NEW FOSSIL WOODS FROM LOWER CENOZOIC VOLCANO-SEDIMENTARY ROCKS OF THE FILDES PENINSULA, KING GEORGE ISLAND, AND THE IMPLICATIONS FOR THE TRANS-ANTARCTIC PENINSULA EOCENE CLIMATIC GRADIENT

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Abstract: Ten embedded fossil logs sampled *in situ* from the middle Eocene volcano-sedimentary rocks close to Suffield Point in the Fildes Peninsula, King George Island, Antarctica, are assigned to *Protopodocarpoxylon araucarioides* Schultze-Motel *ex* Vogellehner, *Phyllocladoxylon antarcticum* Gothan, *Agathoxylon antarcticum* (Poole & Cantrill) Pujana *et al.*, *A. pseudoparenchymatosum* (Gothan) Pujana *et al.* and an unidentified angiosperm wood. Differences in the taxonomic representation and growth-ring characters of the Eocene woods on King George Island and coeval assemblages from Seymour Island, on the western and eastern sides of the Antarctic Peninsula respectively, are interpreted to result from environmental and climatic gradients across the Peninsula Orogen during the early Palaeogene. In particular, a precipitation gradient inferred across the Peninsula at that time might have been induced by a rain-shadow effect.

Key words: fossil woods, Eocene, Antarctica, growth-ring analysis, rainfall gradient, palaeoclimate.

Aʟᴛʜᴏᴜɢʜ Antarctica is largely covered by an ice sheet today, terrestrial plants flourished there from the Devonian (Grindley *et al.* 1980; Woolfe *et al.* 1990; McLoughlin & Long 1994; Xu & Berry 2008), via the late Palaeozoic (Taylor *et al.* 1989; McLoughlin *et al.* 1997; Slater *et al.* 2012, 2015; Tewari *et al.* 2015), Mesozoic (Jefferson 1982; Garland *et al.* 2007; Fröbisch *et al.* 2010; Escapa *et al.* 2011; Bomfleur *et al.* 2011*a*, *b*; Coria *et al.* 2013) and into the Palaeogene (Goin *et al.* 1999; Ashworth & Kuschel 2003; Cantrill & Poole 2005*a*, *b*). Intensified cooling and ice-sheet development after the isolation of Antarctica and the establishment of the South Circumpolar Current at the end of the Eocene saw a dramatic decline in terrestrial vegetation there through the remainder of the Cenozoic (Coxall *et al.* 2005; Anderson *et al.* 2011).

The Antarctic Peninsula has been the subject of intense palaeontological study because it represents the northernmost extent of Antarctica and has yielded abundant Cretaceous and Cenozoic terrestrial fossils (Cantrill & Poole 2005*a*). King George Island, the largest of the South Shetland Islands to the west of the Antarctic Peninsula (Fig. 1), is well known for occurrences of various terrestrial fossils from Upper Cretaceous to Palaeogene deposits. These records include invertebrate trace fossils (Yang & Shen 1999), bird tracks and feather prints (Covacevich & Lamperein 1972; Covacevich & Rich 1982; Li & Zhen 1994; Mansilla *et al.* 2012, 2014), numerous ferns, conifers and angiosperm leaf impressions (Orlando 1963, 1964; Birkenmajer & Zastawniak 1986; Tokarski *et al.* 1987; Chun *et al.* 1994; Zhou & Li 1994*a*, *b*; Li & Zhou 2007; Fontes & Dutra 2010), fossil woods (Lucas & Lacey
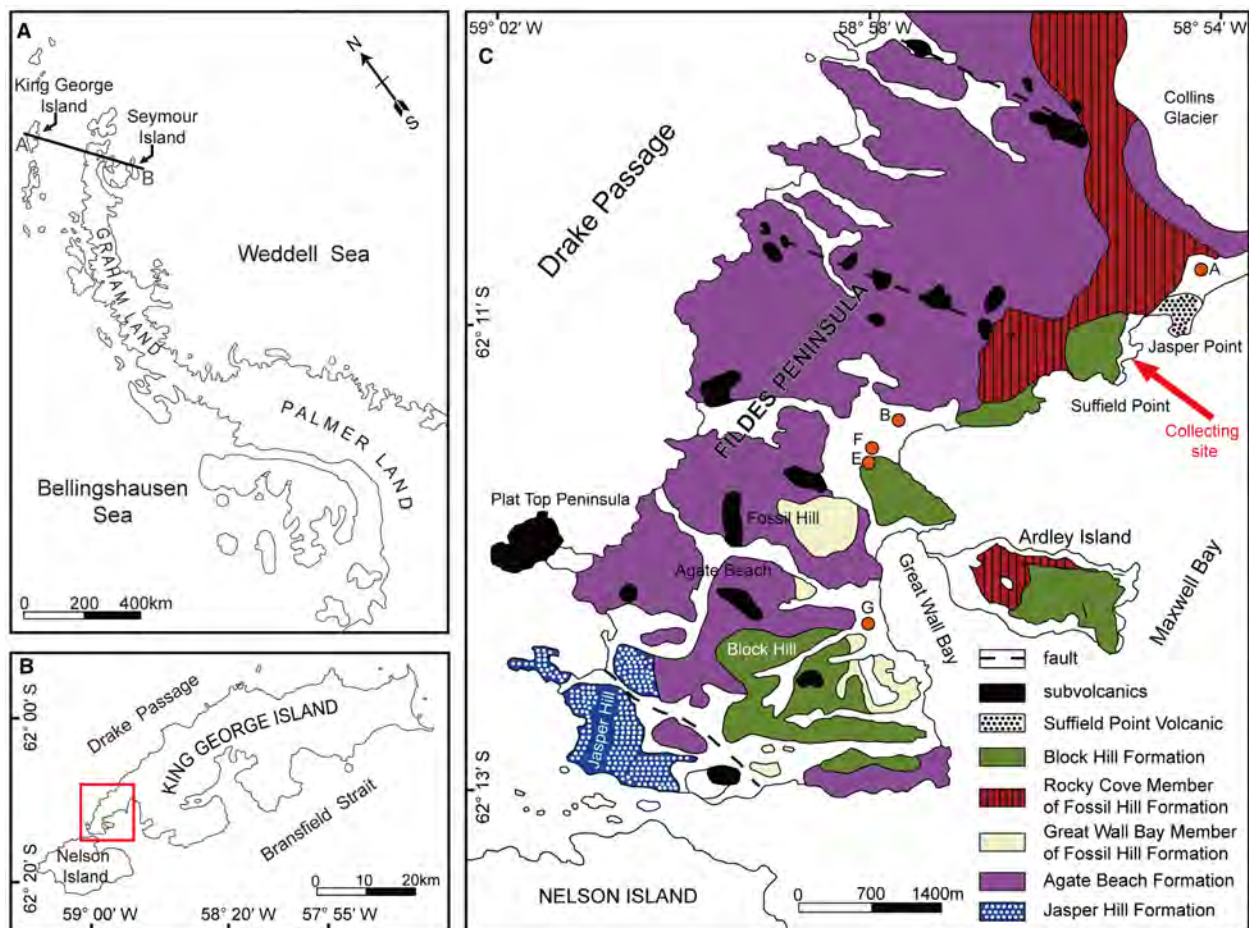
FIG. 1. Geographical and geological maps showing the study area and collecting site. A, geographical map of the Antarctic Peninsula with principal study areas indicated by arrows; AB transect see Figure 11. B, geographical map of King George Island with study area indicated by rectangle. C, geological map of the Fildes Peninsula with collecting site indicated by arrow (A, Artigas Station, Uruguay; B, Bellingshausen Station, Russia; F, Frei Station, Chile; E, Escudero Station, Chile; G, Great Wall Station, China; from Shen 1999).

1981; Torres 1984; Chun & Chang 1991; Zhang & Wang 1994; Poole *et al.* 2001) and spore-pollen assemblages (Cao 1992, 1994).

Much useful information about the Antarctic palaeoenvironments and palaeoclimate (Birkenmajer & Zastawniak 1989; Zastawniak 1994; Dutra & Batten 2000) has been gleaned from the fossil records. Growth-ring characters of fossil woods from this region are particularly important for understanding southern high-latitude climates during the Eocene, since other austral regions (e.g. Victoria Land, New Zealand, Australia) host only sparse occurrences of permineralized woods of this age (Leisman 1986; Bamford & McLoughlin 2000; Francis 2000; Lee *et al.* 2012). In particular, fossil wood, which is quite abundant on King George Island, has provided cursory information about the composition of the high-latitude Palaeogene vegetation (Torres 1984, 1990; Poole *et al.* 2001). Although fossil wood has long been known from the island, relatively little research has been conducted on such material and, of that,

most investigations have used transported (reworked) woody pebbles or loose blocks released by melting glaciers (Torres 1984; Zhang & Wang 1994; Poole *et al.* 2001).

During the January 2015 field season, ten fossil logs embedded in volcano-sedimentary rocks were sampled *in situ* from close to Suffield Point on the Fildes Peninsula, King George Island (Fig. 1). One of these logs had already been noted by previous researchers (Torres 1990), but no anatomical study had been undertaken. Here we describe the anatomical features and identify these woods. We also compare the growth parameters of the Eocene wood assemblages from King George Island with woods documented by other researchers (Gothan 1908; Torres 1990; Torres *et al.* 1994; Pujana *et al.* 2014) from coeval strata on Seymour Island to the east of the Antarctic Peninsula in order to assess whether there were distinctive vegetational and climatic differences between the western (forearc) and eastern (backarc) sides of the Antarctic Peninsula during the early Palaeogene.

GEOLOGICAL BACKGROUND

The Antarctic Peninsula region has a complex tectonic history, summarized in numerous studies (Barker 1982; Lawver *et al.* 1992; Maldonado *et al.* 1994; Robertson Maurice *et al.* 2003; Poblete *et al.* 2011), involving Gondwanan breakup and subsequent convergence with palaeo-Pacific crustal segments. From the mid-Cretaceous to Miocene, convergence of the Phoenix Plate from the west generated tholeiitic to calc-alkaline magmatism that progressively migrated towards the outer portions of the peninsula producing a mountainous spine extending northwards in the direction of South America (Domack *et al.* 2003; Poblete *et al.* 2011). Rifting in the Bransfield Strait (between the Antarctic Peninsula and South Shetland Islands) associated with roll-back of the Phoenix Plate beneath the South Shetland Islands began in the Oligocene (Birkenmajer 1994) or late Miocene and persists to the present (Barker 1982; Barker *et al.* 2003; Solari *et al.* 2008). Thus, upper Mesozoic to Palaeogene deposits on King George Island (and other parts of the South Shetland Islands chain) record sedimentation in a forearc basin to the west of the emerging spine of the Antarctic Peninsula. Since the Late Cretaceous, the Antarctic Peninsula region has been located at roughly the same latitude of 60–65°S (Lawver *et al.* 1992).

The stratigraphy of the Fildes Peninsula, King George Island, is rather complex (Smellie *et al.* 1984). The apparent complexity has been exacerbated by the development of different local stratigraphic schemes by various geologists who have studied the sedimentary successions on the island. Hawkes (1961) established the Fildes Peninsula Group (FPG) for strata in the study area (Fig. 1) and dated this unit to the 'Tertiary'. This group has been considered to consist mainly of extrusive basalt and basaltic andesites, together with agglomerates, tuffs and interbedded sedimentary rocks (Hawkes 1961; Barton 1965; Smellie *et al.* 1984; Birkenmajer 1989). Barton (1965) proposed four stratigraphical sub-divisions for the FPG and dated them as Late Cretaceous to Miocene. He also assumed that the southern part of the peninsula incorporated Upper Jurassic rocks. However, Birkenmajer (1982) amended Barton's Late Jurassic age and assigned a Cretaceous to Pliocene age to the FPG in that area. Pankhurst & Smellie (1983) employed a single formation, the Fildes Formation, for strata exposed in the south-western part of King George Island and confirmed that they are early Eocene in age based on K–Ar geochronology. The Fildes Formation was later reassigned to the latest Paleocene to Eocene by Smellie *et al.* (1984). Subsequently, other researchers have divided the FPG into several formations. Fensterseifer *et al.* (1988) defined the upper Paleocene Schneider Bay and Winkel Point formations in the central-northern region of the Fildes Peninsula. Chinese researchers have employed a more detailed stratigraphical scheme for the FPG. Zheng & Liu (1990) subdivided the FPG into two formations and four members. Shen (1994) reassigned these units to five formations: the Half Three Point Formation of Late Cretaceous age, Jasper Hill and Agate Beach formations of Paleocene age, Fossil Hill and Block Hill formations of Eocene age, and Suffield Point Volcanics of Miocene age. Subsequently, Shen (1999) subdivided the Fossil Hill Formation into two members: the Great Wall Bay Member and Rocky Cove Member (Figs 1, 2).

Although many researchers have attempted to refine the stratigraphic succession of the FPG, it remains poorly resolved, because of strong local faulting, the lack of well-exposed continuous sections (Birkenmajer 1989), sediment homogeneity and conflicting past stratigraphic unit definitions (see Hunt 2001; Cantrill & Poole 2012). Overall, the radiometric and biostratigraphic ages proposed for the FPG generally range from Late Cretaceous to Eocene. However, the upper FPG might include some strata as young as late Oligocene or early Miocene (Pankhurst & Smellie 1983; Smellie *et al.* 1984; Fensterseifer *et al.* 1988; Birkenmajer & Zastawniak 1989; Cao 1994; Shen 1994, 1999; Wang & Shen 1994). The K–Ar age of rocks at Suffield Point, nearby the fossiliferous strata sampled in this study, is middle Eocene (43 ± 1–44 ± 1 Ma; Smellie *et al.* 1984).

