe (1987), Ilic (1991) and searches of the computerised OPCN (Wheeler et al. 1986; LaPasha & Wheeler 1987) and CSIRO Family Key (Ilic 1987) wood databases. Subsequently, comparisons were made with extant wood samples housed in the Jodrell Laboratory, Royal Botanic Gardens Kew; the Wood Anatomy Section in the Herbarium, Utrecht University; and the Federal Research Centre for Forestry and Forest Products, Hamburg.

The wood was described and measurements undertaken in accordance with the IAWA recommendations (IAWA Committee 1989) wherever possible. Vessel element lengths were measured from thin sections as macerations were not possible for the fossils. The fossil specimens are deposited at the British Antarctic Survey, Cambridge, United Kingdom.

RESULTS

Order: Laurales

Family: Lauraceae

Tribe: Laureae

Organ genus: *Sassafrasoxylon* Brezinová et Süß

Generic diagnosis (translated from the German) — Vessels ring-porous, with a multiple ring of earlywood pores; perforation plates simple and scalariform; intervessel pits alternate and bordered. Parenchyma sparsely paratracheal. Rays homogeneous to weakly heterogeneous; uniseriate to quadriseriate; vessel ray pits enlarged, rounded to horizontally elongated and unilaterally bordered; oil idioblasts present.

Type species — *Sassafrasoxylon lipnicense* Brezinová et Süß (1988) from the Miocene of Lipnice, Czech Republic.

Sassafrasoxylon gottwaldii sp. nov.

Holotype: DJ. 1051.5

Paratype: DJ. 451.6

Repository: British Antarctic Survey, Cambridge, U.K.

Type locality: Seymour Island, Antarctica, 064° 15' 53" S, 056° 45' 01" W.

Stratigraphic horizon: López de Bertodano Formation, Maastrichtian.

Etymology: The specific epithet recognizes Professor H. Gottwald and his extensive studies of fossil and extant woods.

Species diagnosis — Growth rings distinct, demarcated by an obvious change in vessel diameter (Fig. 2, 4). Wood ring-porous. Earlywood and latewood vessels mostly circular, solitary and occasionally paired, rarely in radial multiples or clusters of up to three pores; vessel walls are thicker in latewood than in earlywood (Fig. 4). Earlywood tangential vessel diameter medium, mean c. 110 μm (range: 60–155 μm); latewood tangential vessel diameter small, mean c. 30 μm (range: 13–58 μm); mean vessel element length is 270 μm (range: 140–550 μm) in earlywood and 300 μm (range: 172–520 μm) in latewood; mean vessel frequency 29 mm^{-2} (range: 20–33 mm^{-2}) in earlywood and 41 mm^{-2} (range: 24–54 mm^{-2}) in latewood. Perforation plates simple (Fig. 10), very rare scalariform perforations, with relatively few (i.e. < 15) thick bars, (in addition to simple perforations) present in narrow latewood vessels (Fig. 12). No helical thickenings were observed. Intervessel pitting alternate (Fig. 13, 14), very occasionally opposite; pits circular to polygonal, horizontal pit diameter 5–10 μm . Vessel-ray pits with reduced borders, similar to intervessel pits in size and arrangement, rounded to occasionally gash-like, circular to more horizontally elongate (c. 8–13 μm), occasionally crowded within the cross fields [type 1 of Richter (1981)]. Fibres are distributed in more or less regular radial files especially in the latewood (Fig. 2, 4) although they are not always quadrangular in cross section. Mean fibre diameter is 11 μm (range: 5–25 μm). The mean combined fibre wall thickness is

