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# In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: paleoenvironmental setting and paleoclimate analysis

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## Abstract

A structural and ecological study of a standing Triassic forest containing 99 silicified trunks from the Fremouw Formation of Antarctica is detailed. Utilizing quantitative methods, forest density, total forest cover per hectare, mean separation of trees, and basal area per stump were obtained. This information, integrated with sedimentologic, taxonomic, fossil wood, and biomechanical data, has allowed the reconstruction of a plant community that grew at very high paleolatitudes ( $\sim 70\text{--}75^\circ\text{S}$ ). The paleoforest grew along river banks (levees) and within proximal floodplain environments, where a taphocoenosis of permineralized stumps and compression–impression foliage of the *Dicroidium* type has been preserved. In particular, the intimate association of this leaf type with dense, conifer-like wood provides additional confirmation that the *Dicroidium* foliage morphotype was attached to several types of stems. This riparian forest stand was apparently in a mature stage prior to the beginning of preservation. Tree ring analysis, as well as additional indirect evidence, indicates that this Middle Triassic ecosystem in Antarctica experienced a season very suitable for plant growth resulting from an overall favorable climatic regime. This conclusion contrasts with earlier paleoclimate models based on physical parameters in which temperature ranges would make plant or animal growth at these latitudes almost impossible. Finally, Antarctic climatic change from latest Permian through Late Triassic is considered in the context of tectonic and paleogeographic reconstructions of the East Antarctic craton.

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## 1. Introduction

The central Transantarctic Mountains include a number of localities with exquisitely preserved fossil plants, including both compression sites with cuticles (Boucher et al., 1993) and permin-

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eralized peat deposits (Taylor et al., 1989). The present contribution is concerned with the characteristics of the vegetation in a Triassic ecosystem, and is part of a more comprehensive, interdisciplinary approach that was begun with work on the Permian floras in Antarctica (Cúneo et al., 1993), including a Permian in situ forest deposit (Taylor et al., 1992). This method integrates sedimentologic information, which can be used to define depositional settings and taphonomic events (including burial processes of different plant organs), with taxonomic and ecological data, in order to provide a more complete representation of ancient plant community structure.

The present study concentrates on an in situ Triassic forest deposit in the central Transantarctic Mountains, and includes data from paleoforestry, fossil tree rings, and plant biomechanics. Paleoclimate interpretations based on a complete evaluation of the geological and paleobotanical data are also provided. Since relatively little is known about any Triassic ecosystems in Antarctica, this analysis attempts to generate a comprehensive framework upon which succeeding studies can be built. With these baseline data, it will be possible to better understand changes that affected Antarctic ecosystems during times of environmental transition, such as near the Permian–Triassic boundary. The Paleozoic–Mesozoic transition in the Southern Hemisphere was catastrophic for the biosphere, and can be correlated with geologic events, paleoclimate changes and landscape alterations. These differences were reflected in the change in flora from *Glossopteris*-dominated in the Permian to the *Dicroidium*-dominated floras of the Triassic. This condition is different from that in the Northern Hemisphere, where important groups such as the conifers and peltasperms were already present in the Permian and continued to expand into the Triassic (Kerp, 1996). In the Southern Hemisphere, including Antarctica, a different scenario can be envisaged (Archangelsky, 1996) in which the new biotic relationships that developed from the Early/Middle Triassic onwards played a key role for the rest of the period, and probably longer. In this paper, we reconstruct a Middle Triassic forest within its eco-

Table 1  
Gordon Valley forest stumps, transect 1, closest individuals to the point center (stations)

Station	Quadrat	Distance (m)	Diameter (m)
A	1	4.88	0.51
	2	1.83	0.35
	3	9.15	0.28
	4	3.66	0.23
B	1	2.74	0.18
	2	2.82	0.18
	3	5.10	0.18
	4	3.96	0.13
C	1	8.53	0.23
	2	6.10	0.25
	3	3.66	0.25
	4	2.90	0.23
D	1	0.92	0.61
	2	4.88	0.25
	3	10.52	0.25
	4	0.82	0.25
E	1	0.51	0.20
	2	7.01	0.18
	3	4.72	0.36
	4	7.47	0.36
F	1	9.15	0.30
	2	5.64	0.15
	3	8.23	0.18
	4	8.84	0.20
G	1	6.40	0.20
	2	10.36	0.36
	3	4.12	0.15
	4	7.77	0.30
H	1	4.90	0.25
	2	3.66	0.20
	3	4.27	0.36
	4	6.86	0.20
I	1	5.64	0.41
	2	2.74	0.56
	3	5.18	0.20
	4	12.65	0.28
J	1	11.74	0.38
	2	4.57	0.61
	3	6.71	0.56
	4	7.62	0.20
K	1	6.86	0.38
	2	10.36	0.20
	3	0.91	0.51
	4	–	–
L	1	10.67	0.36
	2	3.73	0.36
	3	6.71	0.20
	4	10.06	0.38
M	1	–	–
	2	1.35	0.28
	3	8.23	0.28
	4	10.52	0.36

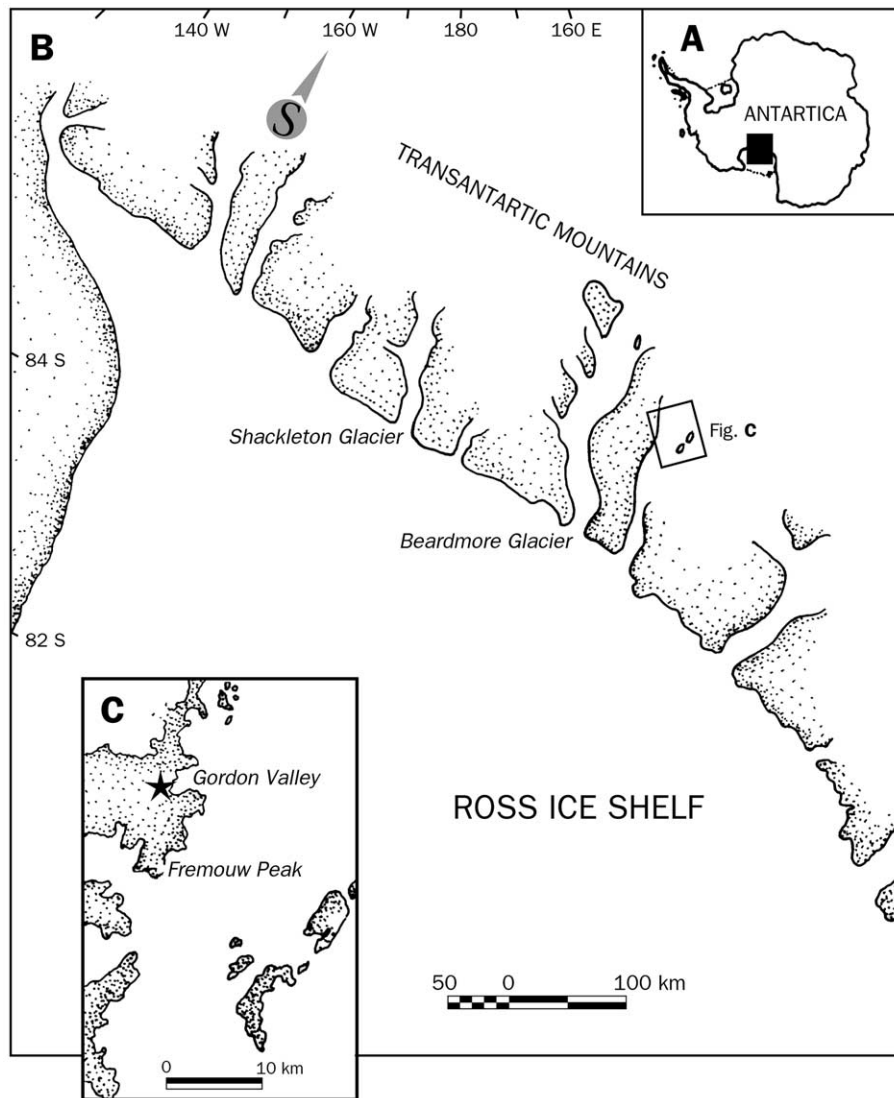


Fig. 1. Location map showing the Gordon Valley locality. Modified from [Hammer \(1990\)](#).

logical context, based on data from tree rings, forest structure, and sedimentology.