The Larsen Basin, initiating on attenuated crust associated with Gondwanan breakup in the Weddell Sea region during the Jurassic (Lawver *et al.* 1992), later developed into a broad backarc basin to the east of the Antarctic Peninsula Orogen associated with subduction of the Phoenix Plate in the west (Hathway 2000). Initial Jurassic sedimentation in the Larsen Basin included a mix of non-marine clastic deposits and volcanics of the Nordenskiöld Formation. Cretaceous–Paleocene sequences of the Gustav and Marambio groups are represented by variably coarse- to fine-grained clastic sedimentary rocks and tuffs, deposited predominantly in neritic settings (Hathway 2000). The Paleocene–Eocene Seymour Island Group is represented by coarse to fine-grained, poorly consolidated sediments deposited in nearshore or estuarine settings (Elliot 1988). Most units in the Larsen Basin succession contain plant fossils (Cantrill & Poole 2005a) attesting to deposition close to the eastern margin of the emergent and well-vegetated Antarctic Peninsula volcanic arc. Fossil woods collected on Nordenskiöld's 1901–1904 Swedish Antarctic Expedition and studied by Gothan (1908) derive principally from Seymour Island in the James Ross Sub-basin of the Larsen Basin. This material, re-studied herein, is associated with few locality details, but later authors have generally inferred its derivation from the Eocene La Meseta Formation (Cantrill & Poole 2005b), although Pujana *et al.* (2014), based on the proximity of units exposed near the reported landing sites of

Ref.\Gr.	Pankhurst & Smellie 1983 Smellie et al. 1984	Fensterseifer et al. 1988	Zheng & Liu 1990	Shen 1994, 1999	
Fildes Peninsula Group				Suffield Point Volcanics	
			Fossil Formation	Block Hill Member	**Block Hill Formation**	
	Fildes Formation			Fossil Hill Member	**Fossil Hill Formation**	Rocky Cove Member
						Great Wall Bay Member
				Agate Beach Member	**Agate Beach Formation**	
		Winkel Point Formation	Great Wall Formation	Jasper Hill Member	**Jasper Hill Formation**	
		Schneider Bay Formation			**Half Three Point Formation**	

FIG. 2. Correlation of stratigraphic units of the Files Peninsula Group on Fildes Peninsula, King George Island, South Shetland Islands, Antarctic Peninsula.

Nordenskiöld's field party, argued for derivation from the underlying Paleocene Cross Valley or Sobral formations. In addition to abundant marine fossils, the La Meseta Formation has yielded a broad range of fossils of nonmarine organisms, including the remains of terrestrial mammals, plants and clitellate annelids (Marenssi *et al.* 1998; Iglesias & Reguero 2012; Reguero *et al.* 2013; Bomfleur *et al.* 2015; McLoughlin *et al.* 2016; Friis *et al.* 2017) that imply nearshore deposition. Although the La Meseta Formation has traditionally been assigned ages ranging from early Eocene to ?earliest Oligocene (Ivany *et al.* 2006), the exposed fossiliferous strata are exclusively of Eocene age (Montes *et al.* 2010).

MATERIAL AND METHOD

Ten fossil wood specimens were collected from the volcano-sedimentary rocks near Suffield Point (62°11.531′S, 58°55.154′W) on the Fildes Peninsula, King George Island, South Shetland Islands, Antarctic Peninsula (Fig. 1). The rocks consist mainly of tuffs or somewhat tuffaceous conglomerates with interbedded mudstones or very fine grained sandstones. The fossil woods occur mostly within the interbedded epiclastic sedimentary rocks or intercalated tuffs. They are embedded horizontally and lack roots or branches, suggesting that they are allochthonous. The specimen diameters range from *c.* 5 to 46 cm, representing isolated branches or trunks. They are carbonized and partially silicified.

Thin-section slides in three orientations (transverse, radial longitudinal and tangential longitudinal) were prepared from each specimen according to the traditional method described by Hass & Rowe (1999). The characteristics used for classifying gymnosperm and angiosperm woods derive from the IAWA list of microscopic features for softwood and hardwood identification (IAWA Committee 1989, 2004). The determination of cross-field pitting types of gymnosperm wood follows the scheme of Philippe (1995). Gymnosperm identification at generic level is based on the revision by Bamford & Philippe (2001) and the key to morphogenera for conifer-like woods by Philippe & Bamford (2008). For the identification of angiosperm fossil wood, the IAWA Modern Wood Data Sheet and IAWA Fossil Wood Data Sheet in the InsideWood website (InsideWood 2004; Wheeler 2011) were used. Photomicrographs were taken using an Axio-Cam HRc attached to a Zeiss Axiophot transmitted light microscope. Conventional adjustments of brightness, sharpness, contrast and saturation of the photomicrographs were undertaken using Adobe Photoshop CS5. The graph and schematic figures were drawn using Adobe Illustrator CS5. Scanning electron micrographs were taken using a JEOL JSM-6610. All specimens and slides of the King George Island material are housed in the collection of the Korea Polar Research Institute, under the accession numbers KOPRIF 25047–25056.

Fourteen woods with prepared thin-sections from Seymour Island and originally assigned by Gothan (1908) to *Phyllocladoxylon antarcticum*, *Podocarpoxylon aparenchymatosum*, *Nothofagoxylon scalariforme*, *Laurinoxylon uniseriatum*, *Laurinoxylon* sp., *Dadoxylon pseudoparenchymatosum* and unidentified conifers and angiosperms were re-studied for comparison with the King George Island

woods. These specimens are held in the palaeobiology collections of the Swedish Museum of Natural History, Stockholm, under the registration numbers SMNH S004052, S004056, S004058–S004062, S004067, S004076, S004083, S004094, S004104, S004107–S004110, S004117, S004149, S005149.

SYSTEMATIC PALAEONTOLOGY

Family ?PODOCARPACEAE Endlicher, 1847
Genus PROTOPODOCARPOXYLON Eckhold, 1921 *nom. cons.*

Type species. Protopodocarpoxylon bedfordense (Stopes) Kräusel, 1949

Protopodocarpoxylon araucarioides Schultze-Motel *ex* Vogellehner, 1968
Figures 3, 4

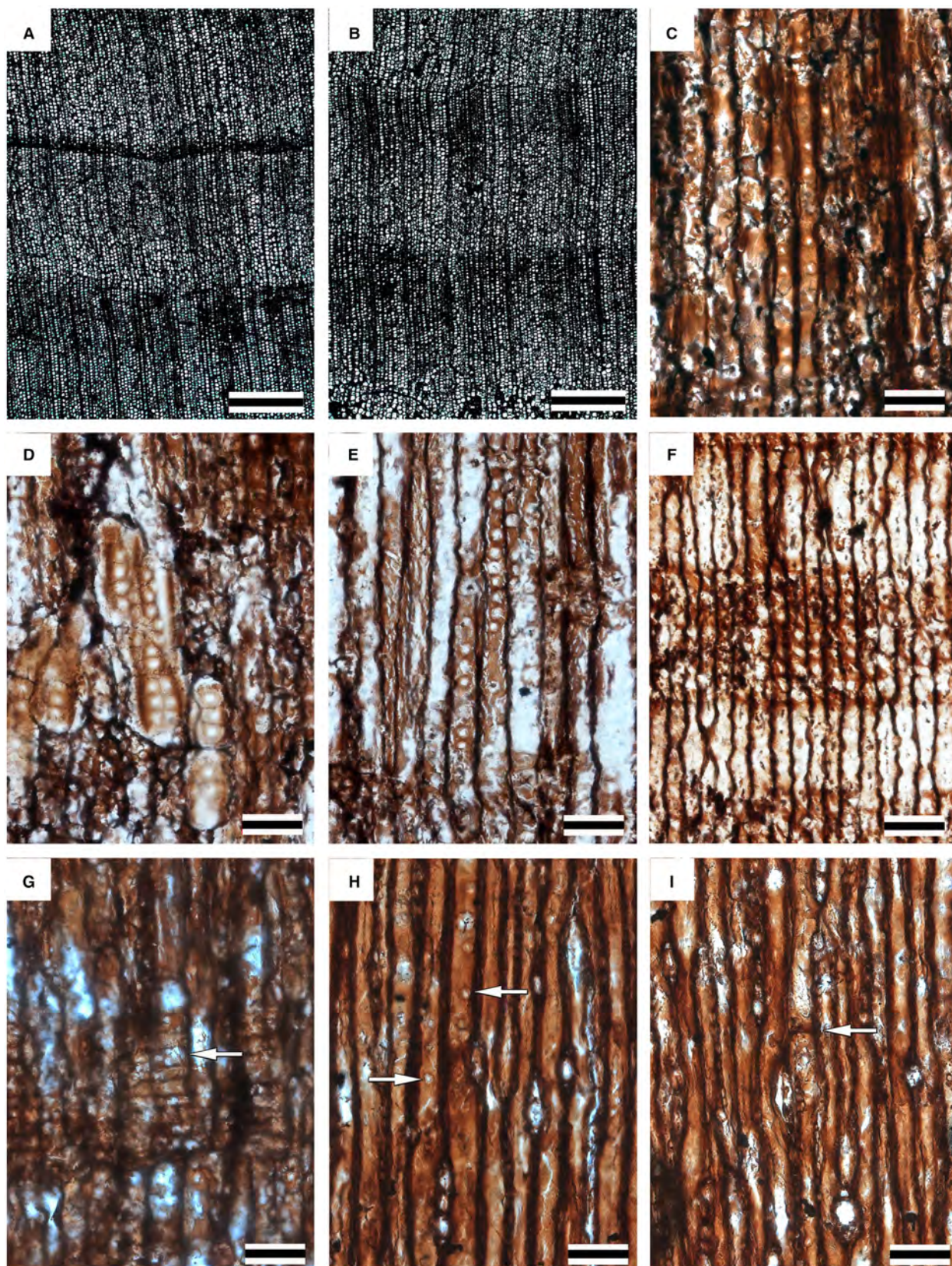*Material.* Fildes Peninsula, King George Island: KOPRIF 25047.

Description. This specimen was sampled from the outer part of a trunk that is *c.* 46 cm in diameter. Growth rings distinct with the naked eye, but both distinct and indistinct rings when viewed with transmitted light microscopy (Fig. 3A–B). The rings are 1.1–4.3 mm (mean 2.4 mm, n = 19) wide. The transition from earlywood to latewood is usually abrupt, but in some cases somewhat gradual. Where abrupt, the latewood zone is narrow (only 1–3 cells wide; Fig. 3A). False rings are present. Earlywood tracheids are quadratic, oblong or polygonal in transverse section, and are 18–39 × 13–36 μm (mean 27 × 26 μm, n = 55) in radial × tangential diameter. Latewood tracheids are small, radially flattened, somewhat thick-walled in transverse section, and 9–23 × 17–31 μm (mean 15 × 24 μm, n = 35) in radial × tangential diameter. Normal and traumatic resin canals are absent. Axial parenchyma cells are present with smooth transverse walls (Fig. 3I). Bordered pits occur on tangential walls of the tracheids, have a circular or oval outline, and are approximately 8–13 μm in diameter (Fig. 3H). These pits are generally spaced, usually uni- or partly biseriate (Fig. 3H). Where biseriate, they are alternate or opposite. Rays are usually uniseriate or rarely partly biseriate, homogeneous, 1–10 cells tall (mean 3.3, n = 60), 21–198 μm (mean 66.3 μm, n = 60) in height, and consist entirely of parenchyma cells (Fig. 3H–I). Ray cells are oblong or circular in tangential section and have smooth end walls. These cells are 10–17 × 13–29 μm (mean 13 × 20 μm, n = 35) in tangential × longitudinal diameter. Bordered pits on the radial walls of the tracheids are spaced, with oval or circular outline, or contiguous with longitudinally flattened outline (Figs 3C–E, 4B). The pits are usually uni- or, in some cases, biseriate and are approximately 10–19 μm in diameter. Where biseriate, they are alternate, opposite or sub-opposite (Fig. 3D). These radial pits have oval apertures. Half-bordered pits are

present in the cross-fields. These pits are usually podocarpoid or somewhat cupressoid in the earlywood cross-fields, about 4–11 μm in diameter, whereas in latewood cross-fields they are more cupressoid (Figs 3F–G, 4C). In some cross-fields, several pits are oopore-like, that is of the simple-type, however, it is assumed that these pits were altered during fossilization. There is usually one, rarely two or very rarely three pits per cross-field in the earlywood.

Remarks. Based on the xylological features, that is podocarpoid (*sensu* Philippe & Bamford 2008) cross-field pits, mixed type of pitting on the tracheid radial walls, absence of resin canals, and smooth ray cell walls, this specimen is assigned to *Protopodocarpoxylon* (Philippe & Bamford 2008).

Protopodocarpoxylon has been reported mostly from the northern hemisphere and rarely from Antarctica. Eckhold (1921) established this taxon initially without assignment of any species. Subsequently, in 1923, he included two species with different cross-field pitting types without designating a type. This resulted in much confusion (Lauverjat & Pons 1978; Philippe *et al.* 2002). Consequently, several fossil woods assigned to *Protopodocarpoxylon* should be transferred to *Brachyoxylon* Hollick & Jeffrey, 1909 based on their araucarioid cross-field pitting (Philippe *et al.* 2002, 2004). Furthermore, Philippe *et al.* (2014) recently established *Shimakuroxylon* to which they transferred *Protopodocarpoxylon orientale* Serra, 1969 and *P. paraorientale* Serra, 1969.