6.5 μm (range: 2.5–12.5 μm) but no fibre pitting was observed. Axial parenchyma is more obvious in latewood when compared with the earlywood; in the latewood the parenchyma is paratracheal vasicentric to occasionally confluent (Fig. 2, 4); in the earlywood it forms a multiseriate initial band including one to several rows of earlywood vessels (Fig. 2). The parenchyma has up to c. 30 cells per axial strand. Rays multiseriate, mainly 2–4(–5) cells wide; mean height 310 μm (range: 120–470 μm), mixed with few uniseriate rays of mean height 130 μm (range: 70–200 μm ; Fig. 8). Rays are composed either solely of procumbent cells (homocellular) or of procumbent body cells with generally one, very occasionally two, rows of square to upright marginal cells [heterocellular; Kribs Heterogeneous Types II and III (Kribs 1935); Fig. 6]. There are between 4 and 8 rays per tangential mm. No deposits or thickened cell walls were observed in the rays. Oil and/or mucilage cells were observed in association with marginal ray cells (Fig. 17, 18), in a single instance also with axial parenchyma (Fig. 15).

DISCUSSION

Systematic affinities

Richter (1981) has studied the anatomy of 41 Lauraceae genera (830 species, over 1600 specimens). Generally wood of the Lauraceae is characterised by 1) paratracheal parenchyma, 2) alternate intervacular pitting, 3) tyloses, 4) fibre pits exclusively in the radial walls except for the *Beilschmiedia*/*Cryptocarya* group (Richter 1981; Richter in Metcalfe 1987). The majority of lauraceous woods have diffuse-porous wood (ring-porous only in *Sassafras*), rays that are 2–4 cells wide, less than 1 mm high and more or less heterogeneous (Kribs Heterogeneous Types I and II), and oil and/or mucilage cells in the form of idioblasts (Richter 1981; Richter in Metcalfe 1987).

The wood of *Sassafras* is similar to most other members of the Lauraceae in having alternate pitting (Fig. 16), simple perforation plates (Fig. 9), paratracheal parenchyma (Fig. 1, 3) oil and/or mucilage cells (Fig. 5, 7). However, *Sassafras* differs from other Lauraceae in having the combination of distinctly ring-porous wood (Fig. 1, 3), simple (Fig. 9) perforation plates but occasionally scalariform (with few, i.e. < 10, bars; Fig. 11) in latewood vessels and commonly 4- or 5-seriate rays (Fig. 7). The fossils both exhibit scalariform perforation plates with slightly more bars (i.e. up to 11) than extant *Sassafras*. Other than this there is no significant difference in wood structural features, qualitatively or quantitatively, between the fossils and the three extant species of *Sassafras* [*S. albidum* (Nutt.) Nees of eastern North America, *S. randaiense* (Hayata) Rehder of Taiwan and *S. tzumu* Hemsley of mainland China]. The extant species of *Sassafras* are indistinguishable from each other in terms of wood anatomy therefore we cannot assign the Cretaceous fossils to a single extant species. Moreover, it cannot be assumed that these *Sassafras*-like fossils belong to the extant genus as they were found as isolated pieces of wood and may represent a stem taxon or another lauraceous genus that developed growth rings in a seasonal, polar environment.

