

# Tree growth at polar latitudes based on fossil tree ring analysis

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Received 29 December 2006; received in revised form 5 June 2007; accepted 14 June 2007

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## Abstract

Permineralized trunks and mature wood samples with well-preserved growth rings are described and analyzed from the Upper Permian and Middle Triassic of the central Transantarctic Mountains. This fossil wood is unique in that the plants lived in an environment with no modern analogue and exhibited luxuriant tree growth above 75°S paleolatitude. Ring width averages 1.69–2.3 mm, with maximum width of 6.83–9.9 mm, an order of magnitude larger than ring widths produced at near-polar latitudes today. Tree rings in both the Permian and Triassic woods show similar structure, consisting almost entirely of earlywood (spring wood), with between 0–12% of each ring classified as latewood (summer wood). The small amount of latewood (0–6 cells) indicates a very rapid transition to seasonal dormancy, probably in response to decreasing light levels at these paleolatitudes. In order to accurately delimit the earlywood–latewood boundary, a comparison was done of classical dendroclimatological techniques and alternative techniques utilized primarily by paleobotanists analyzing fossil woods. We found that classical wood anatomy techniques provided a more accurate explanation of wood development and tree growth for these high-latitude samples. The suggested cool-temperate Late Permian *Glossopteris* flora from this area differs substantially from the warm-temperate Middle Triassic corystosperm flora (leaf type, *Dicroidium*) and very different paleoclimates have been reconstructed for these two time periods. Ring structure and wood growth from both sites, however, are very similar, indicating that these plants were responding to the environment in very similar ways. The structure of the tree rings, including a large number of earlywood tracheids and a very low number of latewood cells, provides evidence that growth at these polar latitudes was limited by light levels rather than water and temperature as occurs in modern high-latitude forests. These fossil tree rings have important implications for understanding woody shoot growth and cambial function at high latitudes during periods of global warmth.

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**Keywords:** Late Permian; Middle Triassic; Antarctica; Tree rings; Paleoclimate; Gondwana fossil flora; Fossil wood anatomy

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## 1. Introduction

Although currently glaciated, Antarctica was covered in vegetation for much of its existence. Plant fossils have been recorded from the Devonian (Edwards, 1990) until

the onset of the present glaciation in the Oligocene and there is evidence of alpine-type assemblages as recently as the Pliocene in continental Antarctica (Francis and Hill, 1996; Ashworth and Cantrill, 2004). Previous studies of Antarctic floras (e.g., Taylor and Taylor, 1990; McLoughlin, 2001) record a floral transition from the Permian to the Triassic similar to that observed elsewhere in Gondwana (e.g., Rees, 2002; Gastaldo et al., 2005). During the Late Permian the Antarctic landscape was dominated by the

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*Glossopteris* flora, which has been described as a cool-temperate assemblage; glossopterid organs (leaves, woody stems, etc.) at some sites represent upwards of 90% of the identifiable plant remains (Cúneo et al., 1993). Floral records from the Lower Triassic of Antarctica are scarce (McLoughlin et al., 1997; Retallack, 2005), but throughout Gondwana there was a major floral turnover at the Permian–Triassic boundary. The glossopterids disappeared almost completely (but see Delevoryas and Person, 1975; McManus et al., 2002) and the Early Triassic was dominated by new clades of pteridosperms. By the Middle Triassic, corystosperm seed ferns were dominant throughout Gondwana (Thomas, 1933; Retallack, 1980; Taylor and Archangelsky, 1985; Maheshwari and Bajpai, 1996). The most common members of this group include *Dicroidium* leaves, *Umkomasia* ovulate organs, and *Pteruchus* pollen organs.

The central Transantarctic Mountains (CTM) region has provided a wealth of information on Permian and Triassic fossil biotas. Two deposits of permineralized peat have yielded extraordinarily well-preserved plant material and provided anatomical details on floral assemblages from these periods (Taylor and Taylor, 1990). The Late Permian peat from Skaar Ridge consists almost exclusively of glossopterid remains, while the Middle Triassic peat from the Fremouw Formation exhibits greater diversity (Taylor et al., 2000). In the latter, all major groups of vascular plants are represented, including four orders of seed plants (Table 1). Both permineralized floras are similar in their floral composition to compression–impression floras of comparable age from across Gondwana, although the Late Permian flora is less diverse than those from lower latitudes. Within the peat are numerous woody axes, including stems and trunks, which exhibit well-preserved growth rings. In addition, isolated wood samples and logs up to 20 m long are relatively common at the same site as the Triassic peat. Because of the presence of the peat deposits, much of the wood can be correlated with other plant organs and assigned to taxonomic groups (e.g., Meyer-Berthaud et al., 1993; Del Fueyo et al., 1995).

Evidence of forest growth in Antarctica consists of forests in growth position, silicified logs, and wood samples; these have been found at a number of localities ranging from the Permian through the Eocene (e.g., Jefferson, 1982; Francis et al., 1993; Falcon-Lang and Cantrill, 2002; Cantrill and Poole, 2005; Poole and Cantrill, 2006). Fossil woods with well-preserved growth rings from several of these sites have been analyzed in detail. Jefferson (1982) was the first to study an Early Cretaceous fossil forest from Alexander Island, Antarctic Peninsula (paleolatitude, ~71°–72°S). This

Table 1

Permineralized peat floras, Central Transantarctic Mountains, Antarctica

<i>Skaar Ridge (Late Permian)</i>	
Glossopteridales—	<i>Glossopteris schopfii</i> (leaves, stems)
	<i>Glossopteris skaarensis</i> (leaves, stems)
	<i>Vertebraria</i> (roots)
	<i>Araucarioxylon</i> -type wood
	Ovulate organs (2 types)
Additional seed plants—	<i>Plectilospermum elliotii</i> (seeds)
	<i>Choanostoma verruculosum</i> (seeds)
Bryophyta—Bryidae—	<i>Merceria augustica</i> (leaves, axes, rhizoids)
Filicales—Skaaripteridaceae—	<i>Skaaripteris minuta</i>
	(stems, roots, sporangia)
Fungi—Basidiomycetes—	white rot, pocket rot in woody axes
	Zygomycetes (hyphae and chlamydospores)
<i>Fremouw Peak (Middle Triassic)</i>	
Corystospermales—	<i>Dicroidium fremouwensis</i> (leaves)
	<i>Kykloxylon fremouwensis</i> (stems)
	<i>Jeffersonioxylon gordonense</i> (woody stems)
	<i>Pteruchus fremouwensis</i> (pollen organ); pollen ultrastructure
	<i>Rhexoxylon</i> -like axis
	<i>Umkomasia resinosa</i> (cupules, ovules)
Petriellales—	<i>Petriellaea triangulata</i> (ovulate cupules)
Coniferales—Podocarpaceae—	<i>Notophytum krauselii</i> (stems, roots, leaves)
	Taxodiaceae— <i>Parasciatopitys aequata</i> (seed cones)
	Voltziales— <i>Leastrobus fallae</i> (pollen cones)
Cycadales—	<i>Antarcticycas schopfii</i> (stems, roots, cataphylls, leaves)
	<i>Delemaya spinulosa</i> (pollen cones)
Additional seed plants—	<i>Ignotospermum monilii</i> (isolated seeds)
Filicales—Cyatheaaceae?/Pteridaceae?—	<i>Schopfiopteris repens</i> (rhizomes)
	Gleicheniaceae— <i>Gleicheniapteris antarcticus</i> (sporangia)
	Gleicheniaceae?— <i>Antarctiapteris sclericaulis</i> (rhizomes)
	Matoniaceae— <i>Tomaniopteris katonii</i> (sori, sporangia)
	Matoniaceae?— <i>Soloropteris rupex</i> (stems)
	Osmundaceae— <i>Ashicaulis (Osmundacaulis) beardmorensis</i> (stems)
	<i>Ashicaulis woolfei</i> (stems, frond fragments)
Other ferns: <i>Fremouwia inaffecta</i> (rhizomes)	
	<i>Schleporia incarcerationata</i> (stems)
Marattiales—	<i>Scolecopteris antarctica</i> (pinnules, sporangia)
Equisetales—	<i>Spaciinodum collinsonii</i> (stems, buds, branches)
Incertae sedis—	<i>Hapsidoxylon terpsichorum</i> (stems)
Fungi—Basidiomycetes—	<i>Palaeofibulus antarctica</i>
	Wood rot in <i>Araucarioxylon</i>
	Zygomycetes (Endogonales—endomycorrhizae):
	Vesicular–arbuscular mycorrhizae
	<i>Sclerocystis</i> -like
	<i>Mycocarpon asterineum</i>
	<i>Endogone</i> -like zygosporangia; <i>Glomus</i> -like chlamydospores
	<i>Gigasporites myriamycetes</i> , <i>Glomites cycestris</i>
Trichomycete	
Ascomycetes?—	<i>Endochaetophora antarctica</i>
Chytridiomycetes—	endobiotic resting spores

For a more detailed list, including references, see Taylor et al. (2000).

material was subsequently studied by other investigators (Creber and Francis, 1987; Creber, 1990; Falcon-Lang et al., 2001), who found that the productivity of this polar forest was similar to forests in temperate latitudes today. Francis and colleagues (Francis et al., 1994) analyzed wood from the Weller Coal Measures (late Early Permian) of the Allan Hills in southern Victoria Land (paleolatitude,  $\sim 80^{\circ}$ – $85^{\circ}$ S) and noted wide annual rings indicative of an equable growing season at these high latitudes during this period. Examination of tree rings in Cretaceous and Tertiary wood from the Antarctic Peninsula also revealed extensive secondary growth (Francis, 1986; Francis and Poole, 2002). These studies, along with data from compression–impression floras, indicate that much of the continent was vegetated for most of its history, even when situated at very high paleolatitudes.