In this study, *Protopodocarpoxylon* species with araucarioid cross-fields, or species later transferred to *Shimakuroxylon*, and other protopodocarpoid woods having poor protologues, illustrations or preservation are not taken into account for comparison with our specimen (Table 1). The remaining seven *Protopodocarpoxylon* species can be compared adequately with our material: *P. araucarioides* Schultze-Motel *ex* Vogellehner, 1968, *P. bedfordense* (Stopes) Kräusel, 1949, *P. fontainei* Serra, 1966, *P. haciniensis* García Esteban & Palacios *in* García Esteban *et al.*, 2006, *P. pedrottii* Biondi, 1978, *P. schurabense* Khudayberdyev *in* Khudayberdyev *et al.*, 1971, and *Protopodocarpoxylon* sp. of Philippe *et al.* (1995). Among these, the taxon with the most similar anatomical features to our material is *P. araucarioides*, which has mixed uni- or biseriate radial tracheid pits, usually one or rarely two podocarpoid pits per earlywood cross-field, rays up to 14 cells tall, and the presence of tangential tracheid pits. Clearly distinct, *Protopodocarpoxylon bedfordense* has mostly uniseriate radial tracheid pits and a single pit per cross-field. *Protopodocarpoxylon fontainei*, unlike the King George Island specimen, has no axial parenchyma, and all biseriate radial tracheid pits are opposite, never alternate. Moreover, it has some strikingly high rays (up to 23 cells). *Protopodocarpoxylon haciniensis* differs from the King George Island material by having up to four pits per cross-field and the absence of
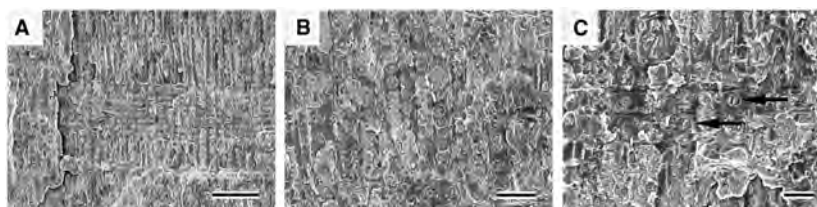
FIG. 4. *Protopodocarpoxylon araucarioides* Gothan. KOPRIF 25047 (from Fildes Peninsula, King George Is.), SEM images. A, radial longitudinal section showing tracheid walls and homogeneous radial parenchyma. B, radial longitudinal section showing spaced or contiguous uniseriate bordered pits on tracheid walls. C, radial longitudinal section showing podocarpoid (*sensu* Philippe & Bamford 2008) cross-field pits (arrows). Scale bars represent: 100 µm (A); 50 µm (B); 20 µm (C).

tangential tracheid pits. *Protopodocarpoxylon pedrottii* has more (up to six) pits per cross-field than the King George Island specimen. *Protopodocarpoxylon schurabense* is distinguished from the Antarctic specimen by having up to four pits per cross-field and rays up to 30 cells tall. *Protopodocarpoxylon* sp. of Philippe *et al*. (1995) differs by having up to four pits per cross-field and rays of relatively few cells high.

Based on these comparisons, assignment to *P. araucarioides* seems justified. *Protopodocarpoxylon araucarioides* being reported from Jurassic deposits in the northern hemisphere (Upper Jurassic of Westphalia, Germany by Müller-Stoll & Schultze-Motel 1989, and Middle Jurassic of Angren, Uzbekistan, by Gomolitzky & Khudayberdyev 1978) does not closely match the new material, from a stratigraphical or biogeographical perspective. However, based on the anatomical characters that underpin fossil wood parataxonomy, we must identify the new specimen as *P. araucarioides*.

Family PODOCARPACEAE Endlicher, 1847
Genus PHYLLOCLADOXYLON Gothan, 1905

Type species. *Phyllocladoxylon muelleri* (Schenk) Gothan, 1905

Phyllocladoxylon antarcticum Gothan, 1908
Figure 5

1919 *Mesembrioxylon antarcticum* Seward, p. 210.
1988 *Phyllocladoxylon antarcticum* Gothan; Torres & Lemoigne, p. 74, fig. 5A–B; pl. 1, figs 1–8.

1990 *Phyllocladoxylon antarcticum* Gothan; Torres, p. 127, pl. 34, figs 1–8; p. 151, pl. 40, figs 1–8.
1994 *Phyllocladoxylon antarcticum* Gothan; Torres *et al*., p. 30, pl. 5, figs 1–8.
1998 *Podocarpoxylon* sp. A; Brea, p. 166, fig. 4A–D.
2014 *Phyllocladoxylon antarcticum* Gothan; Pujana *et al*., p. 126, pl. 1, figs 9–16.
2015 *Phyllocladoxylon antarcticum* Gothan; Pujana *et al*., p. 60, pl. 4, figs 1–5.
2017 *Phyllocladoxylon antarcticum* Gothan; Pujana *et al*., p. 32, fig. 4F–K.
2018 *Phyllocladoxylon antarcticum* Gothan; Mirabelli *et al*., p. 100, fig. 5. 7–12.

Material. Fildes Peninsula, King George Island: KOPRIF 25048–25049, 25051, 25054.

Description. Among the available names, KOPRIF 25048 is best preserved; hence most anatomical information for the systematic description is based on that specimen. Growth rings are distinct and are 0.7–3.5 mm (mean 1.6 mm, n = 20) wide (Fig. 5A). The transition from earlywood to latewood is usually abrupt or somewhat gradual. The latewood is narrow, in general only 2–4 cells wide (Fig. 5A). Earlywood tracheids are squarish, oblong or circular in transverse section and are 17–43 × 13–37 µm (mean 28 × 29 µm, n = 60) in radial × tangential diameter. Latewood tracheids are small and radially narrow in transverse section, and are 10–21 × 14–37 µm (mean 15 × 25 µm, n = 40) in radial × tangential diameter. Normal and traumatic resin canals are absent. Axial parenchyma cells are not evident. Bordered pits on tangential walls of tracheids are present, with a circular or oval outline. These pits are generally spaced, usually uniseriate, about 12 µm in diameter. Rays are usually uniseriate or rarely partly biseriate, homogeneous, 1–17 cells tall (mean 6.3, n = 91), 21–278 µm (mean 101 µm, n = 91) in height, and

FIG. 3. *Protopodocarpoxylon araucarioides* Gothan. KOPRIF 25047 (from Fildes Peninsula, King George Is.), anatomical features of thin-section slides in three directions. A, transverse section showing distinct growth ring. B, transverse section showing poorly defined growth rings. C, radial longitudinal section showing spaced uniseriate bordered pits on tracheid walls. D, radial longitudinal section showing contiguous uni- to biseriate bordered pits on tracheid walls. E, radial longitudinal section showing spaced or contiguous uniseriate bordered pits on tracheid walls. F, radial longitudinal section showing cross-fields with usually one podocarpoid (*sensu* Philippe & Bamford 2008) pit each. G, radial longitudinal section showing (arrow) three pits in a cross-field (rare case). H, tangential longitudinal section showing circular or oval bordered pits on tracheid walls (arrows). I, tangential section showing a smooth transverse wall of axial parenchyma (arrow). Scale bars represent: 500 µm (A–B); 50 µm (C–I). Colour online.

TABLE 1. The list of *Protopodocarpoxylon* woods reported in the world and their generic re-attribution based on their anatomical features.

Species	Age	Country	Anatomical features	Attribution	References (reassigned)
Protopodocarpoxylon araucarioides	Late Jurassic	Germany	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Vogellehner 1968
Protopodocarpoxylon arnatum	Early Cretaceous	China	Poor protologue	?	Zheng & Zhang 1982
Protopodocarpoxylon batuyingziense	Late Jurassic	China	Poor protologue	?	Zheng 2004
Protopodocarpoxylon bedfordense	Early Cretaceous	England	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Kräusel 1949
Protopodocarpoxylon blevillense	Early Cretaceous	France	Araucarioid cross-field pitting	*Brachyoxylon*	Lignier 1907 (Philippe *et al.* 2018)
Protopodocarpoxylon dantzii	Late Cretaceous	Morocco	Araucarioid cross-field pitting	*Brachyoxylon*	Attims & Crémier 1969 (Philippe *et al.* 2004)
Protopodocarpoxylon dariae	Jurassic	Italy	Araucarioid cross-field pitting	*Brachyoxylon*	Biondi 1983 (Philippe *et al.* 2004)
Protopodocarpoxylon feugeuri	Late Cretaceous	France	Araucarioid cross-field pitting	Not *Protopodocarpoxylon*	Boureau & Veillet-Bartoszewska 1955 (**this study**)
Protopodocarpoxylon fontainei	Jurassic	Cambodia	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Serra 1966 (**this study**)
Protopodocarpoxylon guidense	Early Jurassic	Morocco	Araucarioid cross-field pitting	*Brachyoxylon*	Attims & Crémier 1969 (Philippe *et al.* 2004)
Protopodocarpoxylon haciniensis	Early Cretaceous	Spain	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	García Esteban *et al.* 2006
Protopodocarpoxylon jingangshanense	Cretaceous	China	Poor illustration	?	Ding 2000
Protopodocarpoxylon jurassicum	Jurassic	Poland	Xenoxyloid cross-field pitting	*Xenoxylon*	Eckhold 1923 (Philippe & Thévenard 1996)
Protopodocarpoxylon lalongense	Early Cretaceous	Tibet	Araucarioid cross-field pitting	*Brachyoxylon*	Vozenin-Serra & Pons 1990 (**this study**)
Protopodocarpoxylon lamtharii	Early Jurassic	Morocco	Araucarioid cross-field pitting	*Brachyoxylon*	Gazeau 1969 (Philippe *et al.* 2004)
Protopodocarpoxylon macroporosum	Jurassic	Uzbekistan	Poor protologue	?	Junusov *in* Gomolitzky *et al.* 1981
Protopodocarpoxylon microporosum	Jurassic	Uzbekistan	Poor protologue	?	Junusov *in* Gomolitzky *et al.* 1981
Protopodocarpoxylon orientale	Early Cretaceous	Vietnam	Shimakuroid radial bordered pitting	*Shimakuroxylon*	Serra 1969 (Philippe *et al.* 2014)
Protopodocarpoxylon paraorientale	Early Cretaceous	Vietnam	Shimakuroid radial bordered pitting	*Shimakuroxylon*	Serra 1969 (Philippe *et al.* 2014)
Protopodocarpoxylon pedrottii	Early Cretaceous	Italy	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Biondi 1978
Protopodocarpoxylon quinhonense	Early Cretaceous?	Vietnam	Araucarioid cross-field pitting	*Brachyoxylon*	Serra 1971 (**this study**)
Protopodocarpoxylon rochii	Cretaceous	Chad	Araucarioid cross-field pitting	*Brachyoxylon*	Boureau 1952 (Philippe *et al.* 2004)
Protopodocarpoxylon schurabense	Jurassic	Uzbekistan	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Khudayberdyev *et al.* 1971
Protopodocarpoxylon solignacii	Jurassic	Tunisie	Araucarioid cross-field pitting	*Brachyoxylon*	Giraud 1977 (Ouaja *et al.* 2004)
Protopodocarpoxylon subdantzii	Cretaceous	Chad	Araucarioid cross-field pitting	*Brachyoxylon*	Gazeau & Koeniguer 1970 (Philippe *et al.* 2004)

(continued)

TABLE 1. (Continued)

Species	Age	Country	Anatomical features	Attribution	References (reassigned)
Protopodocarpoxylon subrrochii	Jurassic	Morocco	Araucarioid cross-field pitting	*Brachyoxylon*	Attims 1965 (Philippe *et al.* 2004)
Protopodocarpoxylon teixeirae	Cretaceous	Portugal, Morocco, Tunisia	Araucarioid cross-field pitting	*Brachyoxylon*	Boureau 1949, 1951, 1957; Attims & Crémier 1969 (Philippe *et al.* 2004)
Protopodocarpoxylon sp.	Early Cretaceous	Antarctic Peninsula	Podocarpoid cross-field pitting	***Protopodocarpoxylon***	Philippe *et al.* 1995
Protopodocarpoxylon sp.	Early Cretaceous	Antarctica	No details	?	Herbst *et al.* 2007
Protopodocarpoxylon sp.	Jurassic	China (Liaoning)	Poor material	?	Wang *et al.* 2006

consist entirely of parenchyma cells (Fig. 5F). Ray cells are oblong or oval in tangential section, have smooth end walls, and are about 9–13 × 15–23 µm in tangential × longitudinal diameter. Bordered pits on the radial walls of the tracheids are uniseriate, about 17–23 µm in diameter, and mostly spaced or rarely contiguous, with a circular outline (Fig. 5C). Simple large pointed (i.e. phyllocladoid type or 'window-like') pits are present in all the earlywood cross-fields (Fig. 5D). However, slightly bordered pits are also present in the narrowest cross-fields (Fig. 5E). There are one or rarely two pits per earlywood cross-field.

Remarks. The absence of resin ducts, presence of phyllocladoid type or 'window-like' cross-field pitting, abietinean radial tracheid pitting, and smooth horizontal and vertical walls of ray parenchyma indicate that these specimens are referable to *Phyllocladoxylon* Gothan (Philippe & Bamford 2008). To date, the genus has been reported sparsely from Antarctica: *P. antarcticum* Gothan (Gothan 1908; Seward 1919; Torres & Lemoigne 1988; Torres 1990; Torres *et al.* 1994; Pujana *et al.* 2014, 2015, 2017; Mirabelli *et al.* 2018), *P. pooleae* Pujana *et al.* (2014), and *Phyllocladoxylon* sp. (Eklund *et al.* 2004). The anatomical characters of the specimens in this study are mostly consistent with those of *Phyllocladoxylon antarcticum*, which has uniseriate and spaced bordered pits on radial walls of tracheids, large and pointed simple pits in each cross-field, up to 17 ray cells tall, and a lack of axial parenchyma. Additionally, *Podocarpoxylon* sp. A reported by Brea (1998) from the La Meseta Formation of Seymour Island also has similar anatomical features and was considered referable to *Phyllocladoxylon antarcticum* by Pujana *et al.* (2014). *Phyllocladoxylon pooleae* differs from the King George Island specimens by the common occurrence of dark resin plugs in the tracheids. *Phyllocladoxylon* sp. of Eklund *et al.* (2004) is difficult to compare with the King George Island specimens as its anatomy is insufficiently described.

Family ARAUCARIACEAE Henkel & W. Hochstetter, 1865
Genus AGATHOXYLON Hartig, 1848

Type species. Agathoxylon cordaianum Hartig, 1848

Agathoxylon antarcticum (Poole & Cantrill) Pujana *et al.*, 2014
Figure 6

2001   *Araucariopitys antarcticus* Poole & Cantrill, p. 1086, pl. 1, figs 2, 4, 6, 8, 10.
2014   *Agathoxylon antarcticus* (Poole & Cantrill) Pujana *et al.*, p. 130, pl. 3, figs 6–11.
2015   *Agathoxylon antarcticus* (Poole & Cantrill) Pujana *et al.*, p. 59, pl. 2, figs 1–8.
2017   *Agathoxylon antarcticus* (Poole & Cantrill) Pujana *et al.*, p. 30, fig. 3A–J.
2018   *Agathoxylon antarcticus* (Poole & Cantrill) Pujana *et al.*; Mirabelli *et al.*, p. 98, fig. 5. 1–6.