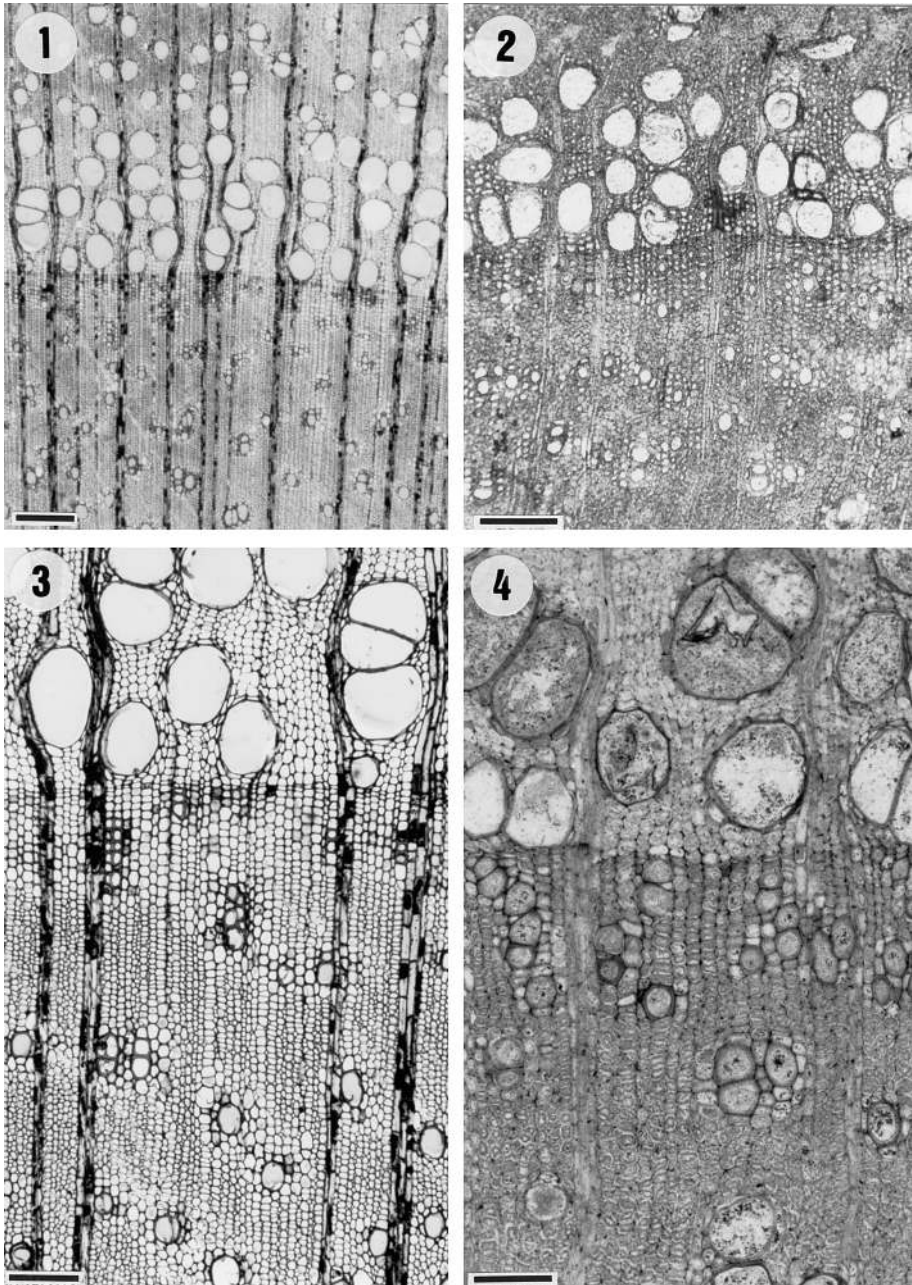


Fig. 1–4. Transverse sections of extant *Sassafras* and fossil *Sassafrasoxylon*. – 1 & 3: *Sassafras albidum* (Kew: 8/52 No. 2 Stern). – 2 & 4: *Sassafrasoxylon gottwaldii* (DJ. 451.6). — Scale bars = 200 μm in Fig. 1 & 2; 100 μm in Fig. 3 & 4.