## 2. Materials and methods

Field work in the upper Gordon Valley ( $84^{\circ}22'23''\text{S}$ ,  $164^{\circ}37'56''\text{E}$ ; [Barrett and Elliot, 1973](#)), Beardmore Glacier region ([Fig. 1](#)), was carried out during the 1990–1991 Antarctic field sea-

son. Silicified stumps and compressed leaves occur near the top of the upper member of the Fremouw Formation (Beacon Supergroup). The section ([Fig. 2](#)) was first analyzed for its fossil plant distribution, and sedimentologic control was established in order to define taphonomic conditions for the paleovegetation. For this phase of the study a facies analysis was carried out by defining origin and evolution of sedimentary deposits and incorporated plant parts. On this basis, the

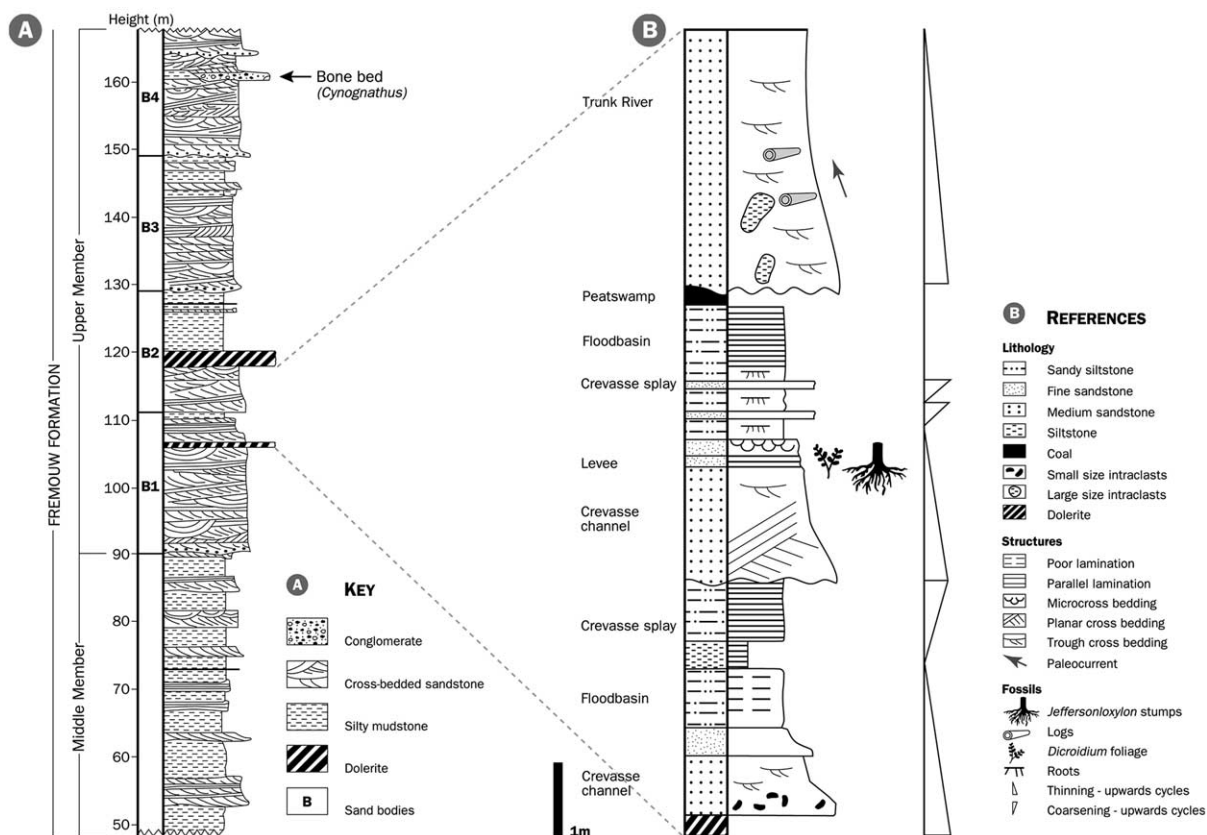


Fig. 2. (A) Lithostratigraphic section of the Fremouw Formation (middle to upper members) at Gordon Valley (modified from Macdonald et al., 1991). (B) Detailed section of part of the upper Fremouw Formation showing distribution of plant horizons.

biostratigraphy of fossil plant horizons was interpreted.

Plant content was analyzed in several ways. First, the density of the in situ permineralized stumps, which occur in two groups on a single stratigraphic level, was measured using the point-centered quarter method (Cottam and Curtis, 1956). This method is used in modern forests and is particularly effective for monodominant stands. An initial transect is made through the stand, and point stations spaced 10 m apart are marked along this line. Each point station is crossed by an imaginary perpendicular line which divides the space into four quadrats (Fig. 3). The distance from each point station to the closest individual stump is then measured for each of the four adjacent quadrats (Tables 1 and 2). At

the Gordon Valley site, two approximately parallel transects 50 m apart were made (Fig. 3A).

Stem diameter was also measured for each stump (Tables 1 and 2). When recorded on modern trees, the diameter is usually taken at breast height, a condition rarely found in standing fossil forests. In the case of the Gordon Valley forest, the diameter was measured at the top of the preserved trunk, being careful to avoid the flare of lateral roots (Plate I, 2). This technique did not affect the accuracy since the diameter at the preserved height of the stumps did not seem to vary markedly from the diameter at chest height, as measured on nearby horizontal trunks. Estimated tree heights were calculated on the basis of regression equations (Niklas, 1994) using known stump diameters (Fig. 4). Parts of six large stumps were

Table 2  
Gordon Valley forest stumps, transect 2, closest individuals to the point center (stations)

Station	Quadrat	Distance (m)	Diameter (m)
A	1	4.57	0.28
	2	3.73	0.36
	3	4.28	0.33
	4	1.22	0.15
B	1	6.40	0.30
	2	5.87	0.25
	3	5.94	0.36
	4	11.18	0.25
C	1	10.06	0.30
	2	2.90	0.18
	3	3.35	0.25
	4	2.82	0.30
D	1	5.33	0.30
	2	–	–
	3	6.86	0.18
	4	7.32	0.30
E	1	6.10	0.30
	2	–	–
	3	–	–
	4	11.43	0.30
F	1	6.86	0.23
	2	–	–
	3	–	–
	4	9.45	0.30
G	1	7.62	0.28
	2	2.90	0.36
	3	–	–
	4	2.90	0.23
H	1	4.88	0.28
	2	14.02	0.20
	3	6.10	0.36
	4	1.68	0.28
I	1	2.52	0.20
	2	5.03	0.23
	3	15.55	0.20
	4	5.94	0.28

collected and sampled for tree ring analysis and wood anatomy.

Stems were sectioned and cellulose acetate peels made of each surface after etching in concentrated hydrofluoric acid. The number of trunks that could be collected for anatomical analysis (six) was limited not only by the size and weight of the individual logs, but also by deteriorating weather conditions which prevented further collecting at the site.

For the plant remains preserved around the base of the stumps as compression–impressions, the quadrat method of [Scott \(1978\)](#) was utilized to determine percentage of plant cover on the bedding plane. This technique consists of clearing off an exposure and applying a 50 × 50 cm square quadrat containing 100 random points over the bedding plane. The presence and identity of plant remains underneath each point are recorded in order to obtain the percentage cover of each species in the quadrat. This process was repeated five more times following a random pattern along the same bedding plane, giving an estimate of plant cover as well as amount of variation in the paleo-leaf litter ([Table 3](#)).

All specimens are deposited in the Paleobotany Division, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS 66045-7534, USA.