Material. Fildes Peninsula, King George Island: KOPRIF 25050.

Description. Growth rings are distinct and 0.4–2.1 mm (mean 0.9 mm, n = 20) wide (Fig. 6A–B). The transition from earlywood to latewood is abrupt. The latewood zone is narrow, 1–6 cells wide. Earlywood tracheids are squarish or circular in transverse section and are 19–37 × 18–42 µm (mean 27 × 30, n = 50) in radial × tangential diameter. Latewood tracheids are small and radially flattened in transverse section and are 7–18 × 11–34 µm (mean 13 × 24 µm, n = 40) in radial × tangential diameter. Normal and traumatic resin canals are absent, nor is there any axial parenchyma. There are no obvious bordered pits on tangential walls of tracheids. Rays are usually uniseriate or rarely partly biseriate, homogeneous, 1–11 cells tall (mean 4, n = 34), 35–245 µm (mean 101 µm, n = 34) in height, and consist entirely of parenchyma cells (Fig. 6F). Ray cells are oblong, oval or circular in tangential section, and have smooth end walls. The cells are about 12–19 × 19–29 µm in
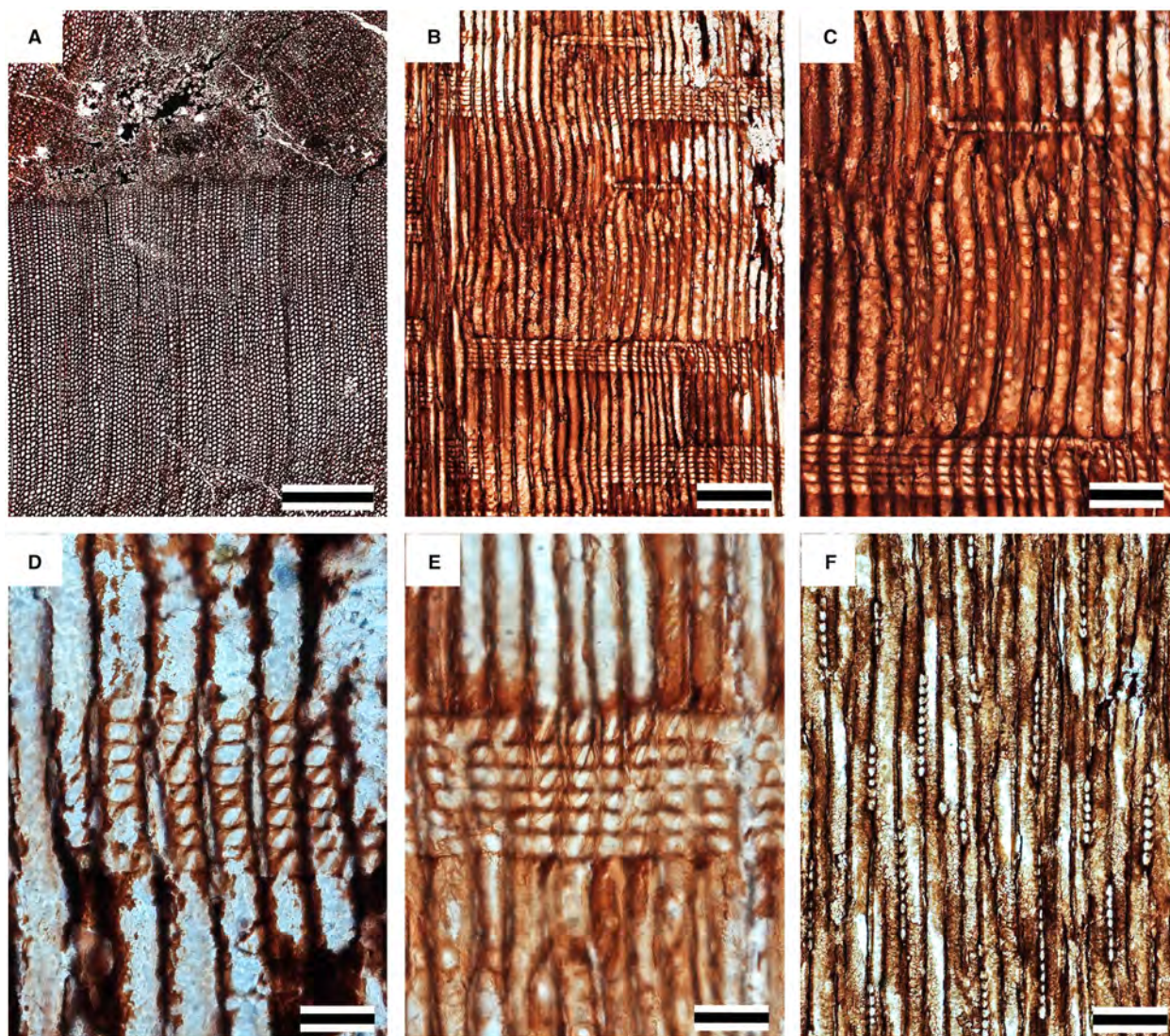
FIG. 5. *Phyllocladoxylon antarcticum* Gothan. KOPRIF 25048 (from Fildes Peninsula, King George Is.), anatomical features of thin-section slides in three directions. A, transverse section showing a distinct growth ring. B, radial longitudinal section showing bordered pits on tracheid walls and cross-field pits. C, radial longitudinal section showing spaced uniseriate bordered pits on tracheid walls. D, radial longitudinal section showing phyllocladoid-type or 'window-like' pits in each cross-field. E, radial longitudinal section showing bordered pits in narrow cross-fields. F, tangential longitudinal section showing uniseriate and homogeneous rays. Scale bars represent: 500 μm (A); 200 μm (B); 100 μm (C, F); 50 μm (D, E). Colour online.

tangential × longitudinal diameter. Bordered pits on radial walls of tracheids are contiguous and commonly uniseriate, or in some cases biseriate or rarely triseriate (Fig. 6C, D). The pits are *c.* 10–15 μm in diameter. Where bi- or multiseriate, they are alternate (Fig. 6D). The cross-fields are of araucarioid type, with two to six contiguous oculipores, which are *c.* 10 μm in diameter (Fig. 6E).

Remarks. The typical araucarioid anatomical features of this specimen confirm its assignment to *Agathoxylon* (Philippe & Bamford 2008). There have been long debates about the nomenclature of araucarioid type fossil wood, variously assigned to *Agathoxylon* Hartig, *Dadoxylon*

Endlicher, 1847, and *Araucarioxylon* Kraus, 1870. Although there is no consensus yet, based on the rules of the International Code of Nomenclature for algae, fungi and plants (ICN; Turland *et al.* 2018), *Agathoxylon* is considered a suitable generic name for this fossil wood type by a majority of current palaeoxylotomists (Rößler *et al.* 2014). Globally, more than 400 fossil-species of araucarioid-type fossil wood have been described (Philippe 2011). Among these, only Antarctic araucarioid fossil woods were compared with the King George Island specimen: *Agathoxylon antarcticum* (Poole & Cantrill) Pujana *et al.* (Poole & Cantrill 2001; Pujana *et al.* 2014, 2015, 2017; Mirabelli *et al.* 2018);
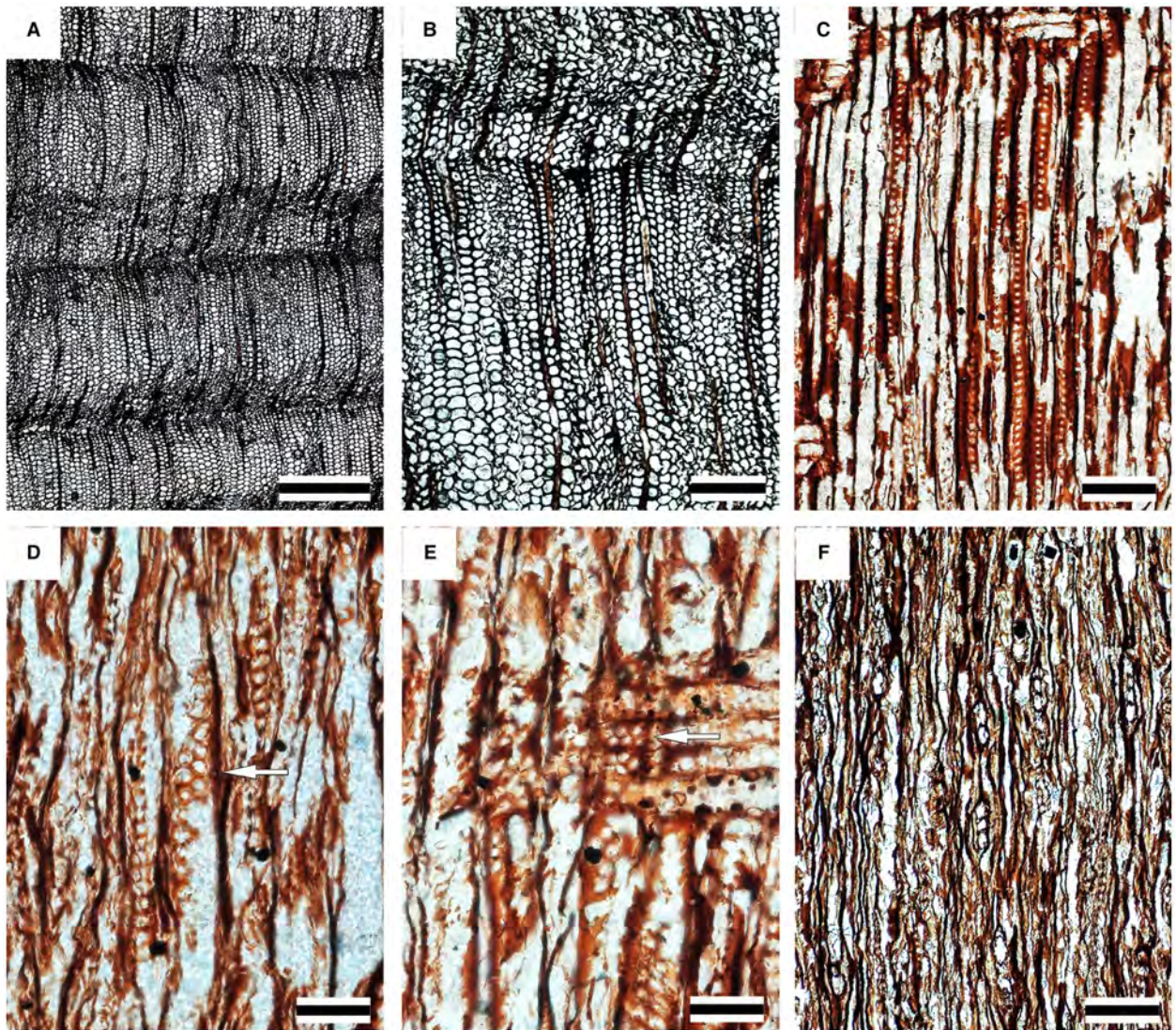
FIG. 6. *Agathoxylon antarcticum* (Poole & Cantrill) Pujana *et al.* KOPRIF 25050 (from Fildes Peninsula, King George Is.), anatomical features of thin-section slides in three orientations. A, transverse sction showing distinct growth rings. B, transverse section showing the abrupt transition from earlywood to latewood. C, radial longitudinal section showing contiguous uniseriate bordered pits on tracheid walls. D, radial longitudinal section showing alternate biseriate bordered pits on tracheid walls (arrow). E, radial longitudinal section showing the cupressoid pits in araucarioid cross-fields (arrow). F, tangential longitudinal section showing homogenous and uinseriate rays. Scale bars represent: 500 μm (A); 200 μm (B); 100 μm (C, F); 50 μm (D, E). Colour online.

A. kellerense (Lucas & Lacey) Pujana (Lucas & Lacey 1981; Pujana *et al.* 2017; Mirabelli *et al.* 2018); *A. pseudoparenchymatosum* (Gothan) Pujana *et al.* (Gothan 1908; Lucas & Lacey 1981; Torres 1990; Torres *et al.* 1994; Pujana *et al.* 2014, 2015, 2017; Mirabelli *et al.* 2018); *Agathoxylon* sp. A (Ottone & Medina 1998); *Araucarioxylon arayai* Torres *et al.* (Torres *et al.* 1982, 1997); *A. chapmanae* Poole & Cantrill (Poole & Cantrill 2001); *A. fildense* Torres (Torres 1990); *A. floresii* Torres & Lemoigne (Torres & Lemoigne 1989); *A. kerguelense* Seward (Torres 1990); *A. novaezeelandii* Stopes (Torres 1990; Torres *et al.* 1994); *A. seymourense* Torres *et al.* (Torres 1990; Torres *et al.* 1994);

Araucarioxylon sp. (Falcon-Lang & Cantrill 2000); *Araucarioxylon* sp. A (Torres *et al.* 1997); *Araucarioxylon* sp. 1 and 2 (Torres & Lemoigne 1988); *Araucarioxylon* sp. 1 and 2 (Falcon-Lang & Cantrill 2001); and two *Dadoxylon* species (Lucas & Lacey 1981; Chun & Chang 1991).

The specimen described in this study is anatomically similar to *Agathoxylon antarcticum* based on its usually uni- or biseriate bordered pits on the radial walls of tracheids, two to six pits in each cross-field, and 1–11 uniseriate ray cells tall. *Agathoxylon pseudoparenchymatosum*, *Araucarioxylon arayai*, *A. chapmanae*, *A. floresii*, *A. kerguelense*, *A. novaezeelandii*, *A. seymourense*, *Araucarioxylon* sp. 1 and

2 of Torres & Lemoigne (1988), and *Araucarioxylon* sp. 2 of Falcon-Lang & Cantrill (2001) differ from the King George Island specimen by their abundant resiniferous tracheids. *Agathoxylon kellerense* differs by its predominantly triseriate bordered pits on tracheids. *Agathoxylon* sp. A of Ottone & Medina (1998) differs by its taller rays of up to 25 cells and frequently biseriate. *Araucarioxylon fildense* has more pits in each cross-field than the King George Island wood. *Araucarioxylon* sp. (Falcon-Lang & Cantrill 2000) is anatomically similar to *A. antarcticum*, but has relatively more biseriate pit rows in the tracheids. *Araucarioxylon* sp. 1 (Falcon-Lang & Cantrill 2001) also has a higher proportion of biseriate pit rows and slightly taller rays. Both *Araucarioxylon* sp. A of Torres *et al.* (1997) and the two *Dadoxylon* species of Lucas & Lacey (1981) and Chun & Chang (1991) are difficult to compare with the new specimen as they are poorly preserved. Based on the collective anatomical characters, the newly described specimen is assigned to *Agathoxylon antarcticum*.