During the late Paleozoic, the paleo-South Pole is commonly reconstructed as situated on the Antarctic continent (Grunow, 1999; Scotese, 2002). Late Permian paleogeographic reconstructions place it either in Northern Victoria Land (Antarctica) or in southeastern Australia. Either of these interpretations would place the CTM at very high latitudes in the Late Permian, certainly above  $75^{\circ}$ S, and probably between  $80^{\circ}$ – $85^{\circ}$ S. During the Triassic, Antarctica rotated slightly away from the pole, but the central Transantarctic Mountains were still situated at high paleolatitudes during the Middle Triassic ( $\sim 70^{\circ}$ – $75^{\circ}$ S). During this time, Gondwana was in transition as the climate changed from icehouse conditions of the Early Permian to a strong greenhouse climate by the Middle Triassic (e.g., Kidder and Worsley, 2004; Galfetti et al., 2007). Fossil forests in the central Transantarctic Mountains during the Permian and Triassic were located at slightly higher paleolatitudes than those described from southern Victoria Land (Francis et al., 1994), and thus represent the highest paleolatitude wood available for ring analysis from Antarctica (see also Cúneo et al., 2003). At these extreme latitudes, trees were growing in a strongly seasonal polar light regime, thus ensuring that growth ring boundaries were formed annually. Although the mid-Triassic Antarctic flora may still have been in a period of recovery from the end-Permian extinctions, to date there have been very few analyses of fossil tree rings from the Triassic of Gondwana (Gabites, 1985; Pires et al., 2005).

In this study we present an analysis of tree rings in Late Permian and Middle Triassic wood from the central Transantarctic Mountains. The Late Permian wood belongs to the plant that bore *Glossopteris* leaves by correlation with leaves in the peat at the site (Pigg and

Taylor, 1993), and because glossopterids are the only known woody plants in the low diversity flora of Skaar Ridge. The most common wood type in the Middle Triassic Fremouw Formation belongs to the corystosperms, and represents the stem of *Dicroidium* (*Kykloxylon*, Meyer-Berthaud et al., 1992, 1993; *Jeffersonioxylon*, Del Fueyo et al., 1995). Due to the exceptional preservation of this material, it is possible to compare ring structure from these two time periods. These specimens not only span a time of great floral turnover, but also provide a record of climate change during an important transitional phase in Earth history.

## 2. Materials and methods

Silicified stems and trunks (Figs. 1–3) were collected from peat deposits and as isolated specimens at Skaar Ridge, McIntyre Promontory, and Fremouw Peak in the region of the Beardmore and Shackleton Glaciers, central Transantarctic Mountains. Most of the specimens are portions of larger axes with only a few containing preserved pith; none of the specimens had preserved extraxylary tissues. Specimens were collected during the 1990–1991, 1995–1996, and 2003–2004 Antarctic field seasons. The Skaar Ridge peat ( $84^{\circ} 49' 15.8''$  S,  $163^{\circ} 20' 18.9''$  E, Buckley Island quadrangle, Barrett and Elliot, 1973) (Taylor et al., 1989) occurs within the Upper Buckley Formation of the Beacon Supergroup and is considered to be Late Permian in age based on palynomorphs and associated compression floras (Farabee et al., 1991). A single, large trunk was collected from McIntyre Promontory ( $84^{\circ} 22' 23''$  S,  $179^{\circ} 45' 58''$  E) during the 1995–1996 field season (Fig. 4). The forest level, where six specimens were found in growth position on the side of a steep cliff face, occurs near the base of the Upper Buckley Formation and is probably Middle–Late Permian (J.L. Isbell, personal communication; Taylor et al., 1997). Due to the difficulty of collecting at this locality combined with the weight of the trunks, only the smallest specimen at the site (no. 12,389, 35.2 cm in diameter) could be retrieved. Triassic peat and wood samples were collected from the col north of Fremouw Peak ( $84^{\circ} 17' 24.1''$  S,  $164^{\circ} 21' 24.2''$  E) (Taylor et al., 1989). This deposit has been dated as early Middle Triassic based on palynomorphs preserved in the peat (Farabee et al., 1990).

All specimens were prepared using the acetate peel technique (Galtier and Phillips, 1999), after etching polished surfaces in concentrated (48–50%) hydrofluoric acid. Selected peels were examined using transmitted light and photographed with a Leica DC500 digital camera. Peels were mounted in Eukitt® on microscope

Table 2

Late Permian tree ring measurements (see text for explanation of values in parentheses)

Specimen #	Peat/trunk	Specimen width (cm)	Total # of rings	Maximum width (mm)	Minimum width (mm)	Mean width (mm)	MS
12,389	Trunk	32.5	27 (115)	5.12	1.03	2.45	0.30
13,089	Peat	9.4	45 (59)	2.27	0.36	1.11	0.32
13,090	Peat	7.4	53 (92)	1.68	0.20	0.82	0.37
13,691	Peat	8.3	30	3.56	0.90	2.02	0.37
15,485	Peat	13.8	16	9.90	2.46	6.49	0.32
15,503	Peat	7.4	27	4.13	0.73	2.15	0.34
15,512	Peat	4.1	15	2.21	0.53	1.27	0.33
15,514	Peat	6.0	25	3.34	0.95	1.81	0.35
Average		9.3	23 (47)	4.03	0.90	2.27	0.34

slides for photography. All specimens, peels and slides are deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Research Center, University of Kansas, under the specimen numbers listed in Tables 2 and 3 (<http://paleobotany.bio.ku.edu/PaleoCollections.htm>). Wright Cell Imaging Facility's ImageJ software (Rasband, 1997–2004) was used to measure ring widths and radial cell diameters. Ring-width measurements were made along a single radius, but in some cases, due to poor cellular preservation, measurements continued along an adjacent radius to obtain the largest number of ring measurements. Some rings within an otherwise well-preserved trunk were too crushed to measure ring width, so these particular rings were excluded from analysis. Since the earliest formed rings in stems generally record rapid and variable growth (e.g., Fritts, 1976), the innermost 3–20 rings, the

so-called juvenile wood, were excluded from the analysis. In addition, the outermost ring was not measured as the ring boundary was often not preserved. Therefore, the total number of rings listed in Tables 2 and 3 represents a conservative minimum. Radial cell diameters were obtained by measuring cells across a single ring from one ring boundary to the next. Two rings per specimen were measured, one file of cells in each ring, one ring towards the middle of the wood and one towards the periphery.

Analyses performed included calculating standard mean sensitivity (Fritts, 1976) and the cumulative sum equation of Creber and Chaloner (1984). Annual sensitivity is a measure of variability in ring width from year to year and mean sensitivity represents variability over the lifespan of the tree. Mean sensitivity (MS) estimates the variability in ring width from

Table 3

Middle Triassic tree ring measurements

Specimen #	Peat/trunk	Specimen width (cm)	Total # of rings	Maximum width (mm)	Minimum width (mm)	Mean width (mm)	MS
11,208	Peat	3.5	26	3.92	0.24	1.32	0.34
11,313	Peat	5.7	8	6.83	4.27	5.30	0.13
11,468	Trunk	9.5	77	2.73	0.08	1.07	0.35
11,475	Trunk	15.3	53	3.69	0.99	2.16	0.22
11,491	Peat	8.1	8	4.52	1.89	3.78	0.24
11,619	Trunk	6.7	62	1.05	0.19	0.57	0.24
11,800	Peat	6.0	68	3.23	0.18	0.82	0.40
11,816	Peat	8.2	54	5.8	0.17	1.22	0.42
11,822	Peat	8.8	39	4.18	1.27	2.36	0.22
11,823	Peat	7.4	14	5.83	2.18	4.41	0.14
12,820	Peat	10.4	50	2.92	0.88	1.88	0.23
12,961	Peat	7.5	58	4.00	0.32	1.44	0.29
12,963	Peat	11.5	105	3.61	0.22	1.02	0.35
12,964	Peat	11.4	122	2.88	0.15	0.98	0.45
12,965	Peat	7.6	72	2.51	0.37	1.08	0.42
13,007	Peat	2.1	31	1.01	0.32	0.65	0.21
13,009	Peat	7.1	78	1.85	0.29	0.79	0.25
13,032	Trunk	18.0	78	4.73	0.42	2.25	0.35
13,655	Trunk	13.6	136	2.24	0.12	0.58	0.44
13,802	Trunk	11.3	43	5.54	0.17	1.19	0.42
13,823	Trunk	9.8	117	2.80	0.13	0.70	0.36
Average		9.0	61.86	3.61	0.71	1.69	0.31



one year to the next over the life of the tree using the formula:

$$MS = (1/n - 1) \sum (|2(x_{t+1} - x_t)/(x_{t+1} + x_t)|)$$

where  $n$  equals the number of rings in the specimen,  $x$  the width of a ring, and  $t$  the ring number. Mean sensitivity values range from 0 to 2. Wood with values of 0–0.3 is considered complacent, i.e., showing little response to environment, while sensitive trees, those seasonally affected by environmental variables, range from 0.3–2 (Fritts, 1976). Although mean sensitivity as a measure of tree environmental response has been questioned in recent years, due to the difficulty of knowing what part of the tree is represented by fossil wood samples (Falcon-Lang, 2005a), we calculated it for comparison to previous fossil tree ring studies which utilized this method (Francis, 1986; Francis et al., 1994).