### 3. Geologic setting

The Fremouw Formation has yielded a diverse taphoflora from a high paleolatitude, including the present permineralized forest in the upper Gordon Valley. The formation is up to 700 m thick and particularly well exposed in the Beardmore Glacier area (central Transantarctic Mountains) ([Fig. 1](#)), where the type locality (Fremouw Peak) occurs. First recognized by [Barrett \(1969\)](#), the Fremouw Formation consists of interbedded sandstone and mudstone, and has been informally divided into three members, based on the proportion of sandstone present ([Barrett et al., 1986](#)). Overall, the formation represents an alluvial plain depositional system within an elongated sedimentary basin ([Collinson et al., 1994](#)); paleocurrents are predominantly northwestward ([Barrett et al., 1986](#)). In general, fluvial deposits become sandier from lower to upper parts of the formation. These deposits are considered to originate from braided streams and are particularly well developed in the upper sections. The upper member, especially interesting because of its paleobotanical content (e.g., [Taylor and Taylor, 1990](#)), includes volcanoclastic sandstone bodies intercalated with siltstone and silty mudstone in Gordon Valley ([Isbell and](#)

Macdonald, 1991). Isbell and Macdonald (1991) suggest that the upper Fremouw member at Gordon Valley, which contains the fossil forest, is a series of superimposed fluvial channels deposited by low-sinuosity braided streams. Both vertebrates and fossil plants are abundant in the Fremouw Formation. Elements of the *Lystrosaurus* fauna have been recorded from the lower Fremouw (Cosgriff et al., 1982), and an interesting fauna containing *Cynognathus* has been described from the top of the upper Fremouw in Gordon Valley, above the fossil forest (Macdonald et al., 1991; Isbell and Macdonald, 1991; Hammer, 1995). Floral remains (*Dicroidium* flora) are found in most of the sequence, but are most abundant in the middle and upper parts (Barrett et al., 1986; Smoot et al., 1987). A permineralized peat at nearby Fremouw Peak occurs near the top of the upper member (Taylor et al., 1989) and has yielded a number of well preserved plant remains (Taylor and Taylor, 1990; Taylor et al., 2000). Palynomorphs within the peat indicate an early Middle Triassic (Anisian) age for this part of the section (Farabee et al., 1990). Kyle and Fasola (1978) and Kyle and Schopf (1982) proposed a Middle Triassic age for the upper member of the Fremouw on the basis of correlation with palynomorph assemblages from the Lashly Formation in southern Victoria Land, Antarctica (Kyle, 1977).

The vertebrate fauna from the upper Fremouw in Gordon Valley includes a mixture of late Scythian (late Early Triassic by correlation with South African faunas) and newer forms (Hammer, 1995). Hammer (1995) suggests that this part of the Fremouw could be Anisian (early Middle Triassic), which correlates well with the palynomorphs from the permineralized peat. The fossil forest lies 50 m below the *Cynognathus* ho-

rizon and is interpreted as equivalent to the permineralized peat from Fremouw Peak; thus it is probably early Middle Triassic. As is true of a number of Antarctic terrestrial deposits, the Fremouw Formation as a whole is poorly constrained, especially when compared to Triassic biostratigraphy on other continents. By comparison, the overlying Falla Formation, which also contains compression fossils (Boucher et al., 1993) and vertebrates (Hammer and Hickerson, 1994), is well dated as Late Triassic to Early Jurassic, based on the intercalation of radiometrically dated dykes of the Kirkpatrick Basalt/Hansen Formation (Elliot et al., 1985).

#### 4. Sedimentology

The Fremouw Formation at Gordon Valley is represented by a section including the middle and upper members (Fig. 2A) with a total thickness of 167 m (Macdonald et al., 1991; Isbell and Macdonald, 1991). Based on sedimentary structures, channel forms, paleocurrent patterns and the absence of large-scale, lateral-accretion bedding, the upper member of the Fremouw Formation was interpreted as a series of stacked fluvial channels deposited by low-sinuosity braided streams (Isbell and Macdonald, 1991). The partial section of this member in which the silicified stumps occur intercalates between the two basal sandstone bodies of the upper member (Fig. 2) and is secondarily bounded by two Jurassic dolerite sills. This section was analyzed in detail and includes volcanoclastic and siliciclastic deposits with coarse-, medium- and fine-grained sandstones, siltstones, claystones and a lenticular coal bed. In total, this part of the section (Fig. 2B) is 7.5 m thick, and shows two small, fining-upward cycles and

Table 3  
Percent cover of the compression–impression assemblage

Quadrat No.	1	2	3	4	5
<i>Dicroidium</i> spp.	52	48	49	55	43
Unidentifiable stems	6	6	6	6	8
Plant debris	4	7	4	7	14
Total cover area (%)	62	61	59	68	65

*Dicroidium* spp. = *D. crassinervis*+*D. stelznerianum*.

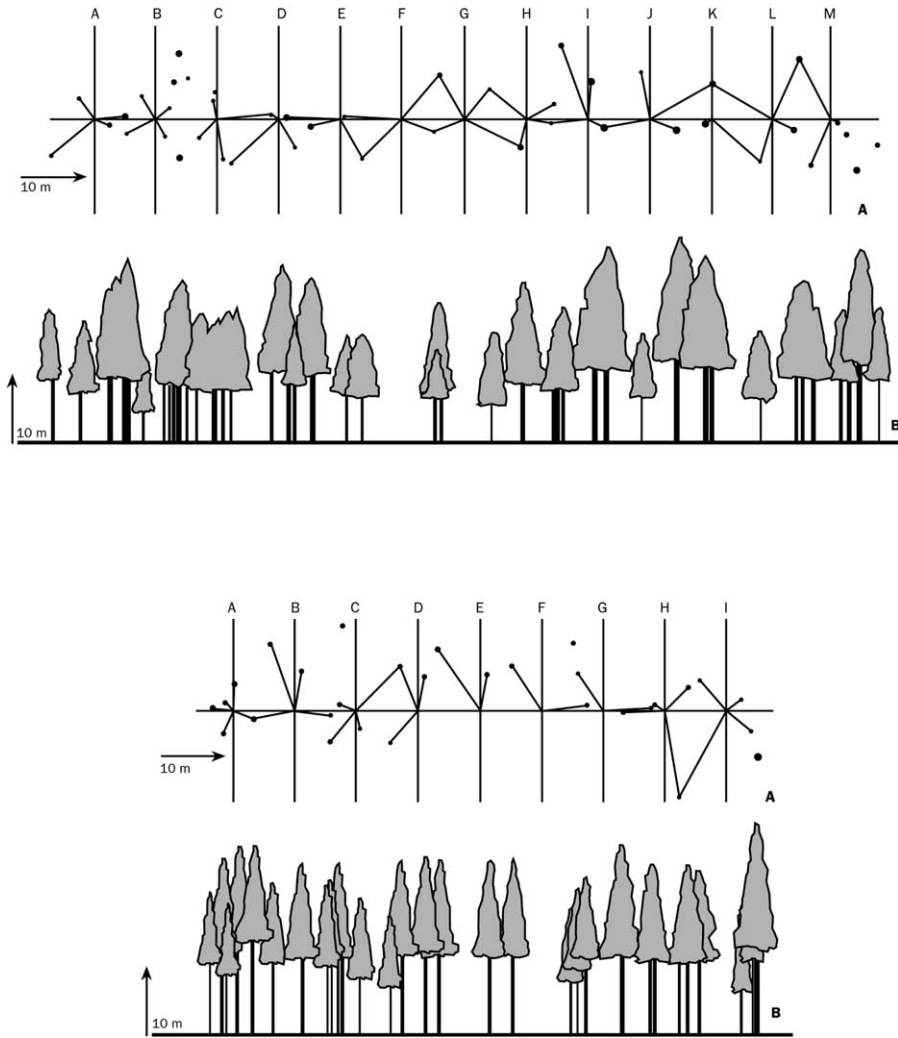
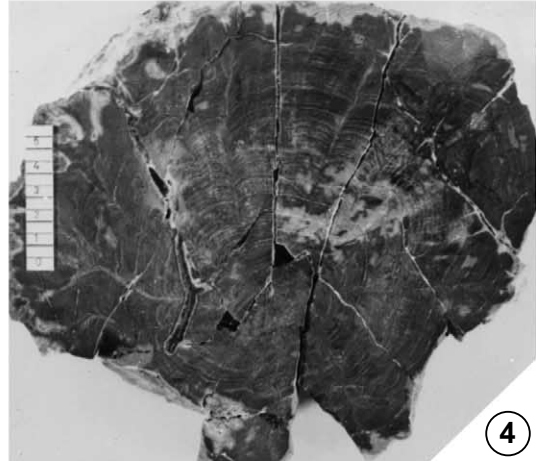