Agathoxylon pseudoparenchymatosum (Gothan) Pujana *et al.*, 2014
Figure 7

1908 *Dadoxylon pseudoparenchymatosum* Gothan, p. 10, pl. 1, figs 1–3, 12–16.

1914 *Araucarioxylon novaezeelandii* Stopes, p. 348, pl. 20.

1919 *Araucarioxylon kerguelense* Seward, p. 185, fig. 714.

1921 *Dadoxylon kerguelense* Edwards, p. 614, pl. 23.

1984 *Araucarioxylon pseudoparenchymatosum*; Nishida, p. 89, pl. 81.

1982 *Araucarioxylon arayai* Torres *et al.*, p. 330, pl. 2, figs 1–4.

1988 *Araucarioxylon* sp. 1; Torres & Lemoigne, p. 79, pl. 2, figs 1–6.

1988 *Araucarioxylon* sp. 2; Torres & Lemoigne, p. 80, pl. 3, figs 1–9.

1990 *Araucarioxylon kerguelense* Seward; Torres, p. 125, pl. 35, figs 1–8.

1990 *Araucarioxylon novaezeelandii* Stopes; Torres, p. 140, pl. 37, figs 1–10.

1990 *Araucarioxylon pseudoparenchymatosum* (Gothan); Torres, p. 142, pl. 38, figs 1–10.

1994 *Araucarioxylon novaezeelandii* Stopes; Torres *et al.*, p. 24, pl. 2, figs 1–9.

1994 *Araucarioxylon pseudoparenchymatosum* (Gothan) Torres *et al.*, p. 22, pl. 1, figs 1–10.

2001 *Araucarioxylon* sp. 2; Falcon-Lang & Cantrill, p. 284, figs 5–6.

2014 *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana *et al.*, p. 129, pl. 3, figs 1–5.

2015 *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana *et al.*, p. 59, pl. 3, figs 1–6.

2017 *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana *et al.*, p. 32, fig. 3K–P.

2018 *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana *et al.*; Mirabelli *et al.*, p. 98, fig. 4. 7–12.

Material. Fildes Peninsula, King George Island: KOPRIF 25053.

Description. Growth rings are variably distinct or somewhat indistinct (Fig. 7A). The width of rings is about 0.8–2.6 mm. The transition from earlywood to latewood is abrupt. The latewood zone is narrow, one or two cells wide (Fig. 7A). Earlywood tracheids are quadratic, circular or crushed in transverse section and are 17–44 × 18–47 μm (mean 28 × 33 μm, n = 55) in radial × tangential diameter. Latewood tracheids are small and radially flattened and are about 9–21 × 19–27 μm in radial × tangential diameter. There are many examples of black or brown resinous contents in the tracheids, from thin resin plugs to thicker resin fillings, especially beside rays (Fig. 7B–D). Normal and traumatic resin canals are absent. Axial parenchyma was not observed. Bordered pits having a circular outline are present on the tangential walls of tracheids (Fig. 7F). These pits are spaced, circular, uniseriate and *c.* 10 μm in diameter. Rays are usually uniseriate or partly biseriate, homogeneous, 1–19 cells tall (mean 7, n = 66), 32–566 μm (mean 199 μm, n = 66) in height, and consist entirely of parenchyma cells (Fig. 7E–F). Ray cells are oblong or quadratic in tangential section and have smooth end walls. These cells are 17–39 × 15–40 μm (mean 30 × 27 μm, n = 35) in tangential × longitudinal diameter. Bordered pits on radial walls of tracheids are mostly contiguous and uni-, bi- or rarely triseriate (Fig. 7C). The pits are about 11–16 μm in diameter. When bi- or multiseriate, they are alternate (Fig. 7C). Circular or oval bordered pits are crowded in cross-fields (Fig. 7D). The cross-fields are of the araucarioid type and their oculipores are about 8–11 μm in diameter. There are two to six such pores per cross-field.

Remarks. This specimen is also referable to *Agathoxylon* based on its araucarioid anatomical features and its similarity to KOPRIF 25050, which is assigned to *A. antarcticum*. However, this specimen differs clearly by the occurrence of abundant resin plugs and resin fillings in the tracheids. This is especially obvious in tracheids flanked by ray parenchyma cells. Although it is a common feature in modern Araucariaceae wood, where resin is produced within the ray and passes to the adjacent tracheids, this anatomical feature has been used repeatedly to distinguish fossil wood (Gothan 1908; Stopes 1914; Torres *et al.* 1994; Pujana *et al.* 2014). We follow this approach in this study. Among Antarctic araucarioid fossil wood, those with abundant resin plugs or resin fillings in tracheids are: *Agathoxylon pseudoparenchymatosum*, *Araucarioxylon arayai*, *A. chapmanae*, *A. floresii*, *A. kerguelense*, *A. novaezeelandii*, *A. seymourense*, *Araucarioxylon* sp. 1 and 2 of Torres & Lemoigne (1988), and *Araucarioxylon* sp. 2 of Falcon-Lang & Cantrill (2001). The specimen in this study is assigned to *Agathoxylon pseudoparenchymatosum* based on its uni- or biseriate radial tracheid bordered pits, two to six cross-field pits, usually uniseriate rays, and medium average ray height.
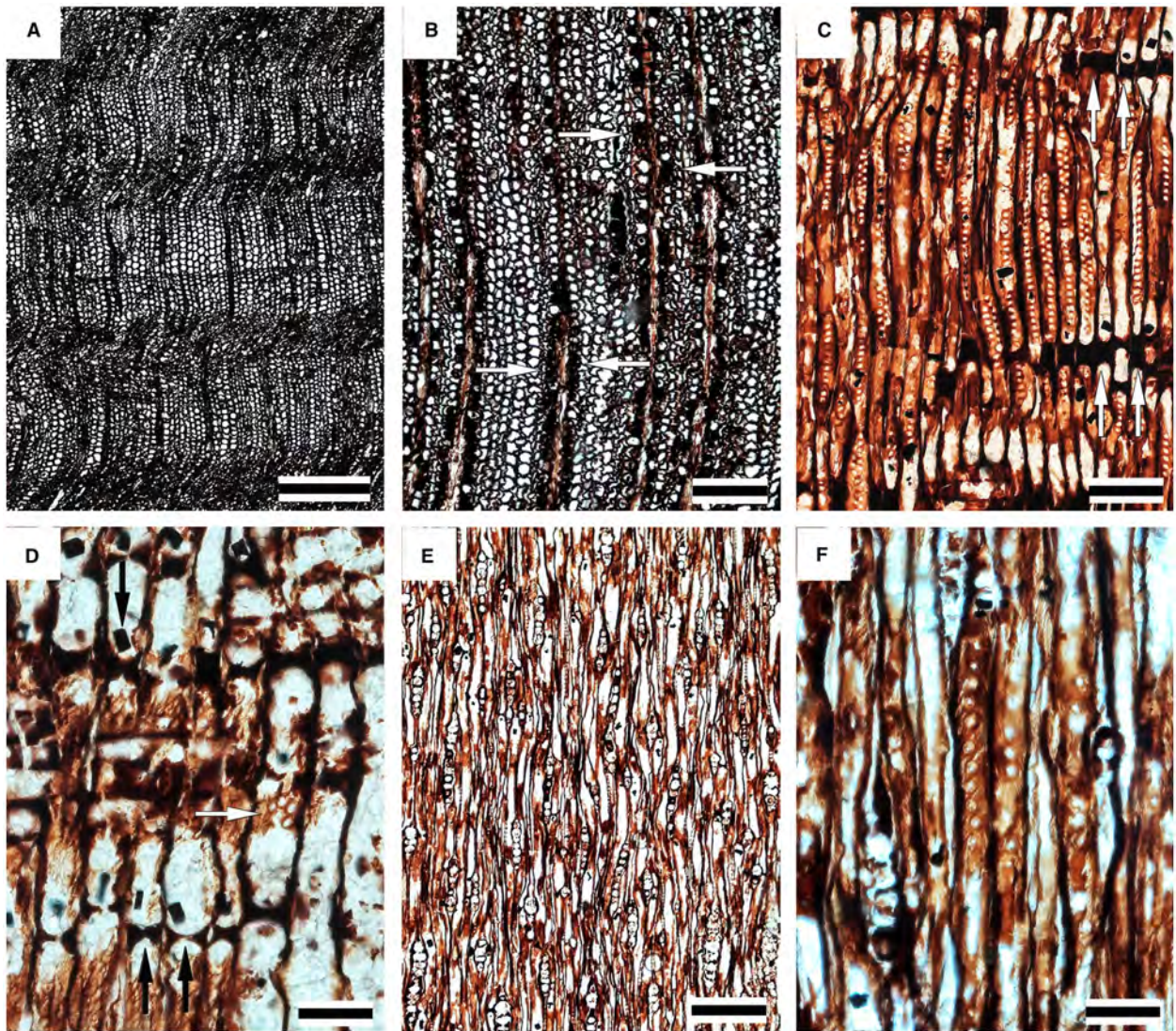
FIG. 7. *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana *et al.* KOPRIF 25053 (from Fildes Peninsula, King George Is.), anatomical features of thin-section slides in three directions. A, transverse section showing the distinct growth rings. B, transverse section showing the abundant black or brown resin-filled tracheids on the periphery of the rays (arrows). C, radial longitudinal section showing the contiguous uni- to biseriate bordered pits on tracheid walls with black resinous substances. D, radial longitudinal section showing araucarioid cross-fields (white arrow) and black resinous substances with resin plugs (black arrow). E, tangential longitudinal section showing uniseriate and homogeneous rays. F, tangential longitudinal section showing oval or circular bordered pits on tracheid walls. Scale bars represent: 500 μm (A); 200 μm (B, E); 100 μm (C); 50 μm (D, F). Colour online.

Araucarioxylon arayai also has very similar anatomical features and we consider it to be a junior synonym of *Agathoxylon pseudoparenchymatosum*. *Araucarioxylon chapmanae* differs by its radial tracheid bordered pits being commonly bi- to triseriate. *Araucarioxylon floresii* differs by the occurrence of axial parenchyma. *Araucarioxylon kerguelense* and *A. novaezeelandii* are similar to *Agathoxylon pseudoparenchymatosum* and were considered its synonyms by Kräusel (1924) and Florin (1940). *Araucarioxylon* sp. 1 and 2 of Torres & Lemoigne (1988) redetermined as *A. kerguelense* by Torres (1990). *Araucarioxylon seymourense* differs by its much taller rays. According to Falcon-Lang &

Cantrill (2001) *Araucarioxylon* sp. 2 is almost identical to *Agathoxylon pseudoparenchymatosum* and we consider the former to be a junior synonym of the latter.

Angiosperm INCERTAE SEDIS
Figure 8

Material. Fildes Peninsula, King George Island: KOPRIF 25056.

Description. On the whole, this specimen is poorly preserved. Growth rings are variably indistinct or distinct and marked by

differences in fibre and vessel dimensions (Fig. 8A). The wood is semi-ring to diffuse porous, vessels being partly solitary or partly in radial multiples of two to four; clusters are absent (Fig. 8A). Some of the solitary vessel outlines appear circular. Nevertheless, the overall poor vessel preservation prevents the confident determination of solitary vessel outlines. Mean tangential diameter of vessel lumina is 93 μm (range 45–149 μm, n = 54). There are 29–43 vessels per square millimeter (mean 35, n = 10). Mean vessel element length is 105 μm (range 48–166 μm, n = 30). Although some of the perforation plates appear simple, the poor preservation prevents the certain determination of perforation plate type (Fig. 8B). Intervessel pitting is usually alternate or rarely scalariform and opposite (Fig. 8C–E). The pit diameter is about 7–15 μm and the alternate pits are polygonal. Vessel-ray pits lack or have only a narrow border: pits circular or angular (Fig. 8D). Helical thickenings are absent. Tyloses and deposits in the vessels are common (Fig. 8E). Axial parenchyma features cannot be determined. Ground-tissue fibres have distinctly bordered pits. Rays are one to three cells wide and heterocellular, but the cellular composition of the rays cannot be determined because of their poor preservation (Fig. 8F).

Remarks. Although several anatomical features are observable, the overall poor preservation of the specimen makes its identification difficult. Key characters, such as the type of perforation plates, the presence and arrangement of axial parenchyma, and the cellular composition of rays could not be observed clearly. Its rather large diameter (*c.* 26 cm) suggests that it was the trunk of at least a small tree, more probably an element of the forest canopy rather than an understory shrub.

DISCUSSION

Comparison of the vegetation and climates between the western (King George Island) and eastern (Seymour Island) sides of the Antarctic Peninsula during the Eocene

The Antarctic Peninsula was an emergent volcanic arc and played a role as a bridge for the exchange of terrestrial biotas between South America and Antarctica during the Cretaceous–Palaeogene interval (Elliot 1983, 1988; Dettmann 1989; Shen 1998; Cantrill & Poole 2012). At that time, the forests of the Antarctic Peninsula were dominated by podocarp and araucarian conifers alongside several woody angiosperms, especially *Nothofagus* (i.e. southern beeches; Francis 1991; Poole *et al.* 2001). Although there was overall floristic similarity across the Antarctic Peninsula during the Paleocene to Eocene interval, the presence of somewhat different vegetation types between the western and eastern sides of the peninsula was suggested by Cantrill & Poole (2005*a*, 2012). To test this hypothesis, fossil wood assemblages were analysed from coeval Eocene deposits on King George Island and

Seymour Island, which represent, respectively, the western and eastern sides of the Antarctic Peninsula (Fig. 1A).