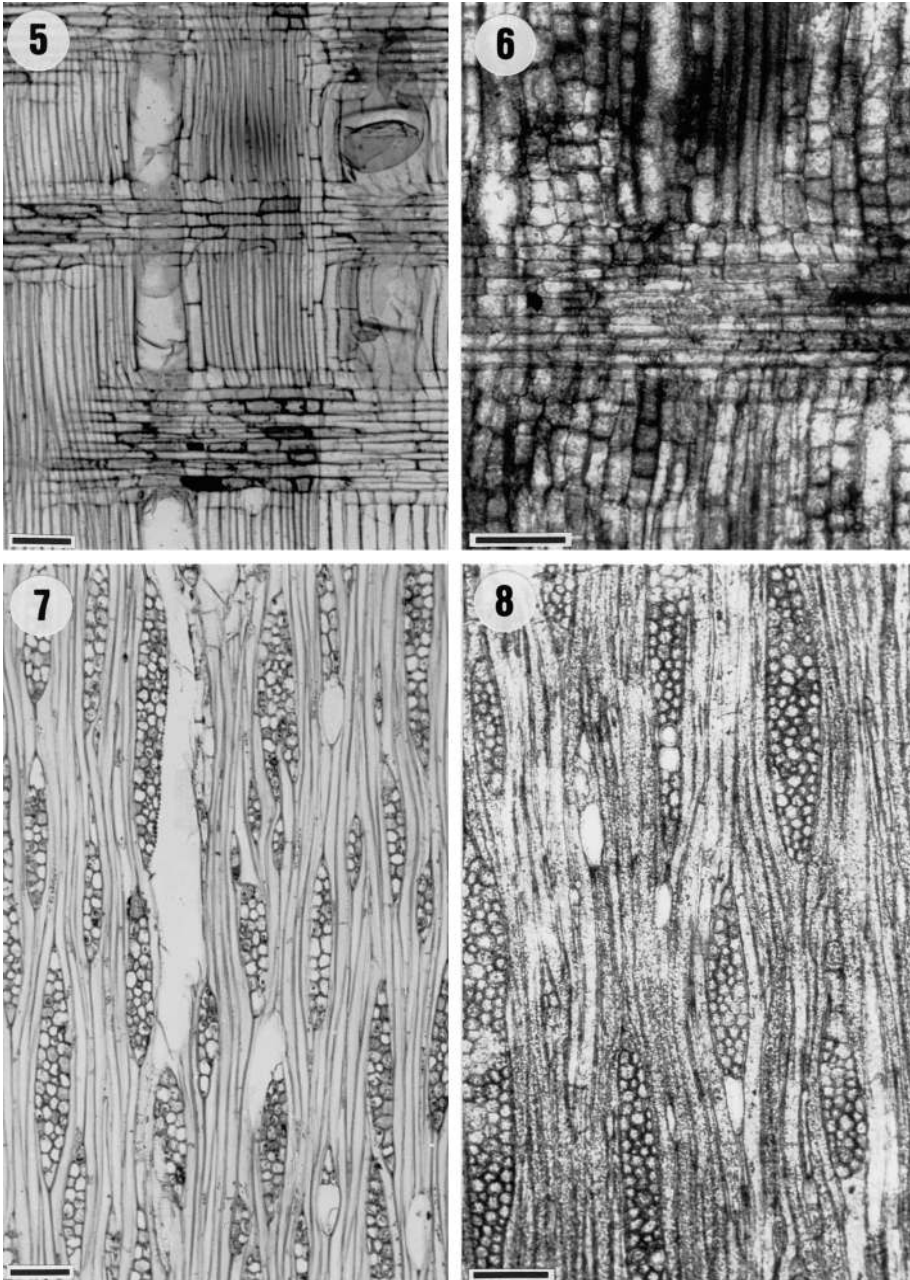


Fig. 5–8. Longitudinal sections of extant *Sassafras* and fossil *Sassafrasoxylon*. – 5: Radial section of *Sassafras randaiense* (Kew: Mus IV Formosa). – 6: Radial section of *Sassafrasoxylon gottwaldii* (DJ. 1051.5). – 7: Tangential section of *Sassafras albidum* (Kew: 8/52 No. 2 Stern). – 8: Tangential section of *Sassafrasoxylon gottwaldii* (DJ. 1051.5). — Scale bar = 75 μ m.