Fig. 3. (A) Two transects through the fossil forest deposit, showing configuration of quadrats and distances to measured stumps from point stations. Note that some stumps were measured from more than one point station and that some quadrats contained no fossil stumps (see text for full explanation). Diameters of black dots are scaled with stump diameters. (B) Vegetation profiles based on the transects in A. Tree heights correspond to estimated heights from Fig. 4, while trunk diameters are based on actual field measurements.

one coarsening-upward microcycle. The two sandstone bodies that represent the base of the first two cycles are 1 and 2 m thick, respectively, and correspond to medium-grained sandstones with scour marks and intraclasts, indicating erosional contacts; sedimentary structures are represented by planar and trough cross-bedding suggesting deposition under a relatively high flow regime. These two sandstone bodies are interpreted as crevasse channels resulting from an avulsion pro-

cess that failed to develop into a major channel. In particular, the second of these bodies follows a previous crevasse-splay deposit represented by the coarsening-up microsequence immediately below (Fig. 2B). This crevasse channel deposit is succeeded by two fine-grained sandstone beds with parallel lamination and small-scale cross-bedding, which show strong rooting associated with *Jeffersonioxylon* stumps and forest litter (*Dicroidium* leaves); the plants are partially encased by these



fine-grained sands. We interpret these deposits as levees associated with a relatively low-sinuosity crevasse channel which resulted from a previously initiated crevasse process. The possibility of considering this channel a meandering stream is rejected, based not only on the absence of critical meandering features such as lateral-accretion surfaces, but also because of the thinness of the deposit. In particular the formation of a meandering stream is unlikely to occur instantaneously in a newly invaded flood basin area because this type of channel requires time to develop (Smith et al., 1989). In the model indicated by Smith and Pérez-Arlucea (1994), crevasse-avulsion channels are bordered by forested levees and separated by marshy ponds with permanent standing water. At the fossil forest site, after the channel was deactivated, fine-grained deposits overlapped previous channel-levee deposition in the context of a high subsidence rate. Finally, migration of the trunk river (top, Fig. 2B) occurred, due to displacement of the braided channel belt on the alluvial plain, probably associated with another avulsion process elsewhere on the plain.

## 5. Taphonomy

Because levee deposits are commonly subjected to erosion by channel migration, they do not represent the most favorable sedimentary environment for preservation of local plant material, and this is confirmed by modern taphonomic studies (Gastaldo et al., 1989). However, other examples indicate that it is sometimes possible to find relatively well preserved plant taphocoenoses included in levee sediments (e.g., Burnham, 1989).

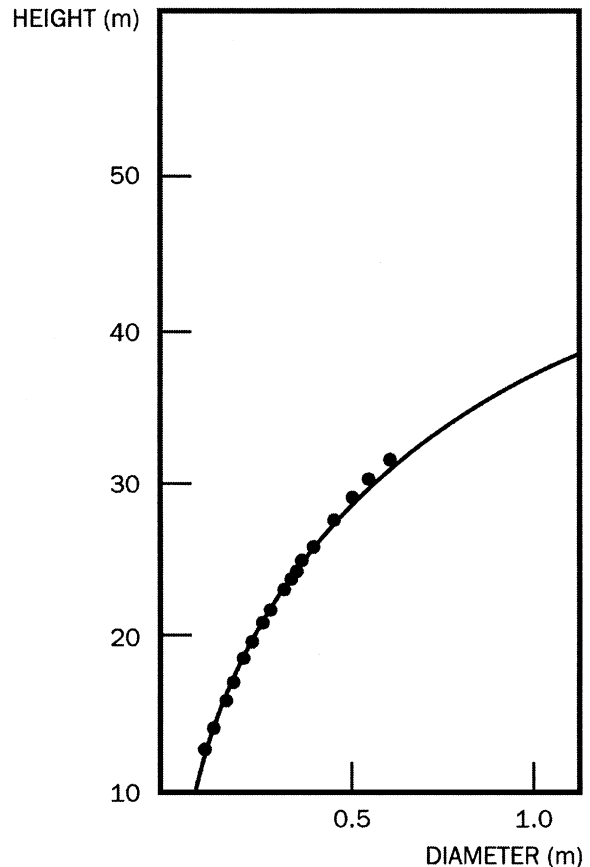


Fig. 4. Regression curve used to calculate estimated heights (based on Niklas' (1994) equations).

Two types of plant taphocoenoses were identified at the paleoforest site: permineralized stumps and compression–impression foliage. The stumps and foliage are included in fine sandstone facies and/or rooted siltstones. In many instances, roots attached to the stumps are preserved and can be followed into underlying beds of medium-grained

## Plate I.

1. Stump in situ with associated paleosol. Scale = 30 cm.
2. Stump in situ showing attached root system. Pen in photo = 14 cm.
3. Two in situ stumps showing spatial separation. Person = 1.8 m.
4. Transverse section of stump (*Jeffersonioxylon gordonense* wood) showing growth rings. Scale in cm
5. Large stump in situ. Pen in photo = 14 cm; stump height ~ 60 cm.

### PYRAMID OF DIAMETER CLASSES (N=99)

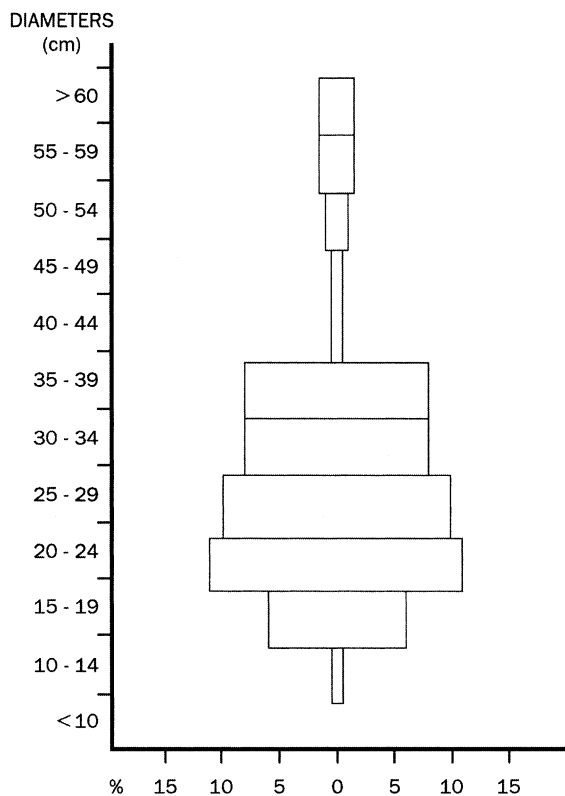


Fig. 5. Pyramid of class diameters taken from 99 fossil trunks.

channel sandstone (Fig. 2, Plate I, 2). Only weakly developed paleosols are present, however, probably due to rapid sediment accumulation (Horner and Krissek, 1991).

The silicified wood has been previously examined and assigned to a new genus, *Jeffersonioxylon* (Del Fueyo et al., 1995). The anatomy of these specimens is typical of coniferous woods (pseudoxyletic), with uniseriate rays and circular bordered pits on the radial walls of the tracheids. *Jeffersonioxylon* appears to be most similar to some podocarpaceous wood (Coniferales) (Del Fueyo et al., 1995). Foliage associated with the stumps is

of the *Dicroidium* type, a form genus [morphotaxon] common throughout the Triassic of Gondwanaland, and considered to belong to the seed fern group, Corystospermales (Taylor, 1996). The fronds are often somewhat fragmented (Plate II), especially those preserved in fine sandstones, indicating some mechanical degradation during the burial process. Two species appear to be present: *Dicroidium stelznerianum* Frenguelli and *Dicroidium crassinervis* (Geinitz) Anderson and Anderson (Boucher, 1995). Both typically occur in mats consisting of multiple layers of leaves. The compression–impression assemblage can be regarded as autochthonous or hypautochthonous in the sense of Gastaldo (1982) or Burnham et al. (1992), in which the litter accumulated on the forest floor and was subsequently buried via inundation. The exclusive occurrence of these leaves in dense mats associated with stumps of the *Jeffersonioxylon* type indicates that the *Dicroidium* fronds were produced by the same plant as the in situ stumps.