The cumulative sum equation, defined as the cumulative sum of tracheid radial cell diameters as they deviate from the mean (CSDM) across a single ring, was proposed by Creber and Chaloner (1984). This method has been used in fossil wood as a method of defining the earlywood–latewood (EW–LW) boundary in wood and as a way to classify ring series by climate (e.g., Creber and Chaloner, 1984; Falcon-Lang, 2000, 2005a):

$$S_i = S_{i-1} + (x_i - x_{ave})$$

where  $S_i$  is the cumulative sum of the radial cell diameters,  $S_{i-1}$  the cumulative sum of the previous cell diameter,  $x_i$  radial cell diameter, and  $x_{ave}$  the mean of radial cell diameters in that ring. In this paper, the cumulative sum calculation was used only to provide a point of comparison among different growth environments based on ring anatomy, as suggested by Creber and Chaloner (1984; see also Brison et al., 2001). In the present study, EW–LW boundary was determined using Mork's (1928) definition, for which Denne (1989) has provided two interpretations that are commonly used in wood anatomical studies. In the first formula, latewood is defined as the point where radial cell wall thickness of an individual tracheid is equal to or greater than four times the width of the cell lumen:

$$2a \geq b \quad (\text{Formula 1})$$

where  $a$ =wall thickness of two adjacent cell walls, and  $b$ =lumen radial diameter. In the second formula, wall thickness must be at least twice the lumen diameter of that

cell for it to be considered latewood:

$$2c \geq b \quad (\text{Formula 2})$$

where  $c$ =thickness of a single cell wall, and  $b$ =lumen radial diameter. To evaluate the utility of these two definitions in fossil material, we calculated the EW–LW boundary using both of Denne's (1989) interpretations. These EW–LW determinations were then compared to the cumulative sum method to determine which formula best defined wood growth and its relationship to the paleoenvironment for the Antarctic specimens.

Using the cumulative sum calculation as a starting point, Falcon-Lang (2000) presented a method to determine whether a gymnospermous wood specimen belonged to an evergreen or a deciduous plant. In his method, when the apex of the CSDM curve occurs to the right of the center of the curve, the plant is evergreen, while deciduous species generally fall to the left of center (Falcon-Lang, 2000, text-Fig. 4). This method was also applied to the Antarctic specimens and compared with data from other methods for determining deciduousness in woody fossil plants.

### 3. Results

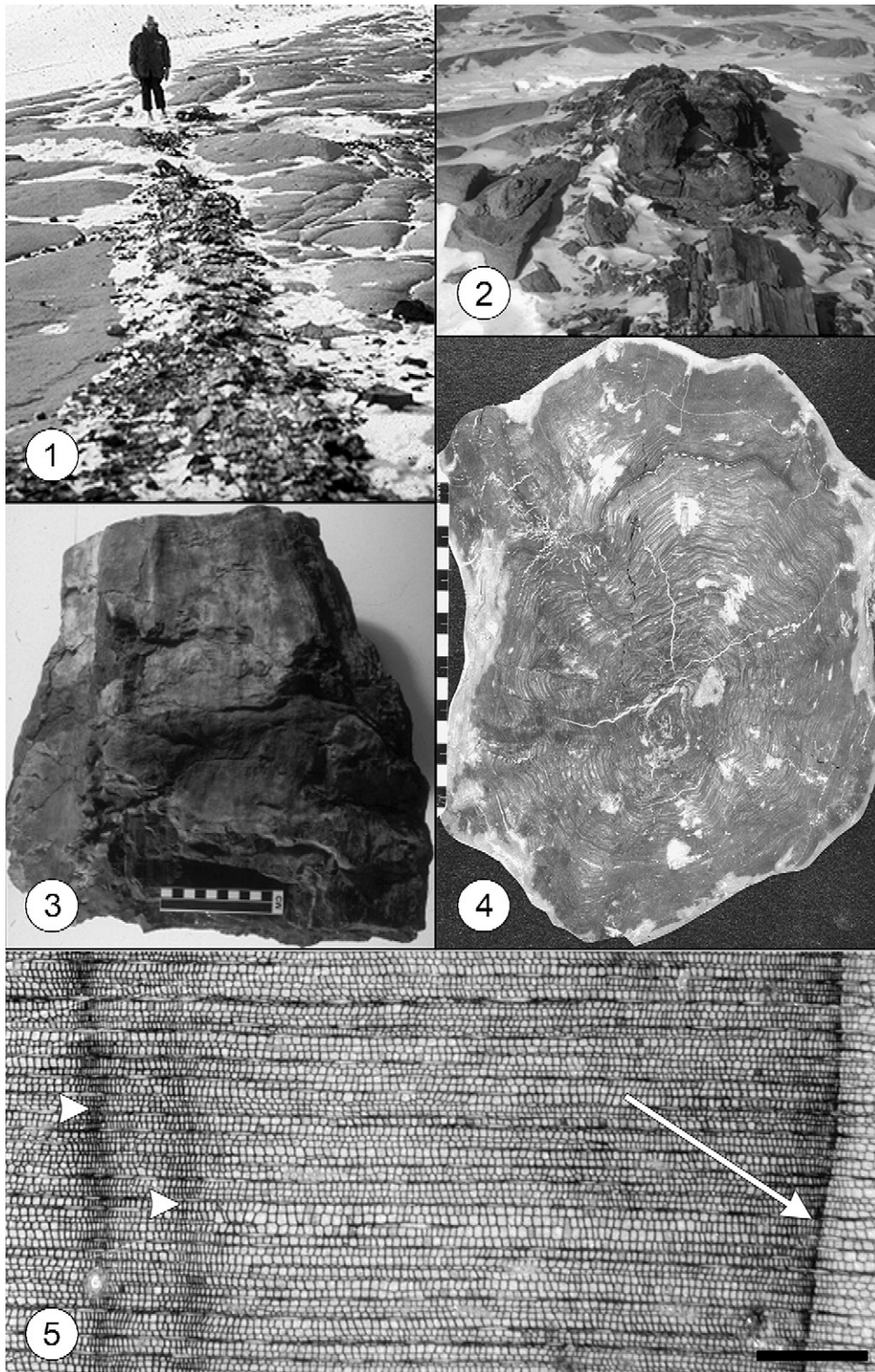
#### 3.1. Permian wood

Eight stems were analyzed from the Permian: seven from the Skaar Ridge peat and one isolated trunk from McIntyre Promontory; all specimens represent stem wood. Since glossopterids are the only woody plants present in this flora, root wood from the peat is identifiable either as the distinctive *Vertebraria* type, with wedges of wood separated by air spaces or, if it is of the 'solid cylinder' type of *Vertebraria* (Neish et al., 1993), by the large number of faint and discontinuous rings. None of the specimens detailed here exhibited these characteristics, so all specimens are considered to be stem wood. The axes ranged from 4.1–35.2 cm in diameter with 15–115+ rings per specimen and an average of 47 rings (Fig. 4). In three specimens, poor preservation prevented measurement of all rings, so values for ring widths represent only the well-preserved rings. The ring boundary is usually visible even in poorly preserved rings, so the total number of rings could be counted (Table 2, number in parentheses). Individual ring widths ranged

Figs. 1–5. Permian and Triassic wood from Antarctica. Fig. 1. Large, permineralized trunk preserved in sandstone, Middle Triassic, Fremouw Peak (~22 m long). Fig. 2. Partially upright stump in channel sandstone, Middle Triassic, Fremouw Peak (~30 cm in diameter). Fig. 3. Large trunk from McIntyre Promontory showing flaring base. Bar scale in cm. Fig. 4. Cross section of trunk in Fig. 3 showing well-preserved growth rings; rings were somewhat compacted during the preservational process. #12,389. White areas represent regions of poor preservation. Fig. 5. Cross section of Permian wood from Skaar Ridge. Center of trunk to left; cambium to right. Arrow=true ring boundary; arrowheads=false rings. #15,485G, slide 15,485γ, Bar scale=0.3 mm.

from 0.20–9.9 mm (mean=2.3 mm, Table 2). False rings were observed in only one specimen (15,485) and were identified by a progressive thickening of tracheid cell

walls, followed by a gradual thinning, with no ring boundary or cessation of growth to signify the end of a growing season (Fig. 5). Although it is often impossible to



determine whether fossil tree rings represent yearly growth increments, the high paleolatitudes of these deposits and the structure of the rings themselves support the hypothesis that each ring represents a single year's growth, so the number of rings therefore represents the minimum age of the tree.