Fossil lauraceous woods

Fossil woods of Lauraceae are known from North America (e.g. Page 1967, Wheeler et al. 1977; Scott & Wheeler 1982; Herendeen 1991), South America (Kräusel 1925; Nishida et al. 1988, 1990), Antarctica (Gothan 1908), India (Lakhanpal et al. 1981; Awasthi & Jafar 1990), Australia (e.g. Leisman 1985; Hill 1986; Christophel et al. 1987; Carpenter et al. 1994; MacPhail et al. 1994) and Europe (e.g. Felix 1883; Süss 1958; Süss & Madel 1958; Huard 1967; Prakash et al. 1971; Brezinová & Süss 1988; Gottwald 1992, 1997). There have been a number of organ genera erected for woods of lauraceous affinity. However, many were synonymised with *Laurinium* Unger by Edwards (1931) although *Ulminium* Unger (1842) has nomenclatural priority. Süss (1958) and later Gottwald (1992) critically re-evaluated fossil lauraceous woods and listed those species with dubious, as well as certain, affinity to members of the Lauraceae. Brezinová and Süss (1988) described a lauraceous fossil wood from the Miocene of the Czech Republic with anatomical similarity closest to that of extant *Sassafras*. Consequently they erected the organ genus *Sassafrasoxylon* for their material. The Antarctic fossils described herein are very similar to the type species and can be included in the organ genus with no emendment to the generic diagnosis. The Antarctic material differs from the type species only in quantitative measurements (e.g. triseriate as opposed to quadriseriate maximum ray width, vessel diameters etc.) which could be accounted for by natural variation. However, the differences in age and geographical location support the erection of a new species of *Sassafrasoxylon* for the Antarctic material.

Distribution

Lauraceae fossils, other than wood, are common in Cretaceous and Tertiary sediments of both the Northern and Southern Hemispheres (e.g. Drinnan et al. 1990; Pole 1993; Hill & Merrifield 1993; Herendeen et al. 1994; Carpenter & Pole 1995; Pole 1996; Beertini & Roiron 1997; Kvacek 1998; Eklund & Kvacek 1998; Pole & Douglas 1999; Herendeen et al. 1999) but the fossil record of *Sassafras*-like organs is restricted to leaves from the Tertiary of North America (Axelrod 1966; MacGinitie 1953), Europe and Asia (Mai 1995). The fossil wood from Upper Cretaceous sediments of the Antarctic Peninsula region is the first and earliest record of *Sassafras*-like wood. Its presence in Antarctica may 1) suggest a minimum divergence age of c. 83 million years for the genus *Sassafras*, or its stem taxon, and 2) imply that this taxon was more widespread in the geological past and has experienced extinction over much of its range.

Today, the Lauraceae consists of about 50 genera and approximately 2500 to 3000 species generally with an arboreal habit, rarely shrubs, distributed throughout tropical and warm temperate regions, with tropical Indo-Malaya and tropical South America being the two major areas of concentration (Richter in Metcalfe 1987; Van der Werff & Richter 1996; Mabberley 1997). They are present in wet forest at all altitudes and are frequently one of the most common tree families especially in the foothills and middle elevations of the Andes (Van der Werff & Richter 1996). Members of the genus *Sassafras* (three species) are restricted today to East Asia and northeastern North America (Mabberley 1997). The North American *Sassafras albidum* (Nutt.)