The stumps were buried by several small-scale depositional events on the fluvial channel levee. Periodic flooding of the alluvial system built up a thick, fining-upward, levee-proximal floodplain deposit. The stability of the river margins was no doubt enhanced by the establishment of relatively dense vegetation, as suggested by the distribution of the stumps (Fig. 3). Sometime after burial rapid permineralization (silicification) of the stumps took place. This process would have been favored by high concentrations of silica in the groundwater due to the erosion of the volcanic arc located on the western margin of the Antarctic craton (Collinson et al., 1994). Interstitial waters, rich in silica, must have saturated the stumps in a relatively short period of time, based on the complete silicification of even the largest stumps. This type of silicification (permineralization) also occurs in other Triassic plant-bearing sequences in Antarctica, in which sandy deposits contain high percentages of volcanic glass (Gabites, 1985; Taylor et al., 1989). Subsequent migration of the fluvial system left distal floodplain deposits on top of the levee deposits, preserving backswamp plant communities principally composed of the herbaceous sphenophyte *Neocalamites* (Fig. 6).

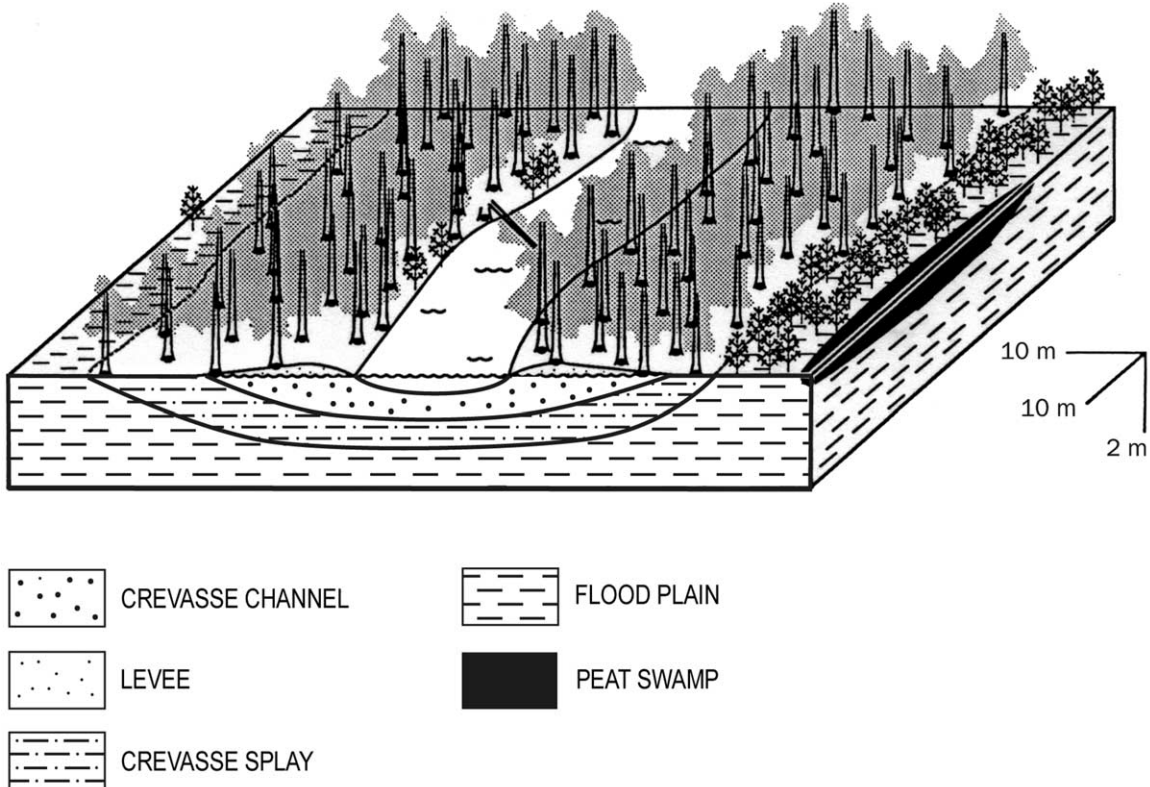


Fig. 6. Reconstruction of a fluvial-dominated terrestrial ecosystem showing the distribution of the stumps in the original forest along the levee and *Neocalamites* in the nearby backswamp area.

## 6. Vegetation analysis

There can be a number of limitations when modern vegetational analyses are applied to fossil systems. In the case of the Gordon Valley paleo-forest, however, the two transects (Fig. 3A), with nine plus 13 point stations, nearly approximate the suggested minimum number of point stations per stand (15) required in modern analyses (Newsome and Dix, 1968), even though some quadrats contain no fossil trunks. Both transects have provided an integrated data set sufficient to be considered statistically useful (Cottam and Curtis, 1956) (Tables 1 and 2). By chance, the two transects are nearly parallel to the paleocurrent features in the channel sandstones immediately below the paleo-forest, and therefore probably parallel the riparian community. Because some stumps were the closest individuals to two

adjacent point stations of the same transect, some were recorded twice (Fig. 3A). This problem has been discussed by Cottam and Curtis (1956), who determined that the results in such instances were not altered by this overlap.

Estimated tree heights were calculated on the basis of regression equations (Niklas, 1994) using known stump diameters (Fig. 4). These are static data that do not consider the presence of neighbors that may influence the growth trajectory of a tree by altering its local light environment (Henry and Aarssen, 1999). This last fact is especially important when high-latitude paleo-forests are analyzed, due to the fact that the shading effect by neighbors was probably more important in that kind of environment. A maximum height of  $\sim 31$  m would correspond to a stump diameter of 61 cm (stump in Plate I, 5), while the minimum diameter measured (13 cm) would have repre-



Plate II. *Dicroidium* fronds collected from area at base of permineralized stumps. Scales in mm.

1. *D. stelznerianum* Frenguelli
2. *D. crassinervis* (Geinitz) Anderson and Anderson

sented an individual up to 12.5 m tall. These size relationships have been corroborated by measurement of similar large, horizontal logs in the surrounding area. In addition, modern conifers show approximately similar correlations in their diameter/height ratios (Niklas, 1993). Considering the distribution of class diameters (Fig. 5), the canopy in the forest community would have varied between 14 and 25 m high, with the majority of individuals (~60%) ranging between 17 and 22 m tall (Fig. 3B).

Tree rings were measured on four randomly sampled individuals (Table 4, Plate I, 4). Although additional trunk samples were collected, the preservation of the wood cells was too poor

for ring analysis. The oldest trunk contained 86 rings (Table 4). Ring widths within a single trunk (specimen No. 11,471 C) range from 0.71 to 7.11 mm (Table 4), suggesting extremely variable growth rates during the life of the tree. However, some of this variation can be explained by the fact that trees tend to produce a large amount of radial growth during the juvenile stage, with diameter growth slowing as the tree matures. It is common when working with climate signals in extant trees to standardize ring widths so that young and older ring widths can be compared (Fritts, 1976). However, this is rarely possible with fossil material due to the small number of well-preserved trunks, and was not done in this study.

Table 4  
Tree ring summary data

Specimen	Number of rings	Ring width	
		Mean (mm)	Range (mm)
11,469 B	10	2.30	1.09–3.22
11,470 A	62	1.41	0.34–3.29
11,470 B top	64	1.49	0.31–2.73
11,471 C	52	2.54	0.71–7.11
11,517 B bot	86	0.92	0.23–3.02

Specimen #11,471 C contains not only the largest single ring (7.11 mm wide), but also nine other rings that are approximately 4 mm wide.