Perhaps the most interesting aspect of these Permian woods is the large number of cells per ring and the small amount of latewood. The number of earlywood cells per ring varied greatly, from 34–234 cells (mean = 119), but the number of latewood cells was always small, from 1–5 cells per ring using Formula 1. One specimen (15,485) had wider rings than the others with 236–238 cells per ring. When this extreme value is excluded, cell numbers range from 36–91 cells per ring (mean = 64). Mean sensitivity of the Permian wood ranged from 0.30–0.37 with a mean of 0.34, and all specimens were classified as “sensitive” (Table 2). Only three specimens (15,485, 15,503, and 15,514) had adequate cellular preservation for tracheid radial diameter measurements. The others were either partially crushed or, more commonly, the cell walls were difficult to resolve, possibly due to incomplete permineralization. Cell diameters ranged from 11–294  $\mu\text{m}$  (mean = 96  $\mu\text{m}$ ). Specimen 15,485 also had extremely large cell diameters, ranging from 27–294  $\mu\text{m}$ . With values far from the other specimens, 15,485 may be responding to the environment in a different way or it may consist of rapidly growing juvenile wood. If this specimen is excluded from the analysis, the range of cell diameters falls to 11–166  $\mu\text{m}$ . Using Creber and Chaloner's (1984) CSDM method, the amount of latewood per ring is very large (all cells to the right of the arrows in Fig. 6A), ranging up to 47% of the ring for all specimens. Using either one of Denne's (1989) two formulae for calculating the amount of latewood (Fig. 6B), it is clear that the decrease in tracheid radial diameter during the growing season is a result of a gradual reduction in lumen diameter and not a thickening of the tracheid walls. Tracheid wall thickness varies slightly throughout the growing season, but remains very close to the wall thickness in the first cells produced in the spring (Fig. 6B). These results confirm that the majority of cells in each ring represent earlywood and not latewood (Fig. 7). Using this method, the number of latewood cells for all specimen ranges from 0–10% of each ring.

### 3.2. Triassic wood

Twenty-one axes ranging from 2.1–18.0 cm in diameter were analyzed from the Middle Triassic Fremouw Formation (Fig. 8). Seven of these included

pith tissue and these ranged from 6.7–18.0 cm in diameter. The number of rings per specimen was 14–136 (mean = 65) (Table 3; specimens with <14 rings were not included in the analysis). Ring widths varied from 0.08–6.83 mm (mean = 1.69 mm) (Table 3, Fig. 9). Due to crushing at ring boundaries, which was common in many of the specimens, only eight Triassic wood specimens were used for cell analysis. As in the Permian wood, there was a large amount of earlywood (14–104 cells) and only a few cells of latewood (0–6 cells, Formula 1) to mark seasonal boundaries (Fig. 10). One trunk specimen (11,475) contained frost rings (Figs. 11, 12) and two axes from the permineralized peat (12,963, 12,964) contained false rings. Mean sensitivities ranged from 0.14–0.45 with an average of 0.31. Approximately half of the stems would be classified as sensitive (Table 2). On average there were 45 cells per ring (range from 14–104). Cell diameters ranged from 11–97  $\mu\text{m}$  (mean = 45  $\mu\text{m}$ ). As with the Permian wood, the CSDM calculation shows a gradual diminution of tracheid radial diameter across each ring (Fig. 13A). Based on our data (Fig. 13B), this size reduction is the result of narrowing cell lumens, rather than an increase in wall thickness, as would have been expected with the formation of latewood. The amount of latewood in the Triassic rings ranged from 0–12% using Denne's (1989) Formula 1.

## 4. Discussion

### 4.1. Comparison of Permian and Triassic wood

Although there are many similarities between the Late Permian and Middle Triassic wood from the central Transantarctic Mountains, the total number of tree rings, on average, is much greater in the Triassic wood than the Permian (~62 vs. 23 average number of rings; Tables 2, 3) indicating a more mature forest in the Triassic than the Permian. There are several other possible explanations for this difference. With one exception, the Permian woods are all preserved in permineralized peat, whereas the Triassic samples from Fremouw Peak are derived from a broader paleoenvironment, including stems in peat nodules, and trunks found in braided river deposits. Wood can be transported for some distance by a river system, especially under flood conditions (Fritz, 1980), so the Fremouw wood may provide a proxy record for a different microenvironment. It is also possible that larger trunks were simply not preserved in the Permian peat as they were in the varied depositional environments of the Triassic wood. As noted in Table 2, several Permian specimens (12,389, 13,089, and 13,090) were too crushed to allow



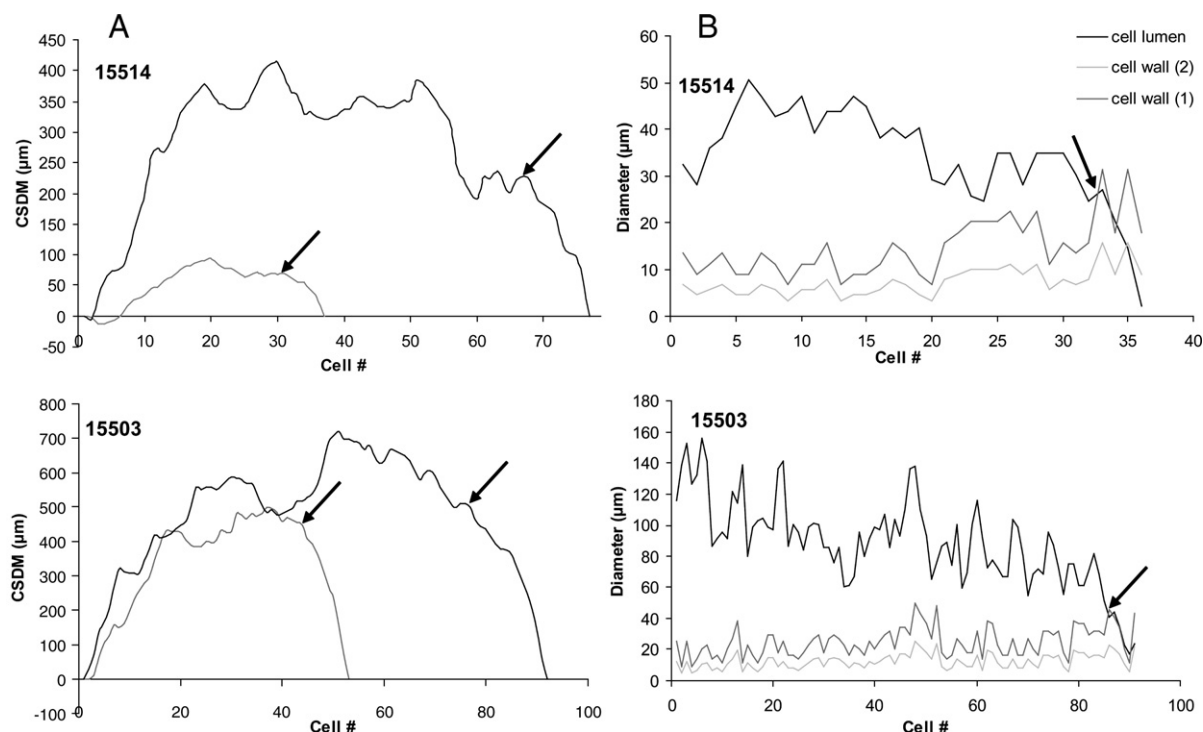


Fig. 6. Different methods of calculating EW–LW boundary using Permian fossil wood (Skaar Ridge). A. CSDM method of [Creber and Chaloner \(1984\)](#). The two graphs show results for two specimens, with two rings measured in each specimen (black and grey lines). EW–LW boundary = the point at which each line turns toward zero (arrows). B. [Denne's \(1989\)](#) two methods based on the same two specimens in A. Thin grey line =  $2a$  of Formula 1; thin black line =  $2c$  of Formula 2. EW–LW boundary = the point at which either thin line crosses the thick line (arrow) (see text for further explanation).

tree ring analysis on the entire cross section. If the estimated totals (i.e., those in parentheses) are included, the average number of rings increases to 47, indicating similar maturity of Permian and Triassic trees at time of preservation. The trunk with the largest estimated number of rings 12,389 (~115), is from the forest site on McIntyre Promontory. In addition, this specimen was the smallest of six standing trunks, indicating that mature forests were growing in Antarctica by the mid-Permian ([Taylor et al., 2000](#)). In contrast, the wood from the Skaar Ridge Permian peat includes only one stem with >90 rings, and the rest have fewer than 45. The wood from Fremouw Formation includes four specimens with more than 100 rings and these occur as both peat specimens and isolated trunks in a fluvial sandstone. With the relatively small sample size from the Permian, concluding that trees grew to greater maturity in the Triassic than in the Permian is premature. It is clear, however, that mature trunks can be preserved in silicified peat deposits based on the large number of rings in some of the Triassic woods from the Fremouw peat.