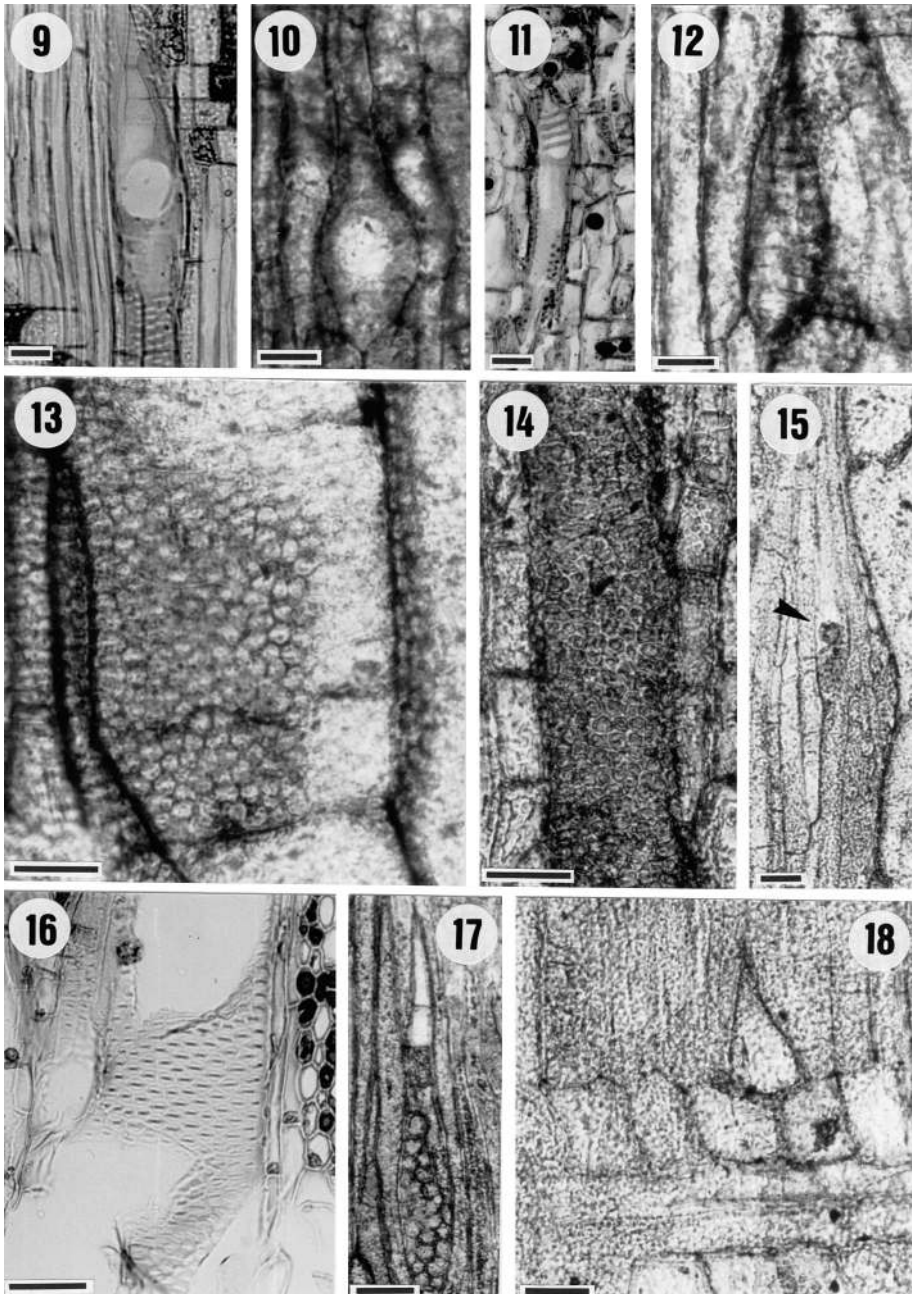


Fig. 9–18. Longitudinal sections of extant *Sassafras* and fossil *Sassafrasoxylon*. – 9: Simple perforation plate in the latewood of *Sassafras albidum* (Kew: 8/52 No. 2 Stern). – 10: Ditto of *Sassafrasoxylon gottwaldii* (DJ. 1051.5). – 11: Scalariform perforation plate in latewood of *Sassafras tzumu* (Kew: Hemsl WL Stern No. 258 7/52). – 12: Ditto of *Sassafrasoxylon gottwaldii*

Nees is a shrub or medium-sized aromatic tree that tends to form thickets in moist upland or valley habitats often in clearings. It is fast growing but short lived and has a spreading crown of short, stout branches with distinctive leaves. This species is the northernmost representative of the Lauraceae (Little 1998). *Sassafras tzumu* and *S. randaiense* are from East Asia; the former common in central and southern China at altitudes from 500 to 1000 m. The latter occurs only as scattered individuals in the broad-leaved forests of the Central Ranges in Taiwan at altitudes of 900 to 2400 m (Li 1963). Both are described as medium-sized deciduous trees and are similar in habit, vegetative characters, inflorescences and fruits to *Sassafras albidum* (Rehder 1920).