The pyramid of diameter classes developed for the fossil forest (based on 99 stumps) suggests that the forest was mature and mostly of a few age classes probably recruited over several decades. This is indicated by the low number of individuals with diameters of less than 15 cm (Fig. 5), as well as the ages of the trees based on tree ring counts (Table 4). The distribution of diameters (Fig. 5) approaches those obtained in modern, mature forest stands (Frangi, 1976), suggesting a riparian community in equilibrium with the regional climate, substrate, topography and water conditions. However, based on the configuration of the pyramid of class diameters (Fig. 5), it is clear that there is a gap between an older cohort of trees with diameters above 40 cm (10% of the stand) and younger trees with smaller diameters (90% of the stand). This suggests a former colonization of the river banks that was interrupted, probably due to environmental changes. Colonization was later resumed when favorable conditions returned. Although an extended sampling area was observed, younger individuals might have been overlooked, or were simply not preserved. However, in this regard, Lehman and Wheeler (2001), studying a Cretaceous forest from Texas, suggest that all of the trunks were preserved similarly by ‘pervasive silicification,’ and consider it unlikely that trees between those preserved could have escaped the permineralization process. Based on this, and taking into account the spacing between trees in Gordon Valley, it appears likely that the original structure of the forest has been preserved almost intact.

Leaf litter analysis also contributes to a reconstruction of the forest community. Quantitative data from five different areas (quadrats) of the sedimentary beds containing the fossil forest indicate that *Dicroidium* fronds cover, on average, about 50% of the bedding plane (Table 3). In fact, *Dicroidium* is the only type of foliage present in the compression–impression assemblage associated with the stumps. No understorey vegetation, which is usually preserved as compressions, was identified in the Gordon Valley forest.

A diagram profile of the forest physiognomy in each transect is shown in Fig. 3. These sections are approximately parallel to the channel/levee, and are based on the distribution of stumps in the stands and estimated heights. The reconstruction shows a concentration of larger (and probably older) individuals in some sectors of the stands, suggesting different phases of growth in the forest community. If both transects are compared, it is clear that the second one (Fig. 3B, bottom) includes smaller individuals. The first transect (Fig. 3B, top) might be interpreted as representing a more proximal location with respect to the main fluvial channel, a characteristic generally recognized in modern channel-backswamp transects (Scheihing and Pfefferkorn, 1984) as well as in fossil cases (Gastaldo, 1987). Since the Gordon Valley forest occurred on a channel levee and proximal floodplain area, it probably bordered a transitional zone with the plant community found on the distal floodplain and backswamp area, which included *Neocalamites* remains (Fig. 6).

## 7. Discussion

### 7.1. Coeval vegetation in Gondwana

Although the *Dicroidium* leaf morphotype was common throughout Gondwanaland in the Triassic, it is clear that an equivalent vegetation was not present over all areas of the supercontinent. Rather, a large number of plant communities (or associations) would have occupied different habitats and could have given rise to phytogeographic zonation. Most studies of Triassic fossil plants in

Gondwana are based on floras from Australia, South Africa, Argentina and India (e.g., Jones and de Jersey, 1947; Menéndez, 1951; Playford et al., 1982; Anderson and Anderson, 1983, 1985; Bose et al., 1990). Studies of floras from Antarctica and New Zealand are less numerous and generally more recent (e.g., Rigby, 1985; Retallack, 1987; Taylor and Taylor, 1990; Truswell, 1992; Boucher et al., 1995). Retallack (1977) reported that levee deposits in the lower Newport Formation, New South Wales included a *Dicroidium* flora, locally dominated by *Taeniopteris*. For the most part the Australian and New Zealand floras, while containing similar elements to the Antarctic floras, appear to be much more diverse. Few of the early reports discuss the possible environment of deposition, but rather concentrate on the listing of species present.

In South Africa, Anderson and Anderson (1985) indicated that low- to medium-diversity forests and woodlands dominated by *Dicroidium*-producing plants lived along levees and other elevated areas during the Early Triassic (Burgensdorp Formation) and early Late Triassic (Molteno Formation). In the Molteno, Cairncross et al. (1995) identified *Dicroidium* remains associated with braided channels that are comparable to the Gordon Valley deposits in Antarctica. However, the South African communities, growing at a much lower paleolatitude ( $\sim 55^\circ\text{S}$  or less) than the Antarctic material, appear more diverse and also include a dense understorey. In Argentina, the taphoflora of the Ischigualasto Formation has been extensively studied. Recently, Zamuner (1991) suggested that one type of *Dicroidium* foliage and the stem type *Rhexoxylon*, which is often found associated (e.g., Archangelsky, 1968), may have grown as riparian vegetation on river banks (levees).

The results of these studies suggest that plants bearing *Dicroidium* foliage may be found in river bank communities in other Gondwanan areas during the Triassic. Although all bore *Dicroidium*-type foliage, several different wood types are represented – evidence that the *Dicroidium* leaf morphotype was produced by different plants (Meyer-Berthaud et al., 1993). In Argentina, *Dicroidium* occurs in the Ischigualasto Formation

associated with stems assignable to *Rhexoxylon* (Archangelsky, 1968). *Rhexoxylon*, which is distinctive for its liane-like anatomy, is also known from South Africa (although not co-occurring with *Dicroidium*; Anderson and Anderson, 1983), but is rare or missing at Antarctic sites where there is an abundance of *Dicroidium* foliage. At Fremouw Peak in Antarctica, *Dicroidium* has been reconstructed as attached to small, coniferous stems (*Kykloxylon*) that exhibit anatomy similar to permineralized *Dicroidium* leaves from the same site (Meyer-Berthaud et al., 1993). Based on this material, these authors suggested that *Dicroidium* may have been borne on one type of stem in eastern Gondwana (*Kykloxylon*), and another type in western Gondwana (*Rhexoxylon*). Based on the taphonomic evidence from the paleoleaf litter at the forest site in Gordon Valley, *Jeffersonioxylon* could represent a third stem taxon linked to *Dicroidium* foliage, or *Kykloxylon* may represent the distal twigs of *Jeffersonioxylon* trunks (Taylor, 1996). Unfortunately, the generally poor preservation of the wood cells does not allow resolution of this question.

## 7.2. Comparison with other polar forests

When we compare known examples of polar paleoforests from both the Northern and Southern Hemispheres (Table 6), some interesting conclusions can be made. First of all, taking into account the relative paleolatitude of the forests, it is clear that for more than 200 million years regions inside the polar circles were suitable for plant and forest growth, although this is not true today. Most of these forests were dominated by trees that produced coniferophytic wood, regardless of their systematic affinities. The various polar forests occupied different paleoenvironments mostly associated with fluvial systems, ranging from levees to backswamps within the flood basins.

The calculated tree densities in these forests range from 300 to more than 2000 trees/hectare, with basal areas of 16–80 m<sup>2</sup>/hectare (Table 6). Among fossil forests from high latitudes, Francis (1991) found densities of 325 and 484 trees/hectare in Tertiary deciduous conifer forests of Arc-

tic Canada, believed to have been growing at  $\sim 78^\circ\text{N}$ . For the same site, Basinger et al. (1994) estimated 1100 trees/hectare. Creber and Francis (1987) estimated 900 trees/hectare for the Cretaceous fossil forest from Alexander Island, along the Antarctic peninsula (Jefferson, 1982), which probably grew at  $\sim 70^\circ\text{S}$  latitude. This forest, however, was only visible in a vertical outcrop which may have influenced the calculation of densities. In addition, many of these density calculations might have been overestimated because of the use of a simple calculation of number of trees present on the exposed surface rather than a statistical estimation of density. Simple methods can sometimes distort the distribution patterns within the forest.

From the data shown in Table 6, it is clear that forests in polar areas were able to grow at densities equivalent to modern temperate or even tropical areas. They did not obtain comparable diameters, however; on average the Gordon Valley trees never exceeded 30 cm, far less than fossil examples from lower latitudes. Mean ring width in the Antarctic forest ranges from 2 to 5 mm, two or more times wider than modern high-latitude tree rings and approaching the average ring size in present-day temperate forests.

Both deciduous and evergreen habits have been noted in polar paleoforests. Spicer and Chapman (1990) found that deciduousness appears to dominate high-latitude floras in those geological time periods when the climate was warmer, such as the Cretaceous (e.g., Askin and Spicer, 1995), while the evergreen habit is more prevalent during colder times, such as the present. In the Permian and Triassic examples from Antarctica, deciduousness was probably the main adaptation to survive the long winter darkness (Taylor et al., 2000) based on both anatomical features and the presence of leaves in leaf mats and in varved deposits (e.g., Gunn and Walcott, 1962).