Ring width averaged 2.3 mm in the Permian samples, but only 1.69 mm in the Triassic wood, even though the

Middle Triassic has been reconstructed as warmer than the Late Permian ([Kidder and Worsley, 2004](#); [Woods, 2005](#)). The results obtained in this study, however, are probably skewed by the low number of Permian stems analyzed as well as by the single Permian specimen (15,485) with very large rings. If ring widths from 15,485 are excluded, the average ring width for Permian wood is only 1.66 mm, similar to those from the Triassic. Trees in high latitudes today, e.g. Alaska ([Oswalt, 1950, 1952](#); [Giddings, 1951](#)) or subarctic Manitoba ([Girardin et al., 2005](#)), generally produce <1.0 mm of ring growth each year. The width of the Antarctic tree rings is similar to those produced in a temperate climate rather than a polar climate of today. The size of the fossil growth rings indicates that these trees were growing with adequate water availability and moderate temperatures throughout the growing season. The small proportion of latewood in these fossils ([Figs. 6B, 13B](#)), however, does not occur in any extant species and supports the reconstruction of a growth environment limited by light availability and characterized by a rapid end to the growing season (see 4.6 below). False rings were found in one Permian (15,485) and two Triassic (12,963 and 12,964) specimens and frost rings in only one Triassic (11,475) trunk.



False rings form in extant wood in response to some environmental perturbations—most commonly drought, but also insect attack or partial defoliation. They can be distinguished from true growth rings by the occurrence of thicker-walled cells followed by production of typical earlywood, without a true cessation of growth as is evident at a ring boundary (Fig. 5). The radial rows of tracheids continue through a false ring, but stop at a ring boundary. In addition, false rings are often discontinuous around the circumference of the stem. Frost rings were identified by a disruption in the orderly production of cells by the cambium (Figs. 11, 12).

Frost rings form in extant plants when there is an unseasonable frost during the growing season. Most frost rings occur early in the spring when the cambium is growing rapidly, but can also occur in the early autumn before winter dormancy. Some or all of the cambial cells are killed by the cold and as the meristem begins to recover from this trauma, the first daughter cells are often large and misshapen, and not in well-defined radial rows (Fig. 11). Eventually, the cambium recovers completely and tracheids appear in regular radial files as they did prior to frost ring formation (Fig. 12). Several authors have noted that frost rings are more common in twigs and in young shoots (e.g., Chapman, 1994; Falcon-Lang, 2005a). The Triassic wood that exhibits the frost ring disruption, however, was a large specimen with 53 rings collected from the channel sandstone on Fremouw Peak, so it may have been moved to this location from higher altitudes upstream before fossilization. The presence of false and frost rings indicates that some unseasonal disruption occurred in these environments. The small number of specimens with either type of ring, however, suggests that perhaps unusual climatic events were not a common occurrence.

Comparing values for mean sensitivity (MS), the Permian woods all show  $>0.30$  MS, indicating a seasonal response to climate. The Triassic woods, however, vary from 0.13–0.45 MS, so some would be classified as sensitive (i.e.,  $>3.0$ ), while others are complacent. Unlike the Permian wood, only 52% of the Triassic specimens could be classified as sensitive, suggesting perhaps a more stable growth environment,

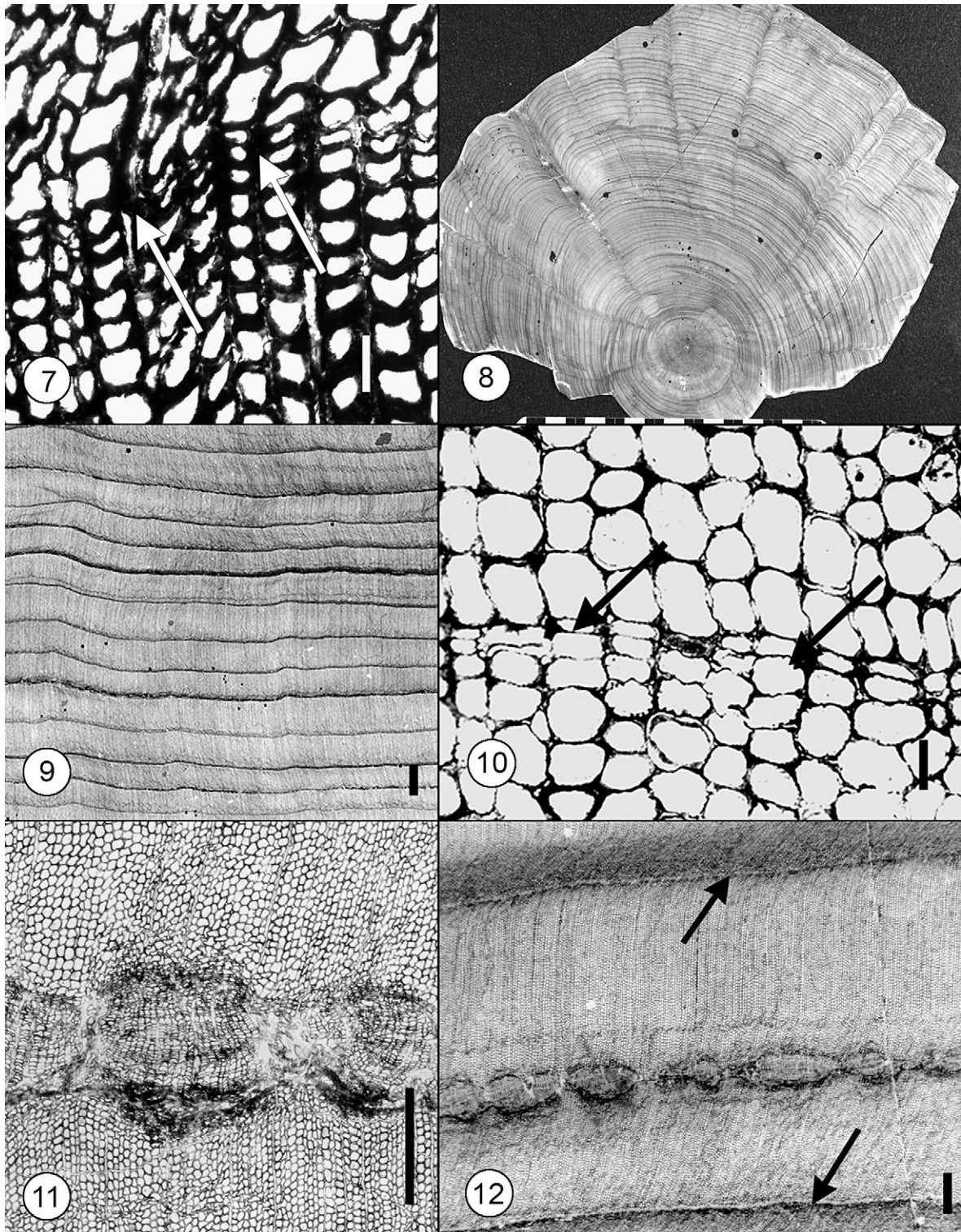
or trees less responsive to climatic changes. The lowest Triassic sensitivities (i.e., in the ‘complacent’ range) occur in samples with very few rings, indicating that perhaps a larger sample taken from a known stem height of more mature specimens is needed for an accurate representation of mean sensitivity. In studies of extant tree rings, the first 50 years of growth are generally excluded from the analysis, due to the variability of growth in the so-called juvenile stages (Fritts, 1976; Schweingruber, 1988). The more mature the tree, the more pertinent the mean sensitivity value is to a tree’s growth response. Excluding those fossil specimens with  $<50$  rings reduces the sample size considerably, but the range of sensitivities is still 0.22–0.45 (mean 0.35).

Ring width is determined both by intrinsic (i.e., genetic) and extrinsic factors. Some trees respond regularly to changes in temperature, water availability, etc. in the environment. Other trees however, record few sensitivity changes throughout the life of that tree (Fritts, 1976). Modern dendrochronology and dendroclimatology analyses are most commonly based on trees at the limit of their growth range, i.e. near treeline, in areas with regular droughts, etc., rather than on trees growing on optimal sites where water availability does not fluctuate much from year to year. Since the Antarctic trees were growing at polar latitudes, it is impossible to speculate on the actual limits of their growth range, although they were growing in an environment with a low angle of sunlight throughout the growing season. The most plausible explanation for the range of sensitivities in the Triassic specimens is that the specimens represented different microenvironments since they were collected from both peat deposits and fluvial sandstones. The range of sensitivity values in the Triassic wood could also be attributed to the presence of more than one natural taxon, each of which may have responded differently to environmental perturbations. All of the wood described in the present study is of the *Dadoxylon*-type, which provides little information on the affinities of the wood except that it is gymnospermous. The diversity of plants from the Triassic peat (Table 1) is much greater than the Permian peat and includes groups that are known to produce large amounts of secondary xylem, e.g.,

Figs. 7–12. Permian and Triassic tree rings. Center of stem towards bottom of figures; outside of stem towards top (all represent peel preparations). Fig. 7. Cross section of Permian wood showing ring boundary (arrows) and small amount of latewood ( $\sim 1$ –3 cells). #13,090B, slide 13,090 $\beta$ , Scale=40  $\mu$ m. Fig. 8. Cross section of Triassic trunk, showing preservation from center of stem and large growth rings. Scale bar in cm. #11,475E. Fig. 9. Cross section of Triassic wood showing fairly uniform ring growth and small amount of latewood before each ring boundary. #11,475E, Scale=2.3 mm. Fig. 10. Detail of Triassic ring boundary showing 1–2 cells of latewood (arrows). #13,007A, slide 13,007 $\alpha$  Bar scale=20  $\mu$ m. Fig. 11. Higher magnification of frost ring in Fig. 12 showing disruption of radial files of tracheids. #11,475A, slide 11,475 $\beta$  Scale=0.5 mm. Fig. 12. Cross-section of Triassic wood showing frost ring (center) and true ring boundaries (arrows). #11,475A, slide 11,475 $\alpha$ . Scale=0.7 mm.

conifers and corystosperms. The Antarctic corystosperms produced wood that was very similar to that of some conifer families (Meyer-Berthaud et al., 1992,

1993; Del Fueyo et al., 1995), making identification of the wood somewhat problematic. To date, however, only corystosperm foliage has been found associated





with large trunks (Del Fueyo et al., 1995; Cúneo et al., 2003). Another explanation for the range of sensitivities in the Triassic samples may be that the local environment was more variable than in the Permian. Even though the plants occurred in a peat-forming environment, there is evidence that the water level in the Triassic peat did fluctuate, based on the presence of *phi* layers in some roots (Millay et al., 1987). These layers are formed in some modern conifers that live in areas with a fluctuating water table (Gerrath et al., 2005).