The fast growing nature and ability to tolerate poor soils may have helped the northward migration. *Sassafras* would not have been out of place in a postulated warm temperate environment (e.g. Crame 1992; Hill & Scriven 1995; Dingle & Lavelle 1998 and the references cited therein; Francis 1999) with suggested mean annual temperatures of 8–15° C, a possible temperature range of less than 16° C, no frosts and high annual rainfall (Birkenmajer & Zastawniak 1989; Askin 1992). These conditions are similar to those experienced by *Sassafras* today. Evidence in support of a temperate climate at c. 60° S in the Cretaceous can also be obtained from the present-day ecological ranges of the nearest living relatives of other fossil plant material which have been found from similar localities, e.g. Podocarpaceae (Dettmann 1989), Atherspermataceae (Poole & Francis 1999), Winteraceae (Poole & Francis 2000), Cunoniaceae (Poole et al. 2000), Nothofagaceae (e.g. Torres 1984; Askin 1992), Aquifoliaceae (Dettmann 1989) and Myrtaceae (Dettmann & Thomson 1987).

CONCLUSIONS

A new species, *Sassafrasoxylon gottwaldii*, has been erected for Late Cretaceous fossil woods from the northern Antarctic Peninsula region with anatomical characters indistinguishable from extant *Sassafras* Nees & Eberm. of the Lauraceae. This is the earliest occurrence, and only record in the Southern Hemisphere, of an organ with features closest to *Sassafras* now restricted to the Northern Hemisphere. This record may suggest that *Sassafras*, or its stem taxon, first appeared in Gondwana and later radiated into the Northern Hemisphere. Therefore the modern distribution of *Sassafras* may represent a relict of a more geographically widespread taxon in the past. The presence of this taxon in the Late Cretaceous sediments of James Ross Island and Seymour Island helps confirm (e.g. Dingle & Lavelle 1998 and references cited therein) the prevalence of a warm temperate climate for the Antarctic Peninsula at the end of the Mesozoic. This record furthers our understanding of a biodiversity and climate no longer represented today.

(DJ. 1051.5). – 13 & 14: Alternate intervessel pitting in *Sassafrasoxylon gottwaldii* (DJ. 1051.5). – 15: Oil cell (arrowed) in *Sassafrasoxylon gottwaldii* (DJ. 1051.5). – 16: Alternate intervessel pitting in *Sassafras albidum* (Kew: 8/52 No. 2 Stern). – 17 & 18: Oil cells associated with rays in *Sassafrasoxylon gottwaldii* (DJ. 1051.5 & DJ. 451.6 respectively). — Scale bars = 20 µm in Fig. 9–12; 30 µm in Fig. 13–15; 50 µm in Fig. 16–18.

ACKNOWLEDGEMENTS

We thank the British Antarctic Survey for the loan of the fossil wood specimens and for the invitation to I.P. to collect material. The Trans-Antarctic Association is also thanked for contribution to field expenses. The continued help of Drs D.F. Cutler, P. Rudall and A.M.W. Menega in allowing access to the modern wood slide collections housed in the Jodrell Laboratory, Royal Botanic Gardens, Kew, and the Herbarium, University of Utrecht, respectively, is greatly appreciated. Drs D. Cantrill, P.S. Herendeen, S. Manchester and E.A. Wheeler are thanked for their constructive comments. This research is made possible by NERC funding which is here gratefully acknowledged.

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