The record of understorey vegetation associated with polar forests is unclear. Shading effects in the relatively dense forest stands, combined with the angle of light at high latitudes, could have been responsible for a lack of understorey. In the case of the Permian forest from the central Transantarctic Mountains, no traces of understorey vege-

tation were found (Taylor et al., 1992). The same is true of the Triassic Gordon Valley forest; however, coeval plant assemblages from the Lashly Formation, even though different in composition, suggest the presence of a tree canopy and a fern understorey (Cúneo et al., 1994). Some late Mesozoic and Tertiary polar forests, on the other hand, did develop a certain amount of understorey (Table 6; see also Thorn, 2001). The lack of understorey in closed polar forest canopies could have been the result of shading effects associated with light conditions in high southern latitudes, including the low angle of sunlight at  $70^\circ\text{S}$ . This fact was invoked by Jefferson (1982) in order to explain the absence of undergrowth vegetation in the forest from Alexander Island (Cretaceous of Antarctica) and by Basinger (1991) for Eocene forests in Arctic Canada. However, Pole (1999) suggests a different interpretation for the Alexander Island forest involving repeated flooding events that precluded the growth of herbaceous or shrubby vegetation on the forest floor. Falcon-Lang et al. (2001) have recently documented an understorey in the Alexander Island forest of ferns and herbaceous angiosperms. Loss of understorey by repeated flooding could have been the case in the Gordon Valley forest, especially considering the sedimentological setting of a levee/floodplain area. It is possible that the original forest included isolated seedlings and very young isolated individuals belonging to the same plant as the *Jeffersonioxylon* stumps and *Dicroidium* foliage. Small flood events could have swept seedlings and other shallow-rooted plants away. Both the low light angle and, more importantly, the environment of growth probably contributed

Table 5

Forest stand data (based on methods of Cottam and Curtis, 1956)

- 
- Mean distance (average separation of trees) = 6.04 m
  - Mean area (free area around each individual) = 36.48 m<sup>2</sup>
  - Total density (individuals per hectare) = 274.12 ind.ha<sup>-1</sup>
  - Mean dominance (basal area per stump) = 0.076 m<sup>2</sup> ind.<sup>-1</sup>
  - Basal area (total forest cover/hectare) = 20.83 m<sup>2</sup> ha<sup>-1</sup>
  - Mean diameter = 27.7 cm
-

to the lack of a preserved understorey layer in the Gordon Valley forest.

Based on the distribution of stumps, suggested tree heights, associated leaf litter and paleoenvironmental features, we suggest that the original forest consisted of plants growing in a relatively open forest structure with a density of 274.12 trees/hectare (Table 5). A comparison with the few other polar forests for which data are available shows that this is a relatively low density (Table 6). However, mean distance (6.04 m) and mean area (36.48 m<sup>2</sup>) values per tree suggest a closer forest physiognomy with a dominant canopy varying from 17 to 22 m in height. These values are similar to those shown by modern temperate red oak and maple forests that yield a spacing of 7–8 m between trees with canopies between 20 and 25 m in height (Halle et al., 1978; Lehman and Wheeler, 2001).

### 7.3. Antarctic Triassic paleoclimate and paleobiogeography

The interpretation of paleobiotas from high or polar paleolatitudes (above 60°) has been some-

what of a dilemma when compared to existing high-latitude ecosystems. A number of fossil discoveries have contributed to our understanding of the biotas and paleoclimates in Antarctica (e.g., Taylor et al., 1992; Webb and Harwood, 1993; Hammer and Hickerson, 1994). It is clear that a climatic amelioration occurred during the Paleozoic/Mesozoic transition in Gondwana, reflecting the shift from an icehouse climate in the Late Carboniferous/Early Permian to warmer greenhouse conditions in the Triassic (Fischer, 1984; Collinson, 1997). The Triassic biota in Antarctica, due to its position at high latitudes, was no doubt one of the first to respond to this change. The climatic shift is reflected in a vegetational change from monotonous glossopterid associations during the Permian to much more diverse Triassic floras. The Early Triassic flora is poorly known, but by the Middle Triassic, ferns, sphenophytes, seed ferns, conifers and even a cycad are known (Taylor and Taylor, 1990). The appearance of the *Lystrosaurus* fauna in Antarctica and South Africa in the Early Triassic also reflects this climate change (Cosgriff et al., 1982; Smith, 1995). Using statistical models, Anderson et al. (1996) estimate

Table 6  
Comparisons of selected polar fossil forests

	Mount Achernar <sup>a</sup>	Gordon Valley <sup>b</sup>	Curio Bay <sup>c</sup>	Alexander Island <sup>d</sup>	Axel Heiberg Island <sup>e</sup>
Location	Antarctica	Antarctica	New Zealand	Antarctic peninsula	Arctic Canada
Paleolatitude	~75–85°S	~65–70°S	~66°S	~65–75°S	~76–78°N
Age	Late Permian	Middle Triassic	Middle Jurassic	mid-Cretaceous	early Tertiary
Wood composition	coniferophytic	coniferophytic	coniferophytic	coniferophytic	coniferophytic
Paleoenvironment	floodplain	levee/floodplain	floodplain	floodplain	swamp
Mean distance	1.95 m	6.04 m	4.26 m	4.21 m	2.97 m
Density	2134 trees/ha	274.12 trees/ha	552 trees/ha	568 trees/ha <sup>f</sup>	1136 trees/ha
Basal area	65.8 m <sup>2</sup> /ha	20.83 m <sup>2</sup> /ha	16 m <sup>2</sup> /ha	?	80.8 m <sup>2</sup> /ha
Mean diameter	11.4 cm	27.8 cm	16.3 cm	8–22 cm	27.4 cm
Estimated height	~10 m	~20 m	14 m	30 m	?
Understorey	none	none	ferns, cycads	ferns, angiosperms	some present
Forest habit	deciduous	deciduous	evergreen?	evergreen	deciduous/mixed
Mean (max) ring width	4.5 (11.38) mm	1.73 (7.11) mm	1.5–2.5 mm	3.04 (12.98) mm	3–5 mm

<sup>a</sup> Cúneo et al., 1993; Taylor et al., 1992.

<sup>b</sup> This paper.

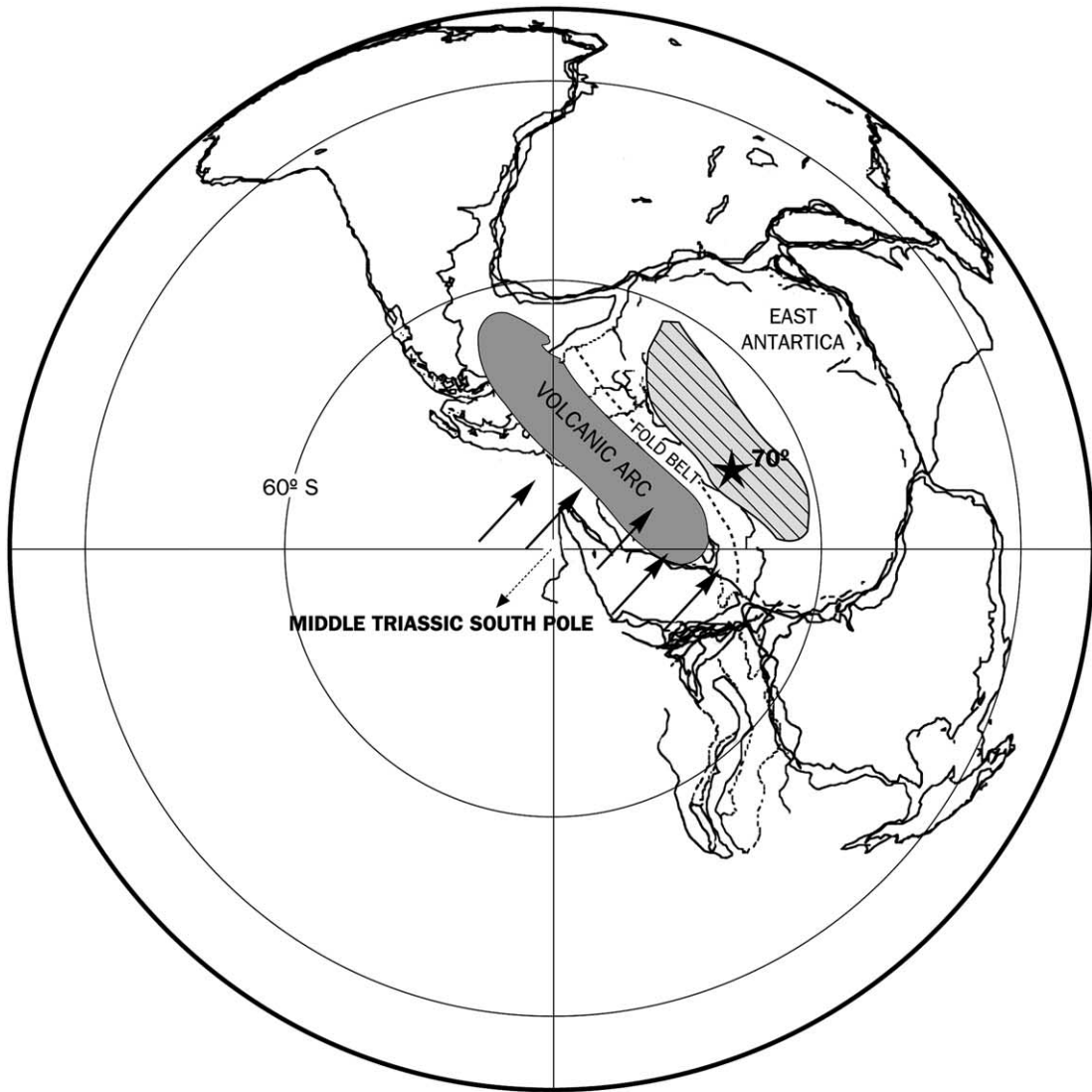
<sup>c</sup> Pole, 1999.