Ontogenetic age may also be a variable in the wide ranges of mean sensitivity and ring widths seen in some fossil woods. Falcon-Lang (2005b) notes that juvenile wood tends to be more variable in terms of sensitivity when compared with more mature wood. The term ‘juvenile’ is something of a misnomer, as all wood represents mature xylem cells. Juvenile wood is simply the wood which formed during rapid, early growth of the saplings, and is also called crown wood (Larson et al., 2001). This wood typically shows more variability in a number of factors, including ring width. Since we attempted to use standard dendrochronological techniques as much as possible, the innermost rings in axes that contained a core of juvenile wood were excluded from analysis, so this variable was controlled as much as possible in the present analysis. With all of these variables potentially affecting mean sensitivity values, the values in this study represent a base line analysis of mean sensitivity with the knowledge that other factors not accounted for here may be affecting the results.

Given that both the Triassic and Permian plants were growing at very high latitudes in a strongly seasonal environment, the number of cells produced per ring is quite large: an average of 64 in Permian woods (238 max) and 45 in Triassic specimens (104 max), another measure of the favorable environment for tree growth. Francis et al. (1994) found rings with up to 194 cells in Permian wood from the Allan Hills, Antarctica. *Larix sibirica*, a temperate wood found at high latitudes today ( $\sim 70^{\circ}$ – $72^{\circ}$ N), produces <20 cells in a growing season (Taylor and Putz, 1993). This large difference indicates either a longer growing season or more favorable conditions for growth, i.e., readily available water and higher temperatures for the Antarctic fossil wood than high-latitude extant trees. Francis et al. (1994) estimated a growing season of at least 48 days during the late Early Permian in Antarctica based on Creber and Chaloner’s (1984) measurement of the production of up to four cells per day in some extant spruce. Among living trees at high latitudes, Oswalt (1960) found that the cambium produced cells for only 50–60 days at one site in Alaska,

whereas an even shorter growing season ( $\sim 30$  days) was measured at another site (Giddings, 1942). The calculated growing season for the present study would be at most 58 days in the Permian and 26 days in the Triassic, based on a maximum growth rate of four cells per day. Gregory and Wilson (1968), however, found that the same species (*Picea glauca*) growing in Alaska and New England produced the same number of cells each growing season, even though the growing season in Alaska was about half as long. They found that the cambium in the Alaskan trees had a higher rate of cell production. Based on these results, it is difficult to estimate the length of the growing season based only on wood production. The large number of cells in the fossil wood, however, indicates that Antarctica’s growing season in both the Permian and Triassic was longer than that seen at high latitudes today, which has important implications for understanding the environmental factors that limited tree growth during times of global warmth vs. today (see below).

#### 4.2. Earlywood–latewood boundary

The Permian and Triassic woods from the CTM exhibit relatively wide growth rings indicating overall favorable growing seasons during both time periods. More importantly, the structure of the rings is fundamentally different from temperate or high-latitude rings produced in extant plants, as the fossil rings consist almost entirely of earlywood with only a small proportion of latewood. There has been much discussion in the literature on determining the EW–LW boundary in tree rings (e.g., Creber and Chaloner, 1984; Denne, 1989, and papers cited therein). Creber and Chaloner determined the boundary by graphing the cumulative sum of deviations from the mean (CSDM) radial cell diameter across a ring; the point at which the CSDM curve declined toward zero was designated as the boundary (Fig. 6A, arrow). Dendrologists and wood anatomists have traditionally determined the EW–LW boundary by the ratio of cell wall thickness to lumen diameter (Mork, 1928; Denne, 1989). In Denne’s (1989) two interpretations of Mork’s (1928) definition, using Formula 2 results in no latewood being present in any of the Antarctic specimens (Figs. 6B, 13B). Using Formula 1, latewood ranges from 0–10% in the Permian wood (Fig. 6B) and 0–12% in the Triassic wood (Fig. 13B). Comparing the method of Creber and Chaloner (1984) with that of Mork’s more commonly used definition (as detailed in Denne, 1989) (Figs. 6, 13), it is clear that the two techniques produce very different results for percent latewood. For example, specimen 15,485 (Permian), would have 50–70 cells of latewood,

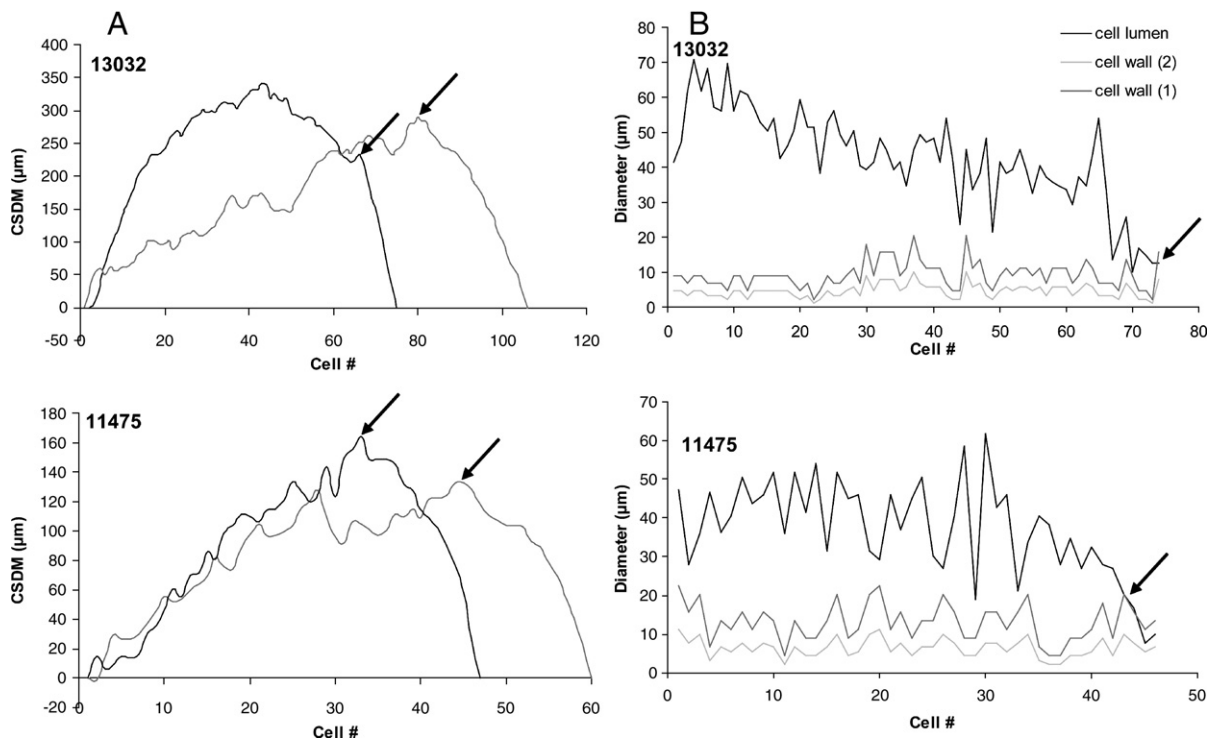


Fig. 13. Different methods of calculating EW–LW boundary using Triassic fossil wood (Fremouw Peak). A. CSDM method (Creber and Chaloner, 1984). The two graphs show results for two specimens (black and grey lines). EW–LW boundary=the point at which each line turns toward zero (arrows). B. Denne's (1989) two methods. Thin grey line=2a, Formula 1; thin black line=2c, Formula 2. EW–LW boundary=the point at which either thin line crosses the thick line (arrow) (see text for further explanation).

which equates to 21–30%, according to Creber and Chaloner's method, but only 4–5 cells using Mork's definition, or 1.7–2.1% (Formula 1 of Denne, 1989). Creber and Chaloner used the CSDM method mainly to determine EW–LW boundary, but they also correlated ring types with certain environments. These ring types (Creber and Chaloner, 1984; Types A–E, O) were based on the trend line calculated from the radial cell diameter only, and not the CSDM curve; the description in the text (Creber and Chaloner, 1984, p. 371), however, does not always match the graphical representation of the types (pp. 372–373). Brison et al. (2001) provided drawings and interpretations of Creber and Chaloner's (1984) ring types but several of these (e.g., Types A, D, and E) are defined differently from Creber and Chaloner (1984) and are sometimes contradictory. For example, Type A of Creber and Chaloner (1984, p. 371) was originally described as having few latewood cells, although their Fig. 5 illustrates a ring with few earlywood cells, and ~69% latewood. Brison et al. (2001) describe Type A as containing few earlywood cells. Types D and E of Creber and Chaloner (1984) were based on the appearance of the ring boundary (distinct vs. faint), whereas Brison et al.