Comparison of wood assemblages. Including the four gymnosperm wood taxa (*Protopodocarpoxylon araucarioides*, *Phyllocladoxylon antarcticum*, *Agathoxylon antarcticum* and *A. pseudoparenchymatosum*) identified in this study, 24 wood taxa have been reported from the Eocene deposits on King George Island (Table 2), whereas, on Seymour Island, 15 Eocene wood taxa have been reported (Table 3). We did not segregate the synonymized taxa among fossil woods listed in Tables 2 and 3, for example *Araucarioxylon novaezelandii*, *A. kerguelense*, *A. pseudoparenchymatosum*, *Dadoxylon kellerense*, *D. pseudoparenchymatosum*, *Podocarpoxylon* sp. A, among others.

At the family level, although two gymnosperm taxa, that is *Protophyllocladoxylon* and *Protopodocarpoxylon*, cannot be assigned definitively to a family (?Podocarpaceae), the gymnosperm wood floras of the two islands are very similar, containing Araucariaceae, Cupressaceae and Podocarpaceae. However, the angiosperm component of the two wood floras clearly differs. On King George Island, seven angiosperm families have been documented based on wood anatomy (Atherospermataceae, Cunoniaceae, Eucryphiaceae, Monimiaceae, Myrtaceae, Nothofagaceae and Rubiaceae) whereas on Seymour Island, only three (Atherospermataceae, Eucryphiaceae and Nothofagaceae) have been reported. Thus, the western side of the Antarctic Peninsula had more diverse angiosperm wood assemblages than the eastern side, notwithstanding potential taphonomic or sampling biases. If this difference reflects genuine compositional disparity in the vegetation, then it is noteworthy that the association of the two families restricted to the western side (Cunoniaceae and Monimiaceae) occurs today within wet temperate *Nothofagus* forests, for example in the Valdivian rainforests of Chile (Markgraf *et al.* 1996; Cantrill & Poole 2012).

To assess whether this low diversity of angiosperm wood assemblages genuinely reflects the parent vegetation, it is worthwhile considering other plant fossil records from Seymour Island. According to Pujana *et al.* (2014), the early Eocene wood assemblages on Seymour Island were dominated by conifers, especially Podocarpaceae, with a few angiosperms. Case (1988) reported a *Nothofagus*-dominated flora with araucarian conifers and ferns based on leaf fossils from the La Meseta Formation on Seymour Island. Doktor *et al.* (1996) described plant remains including ferns, Podocarpaceae, Araucariaceae, Nothofagaceae and Proteaceae with other unidentified angiosperm leaves on Seymour Island. Gandolfo *et al.* (1998) reported leaf fossils assigned to Nothofagaceae, Dilleniaceae, Myricaceae, Myrtaceae and Lauraceae, together with various unidentified angiosperms leaves on Seymour Island. Askin & Fleming (1982) and Askin
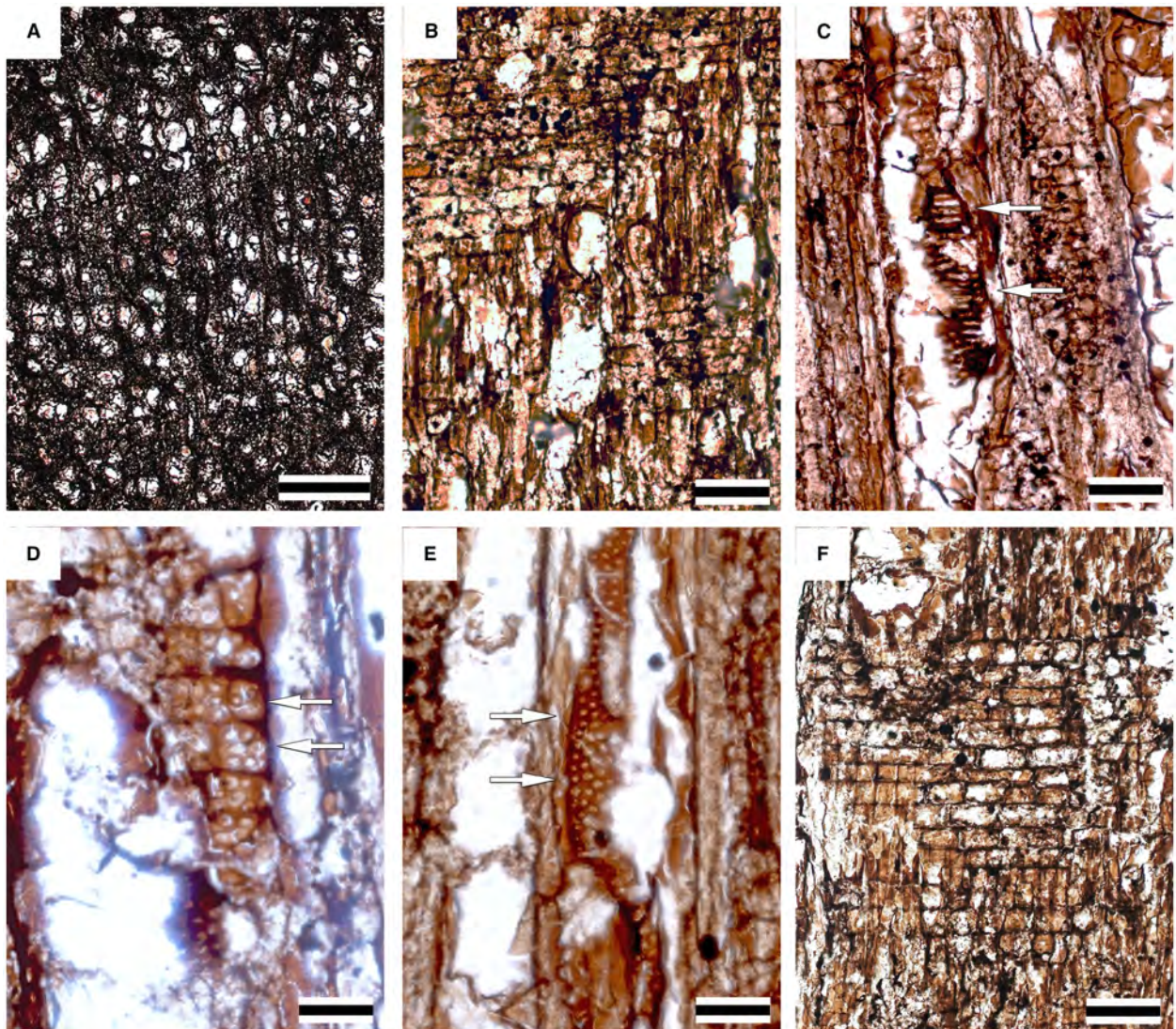
FIG. 8. Angiosperm *incertae sedis*. KOPRIF 25056 (from Fildes Peninsula, King George Is.), anatomical features of thin-section slides in three directions. A, transverse section showing indistinct growth rings and diffuse porous vessels. B, radial longitudinal section showing simple perforation plate-like features. C, radial longitudinal section showing scalariform intervessel pitting (arrows). D, radial longitudinal section showing the reduced borders to apparently simple vessel-ray pits (arrows). E, radial longitudinal section showing typical alternate intervessel pitting (arrows). F, radial longitudinal section showing heterocellular rays. Scale bars represent: 500 μm (A); 100 μm (B, C, F); 50 μm (D, E). Colour online.

(1991) documented Nothofagaceae-dominated pollen assemblages, with subdominant conifers and abundant Proteaceae from the upper Paleocene to upper Eocene Seymour Island Group on Seymour Island. According to a recent study by Warny *et al.* (2019), palynoassemblages from the upper Eocene deposits of the La Meseta Formation on Seymour Island reflect a relatively low-diversity flora dominated by podocarps and *Nothofagus*. These studies suggest that the lower diversity of wood assemblages on Seymour Island during the Eocene does not seem to result from strong taphonomic biases, although the diversity of angiosperms in the middle and understorey layers of the vegetation was somewhat higher than in the canopy based on leaf/pollen assemblages.

Another interesting feature is the predominance of Proteaceae remains on Seymour Island. This family is distributed mainly in the southern hemisphere at present and many representatives are highly sclerophyllous or even xeromorphic plants that can inhabit infertile and dry soils (see Myerscough *et al.* 2015 and references therein). Carpenter *et al.* (2014) showed that this trait was represented within at least one lineage of the family as early as the Eocene. Based on this general ecological trait, Cantrill & Poole (2012) suggested that the

TABLE 2. List of fossil woods occurred from King George Island, South Shetland Islands, Antarctic Peninsula.

King George Island (western side of the Antarctic Peninsula)

Family	Species	Period	References
Araucariaceae	*Agathoxylon antarcticum*	Middle Eocene	This study
	A. pseudoparenchymatosum	Middle Eocene	This study
	Araucarioxylon fildense	Middle Eocene[1]	Torres (1990)
	A. kerguelense[2]	Late middle Eocene[3]	Torres & Lemoigne (1988); Torres (1990)
Cupressaceae	*Cupressinoxylon parenchymatosum*	Middle Eocene[1]	Torres (1990)
	Cupressinoxylon sp.	Middle Eocene[4]	Poole *et al.* (2001)
Araucariaceae	*Dadoxylon kellerense*	Middle Eocene[5]	Lucas & Lacey (1981)
	D. pseudoparenchymatosum	Middle Eocene[5]	Lucas & Lacey (1981)
	Dadoxylon sp.	Middle Eocene[5]	Lucas & Lacey (1981)
	Dadoxylon sp.	Eocene[6]	Chun & Chang (1991)
Podocarpaceae	*Phyllocladoxylon antarcticum*	Middle Eocene	This study
	P. antarcticum	Late middle Eocene[3]	Torres & Lemoigne (1988); Torres (1990)
Podocarpaceae	*Podocarpoxylon fildesense*	Middle Eocene[7]	Zhang & Wang (1994)
	P. fildesense	Middle Eocene[4]	Poole *et al.* (2001)
?Podocarpaceae	*Protopodocarpoxylon araucarioides*	Middle Eocene	This study
Gymnosperm	Gymnospermous wood A	Middle Eocene[5]	Lucas & Lacey (1981)
	Gymnospermous wood B	Middle Eocene[5]	Lucas & Lacey (1981)
Monimiaceae	*Dicotyloxylon birkermajeri*	Late middle Eocene[3]	Torres (1990)
Rubiaceae	*D. pluriperforatum*	Middle Eocene[1]	Torres (1990)
Nothofagaceae	*Nothofagoxylon antarcticus*	Middle Eocene[8]	Torres (1984); Torres (1990)
	N. corrugatus	Middle Eocene[4]	Poole *et al.* (2001)
	N. neuquense	Middle Eocene[4]	Poole *et al.* (2001)
	N. paleoalessandrii	Middle Eocene[1]	Torres (1990)
	N. paleoglauca	Late middle Eocene[3]	Torres & Lemoigne (1988); Torres (1990)
	N. triseriatum	Late middle Eocene[3]	Torres & Lemoigne (1988); Torres (1990)
Nothofagaceae	*Nothofagus scalariforme*	Middle Eocene[4]	Poole *et al.* (2001)
Eucryphiaceae	*Eucryphiaceoxylon eucryphioides*[9]	Middle Eocene[4]	Poole *et al.* (2001)
	Eucryphioxylon fildense	Middle Eocene[1]	Torres (1990)
Atherospermataceae[10]	*Laurelioxylon antarcticum*	Middle Eocene[1]	Torres (1990)
Myrtaceae	*Myrceugenelloxylon antarcticus*	Middle Eocene[4]	Poole *et al.* (2001)
Cunoniaceae	*Weinmannioxylon ackamoides*[11]	Middle Eocene[1]	Torres (1990)
	W. ackamoides[12]	Middle Eocene[7]	Zhang & Wang (1994)
Angiosperm	Dicotyledonous wood	Middle Eocene	This study

[1]Originally considered to be Eocene–Oligocene, here reconsidered to be middle Eocene based on the radiometric age of Smellie *et al.* (1984).

[2]Originally reported as *Araucarioxylon* sp. 1 and sp. 2, but later both redetermined as *A. kerguelense* (Torres 1990).

[3]Originally considered to be Eocene, but later refined to the late middle Eocene (see Cantrill & Poole 2012).

[4]Originally considered to be Eocene, but later refined to the middle Eocene (Poole *et al.* 2003).

[5]Originally considered to be early Tertiary, later refined to the middle Eocene (see Cantrill & Poole 2012).

[6]Originally considered to be early Tertiary, later refined to the Eocene (Kim *et al.* 2006).

[7]Originally considered to be Paleocene, but later corrected to the middle Eocene (Shen 1999).

[8]Originally considered to be Oligocene, but later corrected to the middle Eocene (Shen 1999).

[9]Originally reported to *Weinmannioxylon eucryphioides*, but later transferred to *Eucryphiaceoxylon eucryphioides* (Poole *et al.* 2003).

[10]*Laurelia* which is considered having an affinity with *Laurelioxylon antarcticum* was in the family Monimiaceae, but it is reclassified to Atherospermataceae now.

[11]Originally reported to *Caldcluvioxylon propaniculata*, but later transferred to *Weinmannioxylon ackamoides* (Poole & Cantrill 2001).

[12]Originally reported to *Caldcluvioxylon collinsense*, but later transferred to *Weinmannioxylon ackamoides* (Poole & Cantrill 2001).

prevalence of Proteaceae on Seymour Island during the early Palaeogene provides evidence of drier conditions on the eastern side of the Antarctic Peninsula at that time compared to the western side. Consequently, comparisons of the taxonomic representation of Eocene wood assemblages between King George Island and Seymour Island seem to confirm different environmental conditions on the western and eastern sides of the Antarctic Peninsula.

TABLE 3. List of fossil woods occurred from Seymour Island, Antarctic Peninsula.