<sup>d</sup> Jefferson, 1982; Creber, 1986; Falcon-Lang et al., 2001.

<sup>e</sup> Francis, 1991; Basinger et al., 1994; Greenwood and Basinger, 1994.

<sup>f</sup> Falcon-Lang et al., 2001 described two different forest communities. The density data listed here are from the forest associated with coastal meander-belt sediments.

## SOUTHERN HEMISPHERE PALEOGEOGRAPHY Middle Triassic






-  Approximate distribution of triassic vegetation (recorded)
-  Humid winds
-  Gordon Valley Forest

Fig. 7. Middle Triassic paleomap showing a possible orographic barrier developed along the east Antarctic craton. Modified in part from [Collinson \(1990\)](#).

that biodiversity in the Late Triassic Molteno Formation of South Africa may have approached levels of diversity in the modern flora and suggest a Triassic ‘explosion’ of diversity in the Southern Hemisphere.

Triassic floras of Antarctica reflect climatic changes during this time interval. Based on sedimentological data, the Early Triassic of Antarctica was probably drier than the Middle and Late Triassic (Collinson, 1997). This assumption is strengthened by differences in the vegetation and plant communities, as well as by peat accumulation and subsequent coal formation in the Middle and Late Triassic, suggesting a more humid climate. This change apparently occurred throughout Gondwana, if not worldwide (Ziegler et al., 1993; Francis, 1994; Parrish et al., 1996; Collinson, 1997). In addition, reconstructed paleo-rainfall patterns for the East Antarctic craton suggest an increase from the Early to the Late Triassic (Parrish et al., 1982; Wilson et al., 1994). Drier climatic features in the Early Triassic of Antarctica were likely due to the development of an orographic barrier which began to form in the latest Permian (Collinson, 1990). This mountain chain apparently occupied the western side of the Antarctic craton (Fig. 7) (Cúneo et al., 1991), and was probably highest and thus exerted the strongest climatic influence during the Early Triassic. As a result most of the precipitation was probably discharged on upwind highland slopes, thus preventing humid air coming from the south paleo-Pacific from reaching intracratonic basins. Later erosion of the fold belt lowered the mountains, allowing more humid conditions to prevail inland in the Antarctic craton (Collinson et al., 1994). However, the Triassic climate probably never reached the high humidity levels suggested for the Permian.

The taxonomic diversity and ecological setting of the Middle Triassic vegetation, as shown by the Gordon Valley forest and other contemporaneous plant assemblages in Antarctica, reflect climatic variables that affected the continent. The diversity of vegetation present in the Fremouw Formation (Taylor et al., 2000), as well as the presence of presumably frost-sensitive plants such as the cycad *Antarcticycas* (Smoot et al., 1985), indicate a

higher annual mean temperature than during the Permian. As was probably true for other polar regions during a greenhouse cycle, seasonality in Antarctica was governed primarily by light availability (Taylor, 1989; Creber and Francis, 1996; Taylor et al., 2000). Evidence for seasonality comes from growth rings, not only in the silicified stumps at Gordon Valley, but also from wood in fluvial deposits and permineralized peat (Taylor et al., 2000). Evidence of seasonal deciduousness includes the presence of *Dicroidium* leaf mats (Taylor, 1996) and anatomical evidence for regular and programmed abscission of *Dicroidium* leaves from *Kykloxyton* stems (Meyer-Berthaud et al., 1993). A temperate regime (cool winters and warmer summers), conditioned primarily by sunlight and secondarily by temperature, would be the best fit with the data from Middle Triassic paleobiotas in Antarctica.

The climatic interpretation presented here contrasts with most of the model simulations for this time period (e.g., Wilson et al., 1994), in which an annual temperature range of 50–70°C (winter low of –40° to –50°C; summer high of 20–25°C) has been suggested for the polar latitudes. Such temperature extremes do not correlate with the recorded paleobiota. In an attempt to explain the anomalies between models based on physical parameters and the geological and paleontological record, numerous arguments have been advanced, including migration (of faunas), orbital forcing (Milankovich cycles), reduced obliquity of the Earth’s axis, additional heating induced by methane released from coal deposits, and errors in model design. However, it is clear that heat transport to the poles, especially in winter, must also be considered (e.g., Sloan et al., 1995; Herman and Spicer, 1996). In addition, heating associated with the vegetation itself may have been responsible for a local warming (Woodward et al., 1998). Studies on this subject in modern vegetation (e.g., Sellers et al., 1996) are important for interpretation of future paleoclimatic modeling. More recent models have noted that feedback effects from different vegetation types (e.g., tundra vs. forest), especially at high latitudes, can have a strong effect on the model results, not only through albedo changes, but also from the effects

of increased (or decreased) transpiration (e.g., Otto-Bliesner and Upchurch, 1997; DeConto et al., 1998, 2000).

## 8. Conclusions

Interdisciplinary studies of fossil biotas have proven to be the most informative in understanding community relationships in polar ecosystems. A number of quantitative methodologies taken from modern vegetation analysis, in particular the point-centered quarter method, are especially valuable in the study of an in situ forest deposit. The Gordon Valley forest is important not only because of its excellent preservation but because it grew at very high paleolatitudes ( $\sim 70^\circ\text{S}$ ). The preservation of 99 stumps in situ has allowed for an analysis of the stumps which shows that they grew at a density of 274.12 trees/hectare. Although this density is lower than those described from some other high-latitude fossil forests, the diameter of the trees is larger than most of those described (27 cm). Even with the low angle of sunlight and a period of winter darkness, the Gordon Valley trees produced relatively large annual rings (1.73 mm average), indicating that availability of light and moisture during the growing season was more than adequate. On this basis interdisciplinary studies designed to investigate not only the floristic diversity, but also the ecological distributions of plant communities, represent the most reliable means of understanding past phytogeographic patterns.

The interpretation of ancient climatic regimes based on computer model simulations will necessarily require confirmation from paleobiological data and reliable paleogeographic information. In the case of the Antarctic continent during the Triassic, there is considerable disparity between the physical models and paleontological evidence. In order to improve this correlation it will be necessary to characterize biological features that are unique in high-latitude biotas during times of global warmth. In particular, physiological adaptations to the polar winter influenced by greenhouse gases such as  $\text{CO}_2$  and  $\text{CH}_4$  (e.g., Crowley, 2000) will represent key components in under-

standing the survival of these ancient animal and plant biotas.

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