(2001) differentiated these two types based on an EW–LW transition that was distinct or faint. Much of the difficulty in defining these ring types is due to the use of the CSDM calculation, which includes only radial cell diameter changes, to define the EW–LW boundary. By

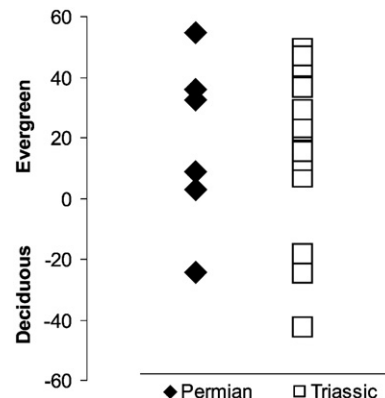


Fig. 14. Calculation of evergreen vs. deciduousness of Antarctic woods using method of Falcon-Lang (2000). Each point represents the difference between the apex of the CSDM curve (see Figs. 6, 13) and the center of the curve (percentage 'skew' of Falcon-Lang) for a single specimen.



using only this measurement, changes in wall thickness and lumen size, two factors known to vary strongly with environment, were not considered in these earlier analyses. For these reasons and others discussed below, we have calculated the EW–LW boundary in the Antarctic fossil wood using Mork's definition (Formula 1 of Denne, 1989).

#### 4.3. *Deciduous or evergreen?*

The interpretation of fossil leaf deposits as representing seasonally deciduous vs. evergreen plants, i.e. those with leaves that remain attached for more than one growing season, is important to paleoenvironmental reconstructions and has been discussed by a number of authors and analyzed from a variety of perspectives. Spicer and Chapman (1990), based on examination of high-latitude floras throughout the Phanerozoic, noted that deciduous plants dominated very high latitudes during times of global warmth, while evergreens were more common during icehouse phases of Earth's climate, such as today. In an attempt to develop a more quantitative method of determining deciduousness in fossils, Falcon-Lang (2000) proposed a method to distinguish between evergreen and deciduous gymnosperms based on the CSDM equation. In the present study, there were only three Permian and eight Triassic samples that were sufficiently preserved to use Falcon-Lang's method. The results span both the evergreen and deciduous ranges (Fig. 14), i.e., above and below the midpoint of the CSDM curve, respectively ( $=0$  in Fig. 14). It is possible, though unlikely, that some of the Triassic wood may represent a different taxon. In the Permian peat from Skaar Ridge, *Glossopteris* is the only woody gymnosperm present. Although *Noeggerathiopsis* leaves and associated wood have been described from the Bainmedart Coal Measures of East Antarctica (McLoughlin and Drinnan, 1996; Weaver et al., 1997), this plant has not been found in the CTM, so different systematic affinities cannot explain these unusual results. There is a great deal of overlap in the ranges for the various species examined by Falcon-Lang (2000; see also Falcon-Lang, 2005a for results from a single tree). For the reasons noted above, and because of the wide variance in our results using this technique, we believe it is problematic to extrapolate this method to fossil woods.

Royer et al. (2003) performed growth chamber experiments and developed a model that simulated light conditions at 69°N and temperatures of the Late Cretaceous–early Paleogene. This study concluded that evergreen plants at this latitude had a slight advantage

over deciduous ones, based on above-ground carbon budget only. More recent work suggests that the carbon budget for evergreen and deciduous trees at high latitudes is similar (Royer et al., 2005), but is distributed differently throughout the year. Deciduous trees exhibited a flux of carbon uptake in late summer, which helped to counterbalance the carbon loss from leaf shedding. These authors note that the presence of high-latitude deciduous plants cannot be explained by carbon budget alone and conclude that without modern analogs, it is difficult to explain how apparently deciduous fossil trees thrived, or to prove experimentally whether deciduous or evergreen trees are more likely to be present at these very high latitudes (Falcon-Lang, 2000; Royer et al., 2003). Both carbon and nitrogen budgets are often measured in extant forests, so these results may be a limitation of the particular models used. Interpretation of deciduous vs. evergreen status has been based traditionally on the presence of leaf mats and especially the occurrence of large deposits of leaves in the 'fall' layers of varved deposits (Spicer, 1989). *Glossopteris* leaves have been found in varved sediments (e.g., Plumstead, 1958; Gunn and Walcott, 1962; Retallack, 1980) and occur in mats in the permineralized peat from the CTM. Spicer and Parrish (1986) and Spicer (1989) found that leaves that are abscised in response to cold tend to accumulate in mats due to a lower rate of decay. Since the Antarctic material is permineralized it is also possible to look for anatomical evidence of seasonal deciduousness such as abscission layers. Meyer-Berthaud et al. (1992, 1993) described a layer of periderm beneath the leaf bases in *Kykloxylon*, the young stem which bore *Dicroidium* leaves, in the Triassic peat from the Fremouw Formation. This periderm was interpreted as functioning similarly to an abscission layer in that transport to the leaf would have ceased after formation of these cells. Thus, the anatomical and sedimentologic data suggest that both the *Glossopteris* and *Dicroidium* 'plants' from Antarctica were seasonally deciduous. Anatomical evidence, either in the leaf base or the stem itself, remains the most exacting method for determination of deciduousness, but unfortunately this level of preservation is rare.

#### 4.4. *Other fossil wood from Antarctica*

Petrified or permineralized wood occurs at a number of localities in Antarctica, both on the continent and the Antarctic Peninsula. Fossil forests in growth position have been described from Alexander Island (Jefferson, 1982) on the Peninsula and from the central Transantarctic Mountains. The Alexander Island forest is Early

Cretaceous whereas the forests from the CTM are Late Permian (Mt. Acherar; Taylor et al., 1992) and Middle Triassic (Gordon Valley; Cúneo et al., 2003). *Glossopteris* wood and logs are widespread in the Permian fluvial coal measures of Antarctica. Well-preserved Early Permian wood with growth rings from the Allan Hills, southern Victoria Land, was analyzed by Francis et al. (1993). The ring structure of both the Allan Hills wood and the Late Permian wood from CTM presented in this study appear very similar. Specimens from both localities exhibit relatively large rings with a small proportion of latewood. The Allan Hills wood exhibited many more cells per ring (115, 141, and 194 cells/ring) than the Skaar Ridge specimens (36–91 cells/ring), but ring widths are similar due to differences in tracheid diameters. Tracheids in wood from Skaar Ridge (mean 81  $\mu\text{m}$ ) are almost three times the diameter of those in the Allan Hills wood (mean 30  $\mu\text{m}$ ). Although the Skaar Ridge site has been reconstructed at a slightly higher paleolatitude, it is difficult to explain why trees from the Early Permian (Allan Hills) produced more cells each season than those from the Late Permian since the paleoclimate of the Early Permian was colder (e.g., Krull, 1999; Isbell et al., 2001; Rees et al., 2002; Isbell et al., 2003a; Montañez et al., 2007), unless there were local environmental factors that contributed to the difference.

The wood described from a small standing fossil forest in the Upper Permian on Mt. Acherar in the CTM (Taylor et al., 1992) is similar in overall growth ring anatomy to the material from Skaar Ridge, as it contains only 1–3 cells of latewood per ring. The Mt. Acherar wood, however, represents young trees, which are known to grow very rapidly, so ring width is large (mean 4.5 mm) and the number of cells per ring is extremely large (~350–400).

Well-preserved *Dicroidium* foliage and a standing forest have also been described from the Middle Triassic of Antarctica, from the upper part of the Fremouw Formation in Gordon Valley, CTM (Cúneo et al., 2003). This material is of equivalent age to the permineralized peat from Fremouw Peak. Large stumps with up to 86 rings and ring widths of 0.92–2.54 mm were recorded with each ring having very little latewood. Gabites (1985) examined tree rings from silicified Middle Triassic wood collected from fluvial deposits of the Lashly Formation, Member B in the Allan Hills. Ring widths ranged from 0.49–2.12 mm and all were classified as complacent based on mean sensitivity calculations (0.15–0.27). Gabites (1985) also described wood from Member C of the Lashly (Late Triassic). Ring widths for the two specimens examined ranged from 0.32–0.57 mm and both were classified as sensitive. Ring widths in the

present study are similar to those studied by Cúneo et al. (2003) and Gabites (1985). Growth response of these plants to the environment was very similar, even though the climate in Antarctica was changing.