Seymour Island (eastern side of the Antarctic Peninsula)

Family	Species	Period	References
Araucariaceae	*Agathoxylon antarcticum*	Early Eocene	Pujana *et al.* (2014)
	A. pseudoparenchymatosum	Early Eocene	Pujana *et al.* (2014)
	Araucarioxylon novaezelandii	Eocene*	Torres (1990); Torres *et al.* (1994)
	A. pseudoparenchymatosum	Eocene*	Torres (1990); Torres *et al.* (1994)
	A. seymourense	Eocene*	Torres (1990); Torres *et al.* (1994)
Cupressaceae	*Cupressinoxylon hallei*	Early Eocene	Pujana *et al.* (2014)
	C. seymourense	Eocene*	Torres (1990); Torres *et al.* (1994)
	C. seymourense	Eocene*	Brea (1998)
Araucariaceae	*Dadoxylon pseudoparenchymatosum*	Eocene	Gothan (1908)
Podocarpaceae	*Phyllocaldoxylon antarcticum*	Eocene	Gothan (1908)
	P. antarcticum	Eocene*	Torres (1990); Torres *et al.* (1994)
	P. antarcticum	Early Eocene	Pujana *et al.* (2014)
	P. pooleae	Early Eocene	Pujana *et al.* (2014)
Podocarpaceae	*Podocarpoxylon aparenchymatosum*	Eocene	Gothan (1908)
	P. aparenchymatosum	Early Eocene	Pujana *et al.* (2014)
	Podocarpoxylon sp. A	Eocene*	Brea (1998)
?Podocarpaceae	*Protophyllocladoxylon francisiae*	Early Eocene	Pujana *et al.* (2014)
Gymnosperm	Gymnosperm woods	Eocene	Gothan (1908)
Atherospermataceae	*Atherospermoxylon bulboradiatum*	Early Eocene	Poole & Gottwald (2001)
	Laurinoxylon uniseriatum	Eocene	Gothan (1908)
	Laurinoxylon sp.	Eocene	Gothan (1908)
Nothofagaceae	*Nothofagoxylon scalariforme*	Eocene	Gothan (1908)
Nothofagaceae	*Nothofagoxylon scalariforme*	Eocene*	Torres (1990); Torres *et al.* (1994)
Eucryphiaceae	*Eucryphiaceoxylon eucryphioides*	Eocene	Poole *et al.* (2003)
Angiosperm	Angiosperm woods	Eocene	Gothan (1908)
	Angiosperm wood 1 (specimen no. D.502)	Eocene*	Francis (1986)
	Angiosperm wood 2 (specimen no. D. 8321.4)	Eocene*	Francis (1986)

*Originally considered to be Eocene–Oligocene, but later refined to the Eocene (see Pujana *et al.* 2014 and references therein).

Palynomorph assemblages from the lower to upper Oligocene formations on King George Island indicated a reduction in floral diversity at the close of the Palaeogene (Warny *et al.* 2019). Thus, the Eocene floras of King George and Seymour islands provide an important window into the last stands of diverse vegetation in the Antarctic Peninsula before the pronounced decline of plant communities at the close of the Palaeogene attributed to glaciation and volcanism in the region.

Comparison of growth-ring widths and patterns. Cantrill & Poole (2012) invoked a rain-shadow effect to explain the environmental differences between the western and eastern sides of the Antarctic Peninsula. During the late Mesozoic and Cenozoic, the subduction of the Phoenix Plate along the western margin of the Antarctic Peninsula led to the development of a magmatic arc and cordillera (Elliot 1988). Elevation of this mountain range may have imposed a rain-shadow effect that led to contrasting climates and vegetation on either side of the Peninsula Orogen. The western side might have been warmer and wetter than the eastern side (Cantrill & Poole 2012). If so, the trees that inhabited the two regions ought to have recorded different climatic conditions in their growth-ring features; for example, in their ring boundary types and ring widths. Although it is impossible to determine whether the fossils from King George and Seymour islands are precisely coeval, the anatomical patterns in the woods should provide general indications of tree growth patterns and environmental conditions for the Eocene on either side of the Antarctic Peninsula. To test this, growth-ring data for Eocene fossil woods from King George Island and Seymour Island were compared (Table 4), and analysed (Figs 9, 10). Although many previous studies did not provide detailed growth-ring data, several studies tabulated or illustrated interesting ring width features, and new data is provided here for both King George and Seymour Island woods (Table 4).

Several fossil woods from King George Island have relatively greater growth-ring width ranges (from 0.4 to 17 mm and rarely up to 23 mm in black solid line; Table 4, Fig. 9) than those from Seymour Island (from

TABLE 4. List of growth-ring characters of fossil woods from King George Island and Seymour Island, Antarctic Peninsula.

W/E	Species	Growth rings				References
		Presence/ Absence	Distinct/ Indistinct	Ranges	Mean or median	
W	*Agathoxylon antarcticum*	Present	Distinct	0.4–2.1 mm	0.9 mm	This study
W	*A. pseudoparenchymatosum*	Present	Distinct or indistinct	0.8–2.6 mm	1.7 mm	This study
W	*Araucarioxylon fildense*	Absent		Not mentioned		Torres (1990)
W	*A. kerguelense*	Present	Distinct	3–6 mm	4.5 mm	Torres & Lemoigne (1988); Torres (1990)
W	*Cupressinoxylon parenchymatosum*	Present	Indistinct	Not mentioned		Torres (1990)
W	*Cupressinoxylon* sp.	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*Dadoxylon kellerense*	Present	Distinct	Not mentioned		Lucas & Lacey (1981)
W	*D. pseudoparenchymatosum*	Present	Distinct	Not mentioned		Lucas & Lacey (1981)
W	*Dadoxylon* sp.	Present	Distinct	Not mentioned		Lucas & Lacey (1981)
W	*Dadoxylon* sp.	Present	Distinct	Not mentioned		Chun & Chang (1991)
W	*Dicotyloxylon birkermajeri*	Absent		Not mentioned		Torres (1990)
W	*D. pluriperforatum*	Present	Distinct	17 mm	17 mm	Torres (1990)
W	*Eucryphiaceoxylon eucryphioides*	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*Eucryphioxylon fildense*	Present	Distinct	4–13 mm	8.5 mm	Torres (1990)
W	*Laurelioxylon antarcticum*	Present	Indistinct	2–3 mm	2.5 mm	Torres (1990)
W	*Myrceugenelloxylon antarcticum*	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*Nothofagoxylon antarcticum*	Present	Distinct	6–8 mm, rarely up to 23 mm	7 mm	Torres (1984); Torres (1990)
W	*N. corrugatum*	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*N. neuquense*	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*Nothofagoxylon paleoalessandrii*	Present	Distinct	12 mm	12 mm	Torres (1990)
W	*N. paleoglauca*	Present	Distinct	1–3.5 mm	2.25 mm	Torres & Lemoigne (1988); Torres (1990)
W	*N. triseriatum*	Present	Distinct	2–6 mm	4 mm	Torres & Lemoigne (1988); Torres (1990)
W	*Nothofagus scalariforme*	Present	Distinct or indistinct	Not mentioned		Poole *et al.* (2001)
W	*Phyllocladoxylon antarcticum*	Present	Distinct	Not mentioned		Torres & Lemoigne (1988); Torres (1990)
W	*P. antarcticum*	Present	Distinct	0.7–3.5 mm	1.6 mm	This study
W	*Podocarpoxylon fildesense*	Present	Distinct	0.65–2.95 mm	1.2 mm	Zhang & Wang (1994)
W	*P. fildesense*	Present	Distinct	Not mentioned		Poole *et al.* (2001)
W	*Protopodocarpoxylon araucarioides*	Present	Distinct or indistinct	1.1–4.3 mm	2.4 mm	This study
W	*Weinmannioxylon ackamoides*	Present	Distinct	0.5–2.5 mm	1.5 mm	Torres (1990)
W	*W. ackamoides*	Present	Distinct	0.5–2.4 mm	1.05 mm	Zhang & Wang (1994)
W	Unidentified angiosperm wood	Present	Distinct	Unmeasured		This study
W	Gymnospermous wood A	Present	Distinct	Not mentioned		Lucas & Lacey (1981)
W	Gymnospermous wood B	Present	Distinct	Not mentioned		Lucas & Lacey (1981)
E	*Agathoxylon antarcticum*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*A. pseudoparenchymatosum*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*Araucarioxylon novaezelandae*	Present	Distinct	1.5–2.5 mm	2 mm	Torres (1990); Torres *et al.* (1994)
E	*A. pseudoparenchymatosum*	Present	Distinct	0.8–2.5 mm	1.65 mm	Torres (1990); Torres *et al.* (1994)
E	*A. seymourense*	Present	Distinct	1–2.5 mm	1.75 mm	Torres (1990); Torres *et al.* (1994)
E	*Atherospermoxylon bulboradiatum*	Present	Distinct	Not mentioned		Poole & Gottwald (2001)
E	*Cupressinoxylon hallei*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*C. seymourense*	Present	Distinct	0.5–2.3 mm	1.4 mm	Torres (1990); Torres *et al.* (1994)

TABLE 4.   (Continued)

W/E	Species	Growth rings				References
		Presence/ Absence	Distinct/ Indistinct	Ranges	Mean or median	
E	*C. seymourense*	Present	Distinct	0.17–0.95 mm	0.56 mm	Brea (1998)
E	*Dadoxylon pseudoparenchymatosum*	Present	Distinct	0.2–3.3 mm	1.2 mm	Gothan (1908); this study
E	*Eucrphiaceoxylon eucryphioides*	Present	Distinct	Not mentioned		Poole *et al.* (2003)
E	*Laurinoxylon uniseriatum*	Present	Distinct	0.8–1.5 mm	1.2 mm	Gothan (1908); this study
E	*Laurinoxylon* sp.	Present	Distinct	Unmeasured		Gothan (1908); this study
E	*Nothofagoxylon scalariforme*	Present	Distinct	0.6–3.0 mm	1.9 mm	Gothan (1908); this study
E	*N. scalariforme*	Present	Distinct	0.4–3 mm	1.7 mm	Torres (1990); Torres *et al.* (1994)
E	*Phyllocladoxylon antarcticum*	Present	Distinct	0.1–5.0 mm	1.8 mm	Gothan (1908); this study
E	*P. antarcticum*	Present	Distinct	1–2.6 mm	1.8 mm	Torres (1990); Torres *et al.* (1994)
E	*P. antarcticum*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*P. pooleae*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*Podocarpoxylon aprenchymatosum*	Present	Distinct	0.64–2.4 mm	1.4 mm	Gothan (1908); this study
E	*P. aparenchymatosum*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	*Podocarpoxylon* sp. A	Present	Distinct	0.07–2.6 mm	1.34 mm	Brea (1998)
E	*Protophyllocladoxylon francisiae*	Present	Distinct	Not mentioned		Pujana *et al.* (2014)
E	Gymnosperm woods	Present	Distinct	0.1–2.1 mm	1.1 mm	Gothan (1908); this study
E	Angiosperm woods	Present	Inistinct	1.2–2.0 mm	1.5 mm	Gothan (1908); this study
E	Angiosperm wood 1 (D.502)	Present	Distinct	0.4–3.3 mm	1.32 mm	Francis (1986)
E	Angiosperm wood 2 (D.8321.4)	Present	Distinct	2.5–8.4 mm	5.7 mm	Francis (1986)

W = western side, E = eastern side of the Antarctic Peninsula.

0.07 to 8.4 mm in white with black border solid line; Table 4, Figs 9, 10B–C). The mean growth-ring width of fossil woods from King George Island is 4.54 ± 4.7 mm (n = 15), clearly greater than the corresponding 1.7 ± 1.09 mm (n = 17) for woods from Seymour Island (Fig. 10E, G, H). The huge standard deviation for the King George Island woods, however, makes interpretation difficult. It should be noted that, on both sides of the Antarctic Peninsula, gymnosperms have narrower mean ring widths (2.05 mm (west) and 1.45 mm (east)) than angiosperms (6.2 mm (west) and 2.15 mm (east)). The Seymour Island fossil wood assemblages are more gymnosperm-rich (65%) than those from King George Island (40%). Hence, the narrower mean ring width recorded in the Seymour Island assemblages might be partly a taxonomic artefact. Maximum ring width is a marker of environmental tolerance or permissiveness for tree growth. On both sides of the Antarctic Peninsula Orogen, this maximum is attained by a dicot angiosperm, with 23 mm in the west compared to only 8.4 mm in the east. Minimum ring width is probably not controlled exclusively by climate, but, nevertheless, it is notable that this parameter is represented by lesser values on the eastern side (0.07 mm) than on the western side (0.4 mm) of the peninsula, both values being expressed in a gymnosperm. Overall, the growth-ring widths of fossil woods from King

George Island vary more widely than in woods from Seymour Island, although angiosperm wood 2 (sample no. D.8321.4; Francis 1986) has exceptionally wide growth-ring ranges among fossil woods from Seymour Island (Table 4, Fig. 9), and isolated broad rings occur in the early stages of growth of some conifers (Fig. 10D). Growth-ring boundary features vary substantially in the Seymour Island woods; from very subtle rings with minimal latewood (Fig. 10A, H), to strongly defined rings with moderate to very thick latewood (Fig. 10C, F, I). False rings are sparsely represented in the Seymour Island woods. Although these growth-ring data are difficult to interpret unequivocally, it is striking that mean values, minima, and maxima all suggest relatively more favourable growth conditions and, by inference, milder climates on the western side of the Antarctic Peninsula cordillera.