#### 4.5. Permian–Triassic paleoclimate in Antarctica

From the Permian into the Triassic, Gondwana was in transition from an icehouse to a greenhouse climate as the Late Carboniferous–Early Permian glaciation waned and ecosystems began to recover. These changes have proved a challenge when correlating paleoclimate based on physical models with that based on paleobotanical data. Paleoclimate models for the Late Permian generate temperatures at low latitudes that agree with paleobotanical evidence (e.g., Kiehl and Shields, 2005), but high-latitude reconstructions show discrepancies between the models and paleobotanical data. Rees et al. (2002) noted that their model for the Late Permian (Wordian), which predicted a tundra environment at high southern latitudes, did not match the paleobotanical data even at 8X present-day  $\text{CO}_2$  levels. Although Antarctica may have been a tundra environment in the Late Permian, the wide geographical range of the woody *Glossopteris* plant argues against this hypothesis. In the earliest models, Antarctica was reconstructed as a glacial–tundra environment (Crowley et al., 1987). Yemane (1993) suggested that these high-latitude climates could have been milder than model predictions if continental interiors included either large lakes or possibly interior seaways. Climate can also be ameliorated by the type of vegetation present, as illustrated in a simulation model of high latitudes during the latest Cretaceous (Otto-Bliesner and Upchurch, 1997; Upchurch et al., 1998). By including a forest biome rather than tundra in the model parameters, feedback from albedo changes produced a much warmer climate at high latitudes (+4.1–4.2 °C in the Northern Hemisphere; +3.4 °C in the Southern) and globally (+2.2 °C). More recently, Kiehl and Shields (2005) produced a paleoclimate model for the Permian that incorporated a number of additional factors, such as a fully coupled land and ocean system, as well as paleogeographic features and high  $\text{CO}_2$ . Their model produced warmer temperatures at high latitudes than any previous simulations, with a mean annual temperature at these latitudes of ~10 °C. As paleoclimate modeling becomes more sophisticated, resolution between the biological data and the model simulations is converging.

Triassic climate reconstructions for the Antarctic region based on physical models have generally agreed

with paleobotanical data, including the results of tree ring analysis. During the Middle Triassic, the central Transantarctic Mountains area has been reconstructed as a warm-temperate climate capable of supporting trees (Retallack et al., 1996). The Triassic was the beginning of a continuing warm period in Earth's history and no severe climate changes (i.e., icehouse conditions) occurred throughout the Mesozoic. During the Triassic the CTM were at slightly lower latitudes than during the Permian (Powell and Li, 1994; Grunow, 1999). With the formation of Pangea, continental interiors have been modeled as arid (Crowley et al., 1989), yet tree growth in the CTM suggests that these plants did not experience extremes of either drought or cold.

There is little difference in the amount of wood produced in trees from the Late Permian and the Middle Triassic, and no difference in the structure of the rings themselves. This is surprising given the large differences in paleoclimate that are suggested not only by physical models, but also by the greater diversity of plants in Middle Triassic floras from Antarctica. Perhaps the similarities in wood growth suggest that the Late Permian in Antarctica was warmer than any model has yet predicted, although floral diversity does not support this hypothesis. Isbell et al. (2003a,b) have hypothesized that the model of a massive ice sheet centered on the CTM no longer fits the more recent paleontological and sedimentary data (see also Babcock et al., 2002). Evidence emerging from Australia also supports a reconstruction of discrete glacial events with periods of interglacial or periglacial conditions (Fielding et al., 2005; Montañez et al., 2007); these studies, however, have concentrated on the Late Carboniferous–Early Permian and not the Late Permian. For many years, low floral diversity in the Permian of Gondwana has been attributed to a cold climate, and vice versa, with no independent data to corroborate this theory. The glossopterids moved in rapidly after the retreat of the ice sheet and perhaps remained dominant throughout the Permian in Antarctica because once established, their densely borne, large strap-shaped leaves shaded out competitors (Taylor, 1996). While these generalists were able to colonize almost all environments in the Permian of Gondwana, the series of climate perturbations that occurred around the *P–T* boundary, including the continuously warming climate, may have contributed to their extinction. As the temperate glossopterid forests disappeared, more warm-adapted seed ferns colonized Antarctica, perhaps migrating from lower latitudes (Kerp et al., 2006), resulting in a large increase in plant diversity through the Triassic. Although the variety of plants growing during the Middle Triassic of Antarctica is vastly different from

the Late Permian, the ring structure clearly indicates that these plants were responding to their environments in a similar way, providing evidence that other factors besides temperature were limiting tree growth during these time periods.

#### 4.6. Interpretation of tree growth at high latitudes

In order to understand the unique structure of the Antarctic tree rings and interpret its meaning, it is important to examine modern tree growth and wood production in the context of physiological ecology. Tree rings from Antarctica all have a similar structure of predominantly earlywood with a small amount of latewood produced at the end of the season. This structure, coupled with the high paleolatitudes of these floras, supports the hypothesis that woody plants in both the Late Permian and Middle Triassic of Antarctica were limited by light, rather than by a combination of temperature and water availability as are woody plants at high latitudes today.

In a series of classic papers, Larson (1960, 1962) and subsequently others (e.g., Lindstrom, 1996) showed that earlywood production in conifers is correlated with elongation growth in the apical meristems and consequent high auxin levels, whereas latewood production is correlated with cessation of terminal growth and the resulting lower auxin concentrations in the cambium. In temperate zones today, changes in day length during the growing season are involved in triggering this change (Larson, 1962). At very high latitudes, however, day length during the summer is continuous. With no substantial changes in day length, Larson's physiological model suggests that wood production at polar latitudes should exhibit continuous production of earlywood, as long as other factors are not limiting to growth. In modern boreal woody plants, however, temperature and water availability are limiting factors, and woody plants do not grow above  $\sim 72^\circ\text{N}$  latitude (lower in the southern hemisphere), so day length does change during the growing season. In the higher latitude forests of Antarctica, however, the ring structure demonstrates that these plants continued elongation growth throughout the growing season, ceasing only at the very end of the summer, at which time the few rows of latewood cells (1–5) would have been produced. Using Mork's traditional method to calculate EW–LW boundary, this type of growth is clearly evidenced in the Antarctic woods—large amounts of earlywood followed by a very low percentage ( $\sim 0$ –12%) of latewood before the ring boundary. Using the method outlined by Creber and Chaloner (1984), however, it is difficult to

reconcile up to 59% latewood (for both Permian and Triassic wood) with the physiology of tree growth in this extreme environment. With almost half of the ring latewood, elongation growth would have had to cease in the middle of the growing season, yet there is no evidence of cell wall thickening, as normally found in latewood, until the very end of the season, i.e., the last few cells in the ring. For these high-latitude woods, the traditional calculation of the EW–LW boundary provides a more accurate interpretation of tracheid production and tree growth than the method utilized in many previous studies of fossil tree rings.

Using Larson's (1962) model, the small amount of latewood in Antarctic wood, and that seen in other high-latitude woods (e.g., Parrish and Spicer, 1988), can be attributed to a growing season which ended only as a result of inadequate light levels for photosynthesis (Taylor et al., 1992; Francis et al., 1993), rather than by a combination of water and temperature as in modern boreal forests. At these paleolatitudes, this physiological switch must have occurred as the sun, already low on the horizon, moved rapidly below the horizon, at which time photosynthesis could not occur, triggering leaf drop and winter dormancy. Experimental studies and models have shown that given temperatures above freezing, trees are capable of surviving winter darkness (Read and Francis, 1992; Beerling and Osborne, 2002; Royer et al., 2003), although cold, dark winters are more easily tolerated (Read and Francis, 1992).

## 5. Conclusions

Paleobotanical evidence, sedimentological analyses, and physical models are increasingly resolving reconstructions of past climates. In spite of the advances in these disciplines, problems remain in data interpretation. As demonstrated by this analysis of Late Permian and Middle Triassic tree rings from Antarctica, it is important to include aspects of the growth and physiology of plants when considering paleoclimate reconstructions. This is especially critical when no modern analogue environment exists, as with these polar latitude fossil forests.

Research on modern wood has shown that the proportion of earlywood to latewood in growth rings is generally correlated with environmental factors. Thus, the position of the EW–LW boundary is important in extrapolating environmental parameters, such as growing season, for fossil woods. We have shown here, however, that some previous studies have defined this boundary incorrectly. Using Mork's (1928) and Denne's (1989) standard technique to define the EW–LW boundary yields paleoenvironmental hypotheses which corre-

late well with observed wood anatomy. The occurrence of anatomically preserved plants and wood samples in permineralized peat from Antarctica offers an opportunity to examine both primary and secondary plant growth and development within a climatic regime that does not exist today. Parameters controlling high-latitude growth today (water availability and temperature) are different from those in periods of global warmth (light levels), indicating that many factors, individually or jointly, can control a tree's response to the environment. As more plants from these sites are reconstructed and ideas about the composition of the community and ecosystem refined, it should be possible to better understand not only deep-time climates, but also how plants of the past responded to these unique environmental conditions.

## Acknowledgements

Based upon work supported by the National Science Foundation (OPP-0126230, OPP-0229877). We thank past members of Antarctic field parties for field work and helpful discussions, especially N.R. Cúneo, Museo Paleontológico E. Fergulio, Trelew, Argentina; J. Isbell, University of Wisconsin-Milwaukee; and T.N. Taylor, University of Kansas. We also thank J. Ward and C. Springer, University of Kansas, for interesting discussions on ecophysiology and two anonymous reviewers for helpful comments and suggestions. Special thanks to David Buchanan and Tim Culley, who collected the trunk from McIntyre Promontory, with the assistance of Helicopters New Zealand.

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