Generally, wide growth rings indicate rapid tree growth linked to favourable climates and substrates (Poole & van Bergen 2006). Rapid growth is impossible without an adequate supply of water and at least mild temperatures. Trees in their main growth phase typically have relatively wider rings compared to older trees or young seedlings. However, among the King George Island fossil woods, *Dicotyloxylon pluriperforatum* with growth rings up to 17 mm wide and *Nothofagoxylon paleoalessandrii* with rings up to 12 mm wide are represented by large trunks,
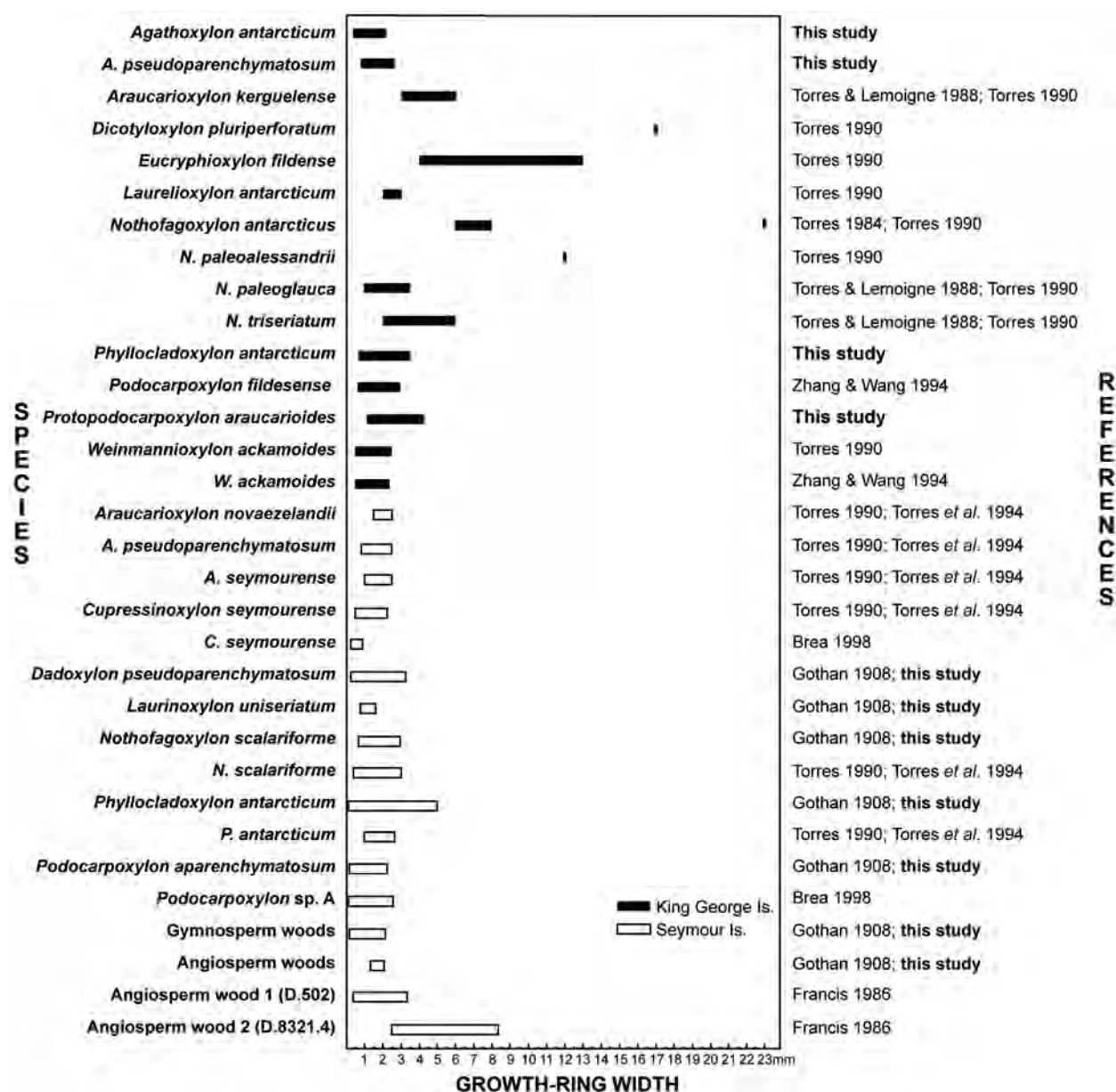
FIG. 9. Graph showing the growth-ring widths of fossil woods from King George Island and Seymour Island.

c. 40 cm in diameter (Torres 1990). Thus, they represent well-established trees, having surpassed their exponential diameter-growth phase. In addition, among the gymnosperm woods shared by the two islands, *Protopodocarpoxylon araucarioides* from King George Island (c. 46 cm diameter trunk), also has relatively broader growth rings than other gymnosperm woods. A specimen of *Phyllocladoxylon antarcticum* (SMNH S005149) from Seymour Island having up to 5 mm ring widths (Table 4; Gothan 1908; this study), could be derived from the early stage of development of a young tree, because this width is abnormal among *P. antarcticum* specimens from that area. Most fossil woods with wide growth rings from

King George Island are not young trees and their broad growth rings reflect genuinely favourable growth conditions.

A similar picture is evident in the *Araucaria araucana* forests growing in the Andes. According to Muñoz *et al.* (2014), the plant productivity of *A. araucana* trees in the North Patagonian Andes decreases from the western side to the eastern side of the cordillera and this coincides with the rainfall gradient affecting the region, with the western side receiving much higher annual precipitation. The mean tree ring width of the *A. araucana* trees is also smaller on the eastern side compared to the western side of the Andes (Muñoz *et al.* 2014).
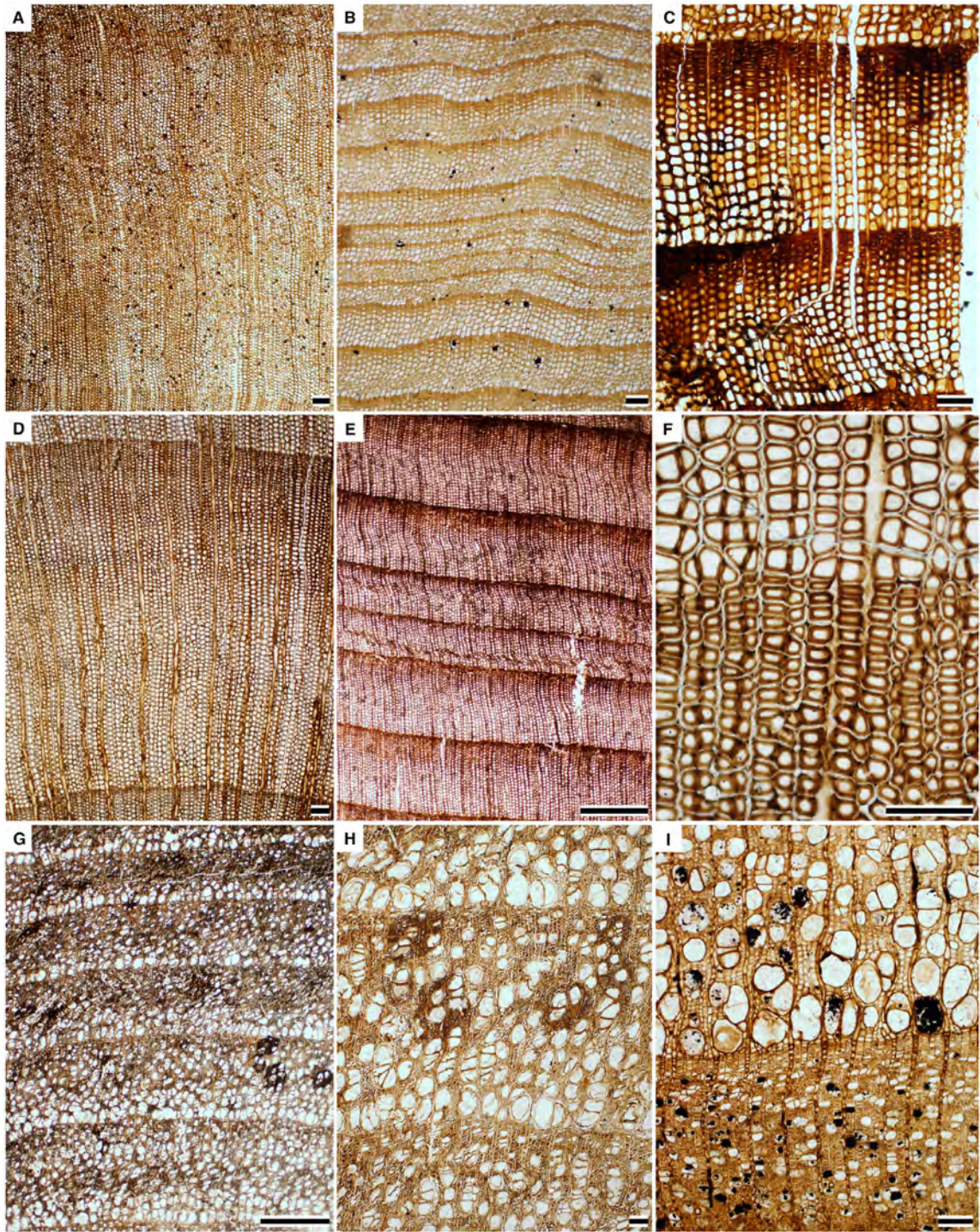
FIG. 10. Growth-ring features of Eocene woods described by Gothan (1908) from 'Cape Seymour', north-eastern Seymour Island. A–C, *Phyllocladoxylon antarcticum* Gothan, SMNH S004055-02/S004117-01/S004094-02; A, transverse section showing ill-defined growth rings; B, transverse section showing variable narrow growth rings; C, transverse section showing well-defined growth rings and prominent latewood. D, F, *Dadoxylon pseudoparenchymatosum* Gothan, SMNH S004104-04; D, transverse section showing very broad growth ring; F, transverse section showing growth-ring boundary with prominent latewood. E, *Podocarpoxylon aparenchymatosum* Gothan, SMNH S004109-01; transverse section showing variable growth rings. G–H, *Laurinoxylon uniseriatum* Gothan, SMNH S004108-03; G, transverse section showing relatively uniform narrow growth rings; H, transverse section showing growth rings with relatively narrow latewood. I, *Nothofagoxylon scalariforme* Gothan, SMNH S004067-01; transverse section showing a growth-ring margin with prominent latewood. Scale bars represent: 100 μm (A–D, F, H–I); 1 mm (E, G). Colour online.
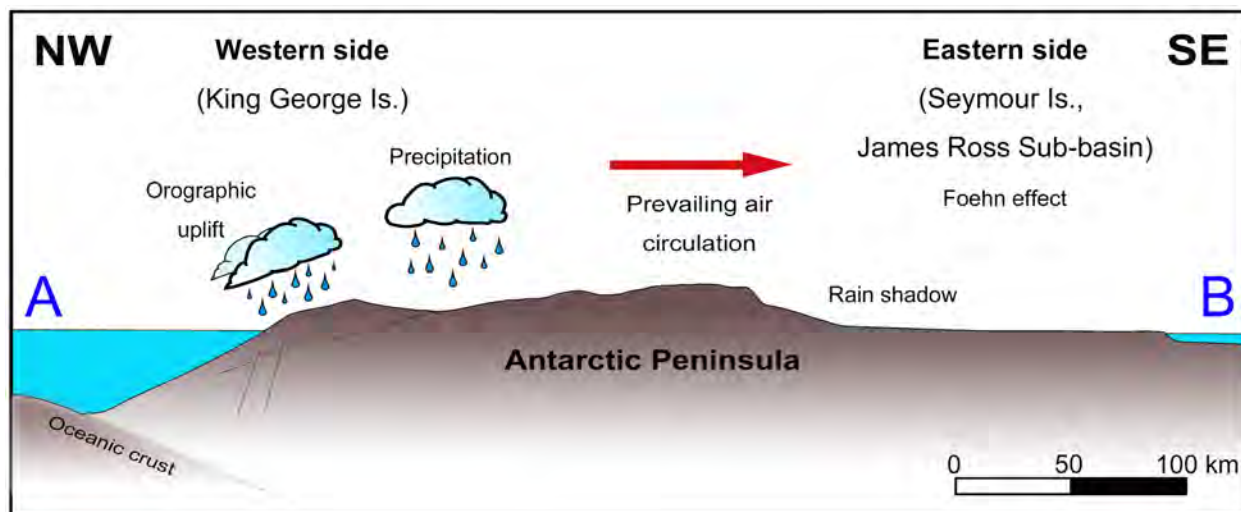
FIG. 11. Palaeotopographical and palaeoclimatological model for the Antarctic Peninsula during the Eocene (adapted from the schematic cross-section by Elliot 1988); for location of transect see line AB in Figure 1A. Colour online.

Another interesting growth-ring feature is the absent or indistinct growth-ring boundaries evident in several fossil woods from King George Island. Among specimens from this island, two fossil woods lack growth-ring boundaries, two have indistinct growth-ring boundaries, and three fossil woods contain both indistinct and distinct growth-ring boundaries (Table 4). Such features are not easy to interpret and might be the result of stochastic genetic effects or episodic climatic events. The two woods lacking clear growth rings are from a conifer and a dicot angiosperm, which suggests an environmental driver of growth rather than a genetic peculiarity of a single botanical group. However, it should be noted that both reports are from the same source (Torres 1990) and it is surprising that the absence of growth rings has not been reported in studies of King George Island fossil wood assemblages by other researchers. Despite these caveats, the more pronounced and narrower growth rings in most Seymour Island woods are consistent with the hypothesis that the leeward eastern side of the Antarctic Peninsula experienced stronger seasonal climatic variations than the windward western side where conditions were milder and precipitation more regular.

Although the extent of growth-ring data for Antarctic fossil woods is still sparse, a pattern of more uniform growth-favourable conditions vs more seasonal conditions incorporating more episodic precipitation is emerging from fossil assemblages from King George Island and Seymour Island respectively. The most likely cause of this contrast in growth conditions is the rain-shadow effect induced by an elevated topography along the emerging Antarctic Peninsula Orogen during the early Palaeogene (Fig. 11).

CONCLUSIONS

During the early Palaeogene, despite its high southern palaeolatitudinal position, the Antarctic Peninsula hosted a rich forest vegetation of woody conifers and angiosperms. Somewhat different associations of woody species developed on the western and eastern sides of the Antarctic Peninsula. Woody angiosperm diversity was relatively high on the western side of the Peninsula compared with the eastern side. This difference suggests that these regions experienced somewhat contrasting environmental conditions. The elevated topography of the Antarctic Peninsula Orogen probably induced a rain-shadow effect during the early Palaeogene. Consequently, precipitation on the western side of the Antarctic Peninsula became relatively higher and more consistent than on the eastern side. These climatic conditions influenced the growth signatures of woody species on both sides of the Peninsula. In addition, this study of Eocene woods on the Antarctic Peninsula documents the regional patterns of floral-diversity and tree-growth syndromes in the last stage of moderately diverse vegetation before the cooling crisis that initiated ice-sheet development on Antarctica in the Oligocene.

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