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# TRIASSIC FLORAS OF ANTARCTICA: PLANT DIVERSITY AND DISTRIBUTION IN HIGH PALEOLATITUDE COMMUNITIES

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## ABSTRACT

**Continental Triassic sequences in Antarctica are among the most continuous and best represented in Gondwana. Triassic fossil plants have been collected sporadically from Antarctica since the beginning of the twentieth century, but our knowledge of the vegetation during this time has dramatically increased during the last three decades. Here we review the fossil record of Triassic plants as representatives of natural groups from sites along the Transantarctic Mountains, using the fossils as evidence for successive vegetational changes through the Triassic, taking into account that these plant communities were living under particular high-latitude (70° or higher) paleoclimatological conditions, including a polar light regime. Even though our knowledge of the Triassic floras of Antarctica is still incomplete, this survey shows that these floras were remarkably diverse. Lycopsids, equisetaleans, ferns, seed ferns, ginkgoaleans, and conifers were major components of the landscape in Antarctica during this time. The diversity of gymnosperms is exceptional, with almost every major clade of seed plants present, despite the high paleolatitude; however, each clade is often represented by only one or a few genera. The occurrence of permineralized peat, along with compression-impression floras, has increased our knowledge of the morphology, reproductive biology, and evolution of many of the plants in these floras. In general, floral changes in Antarctica during the Triassic can be recognized elsewhere in Gondwana, especially in South America, although a strict correlation based on macrofossils is still not possible. Thus, this contribution represents the first attempt to bring together information on Triassic floras from continental Antarctica (excluding the Antarctic Peninsula) within a biostratigraphic framework and thereby to compare these floras with those from lower latitudes.**

## INTRODUCTION

The first fossil plants described from the Transantarctic Mountains included specimens of *Glossopteris* leaves and wood fragments collected by British explorer Captain Robert Falcon Scott's field party on their return trip from the South Pole (Terra Nova Expedition, 1910–1913; Seward, 1914). Scott's field notes indicate that these plant fossils, later determined to be Permian, were collected from Mount Buckley on the Beardmore Glacier in the central Transantarctic Mountains (CTM) (Seward, 1914). Although Triassic wood and various plant compressions or impressions have been collected since the first geologic expeditions to the continent, there have been just a few summaries of Antarctic Triassic plants or floras (e.g., Truswell, 1991). One of the earliest Antarctic researchers focusing primarily on plant fossils was James M. Schopf, who participated in expeditions to Antarctica during the 1960s (e.g., Schopf, 1968, 1970). Schopf worked for the U.S. Geological Survey at The Ohio State University and amassed a large number of Antarctic plant fossils during his career. His collection—now at the University of Kansas—includes plants preserved as impressions and compressions, palynological samples, and silicified wood from numerous sites, including southern and northern Victoria Land (SVL, NVL) and the CTM.

Certainly one of the most significant contributions of Schopf's fieldwork in Antarctica was the discovery of permineralized peat from two sites in the CTM (Schopf, 1970, 1978). One of these peats occurs on Skaar Ridge (Mount Augusta of Schopf, 1970), and is considered to be Late Permian based on the *Glossopteris* flora and comparison with megafloras and palynomorphs from Mount Achernar in the region (Farabee et al., 1991; Cúneo et al., 1993). The second peat locality occurs on the north side of Fremouw Peak and has been dated as Middle Triassic based on palynomorphs in the peat (Farabee et al., 1990). Plant material from this site is anatomically preserved in opaline silica and has been the focus of numerous studies beginning in the late 1970s (Schopf, 1978) and extending to the present. In addition to the permineralized peat, the record of Triassic plants in continental Antarctica includes numerous impression and compression specimens that have been collected from more than 20 localities at various stratigraphic positions ranging from Lower to Upper Triassic. Taken together, these collections represent a significant data set that provides the opportunity to place the Triassic vegetation of Antarctica within a framework in which the biological and geological importance of these plants can be fully integrated.

The focus of this paper is to establish the presence of natural groups in the Triassic communities of Antarctica based on megafloral evidence from CTM, southern Victoria land, and northern Victoria land. Many plant groups summarized here were previously noted as being present in the Triassic of Antarctica (Rigby and Schopf, 1969); in many cases, however, the evidence was only briefly discussed, as in the case of the lycopsids, and neither figured nor formally described (e.g., in the case of the dipterid ferns). The purpose of this paper is to present the first detailed documentation of the systematic composition of these floras and to provide a context for a broader analysis of Gondwanan floras at an important time in Earth history and plant evolution.

## MATERIALS AND METHODS

### Collections

The present survey is largely based on material housed in the Paleobotanical Collections (KUPB, specimens with prefix T) of the Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence (http://paleobotany.bio.ku.edu/PaleoCollections.htm). This material was collected during many field trips to Antarctica since the 1980s and includes specimens collected by Schopf during the 1969–1970 field season. The entire collection comprises ~2600 compression-

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impression (specimens with prefix T) and ~3500 permineralized specimens (numbered in figure captions) from >20 localities.

Additional specimens included in this study are housed in the collection of the Forschungsstelle für Paläobotanik, Institut für Geologie und Paläontologie, Westfälische Wilhelms-Universität Münster. This material was collected during the 9th German Antarctic North Victoria Land Expedition (GANOVEX IX, specimens with prefix GIX) in 2005–2006 and includes ~200 compression-impression and 30 permineralized specimens from five sites.

The distribution of taxa also includes additional literature citations of floristic elements from other Triassic localities of SVL and CTM (i.e., Plumstead, 1962; Townrow, 1967a; Gabites, 1985; Rigby, 1985; Retallack et al., 2005) and some comparison with Triassic floras known from the Prince Charles Mountains (PCM) in East Antarctica (e.g., Cantrill et al., 1995; McLoughlin et al., 1997). Considering that no uniform taxonomic concept was used within some groups, especially in the older literature, we will use the most recent classifications based on phylogenetic analyses wherever possible. For example, Gabites (1985) mentioned and illustrated *Xylopteris elongata* from several levels of the Lashly Formation, SVL. Leaf morphospecies placed in *Xylopteris*, however, are considered to be part of the genus *Dicroidium* based on morphological features and cuticles (Archangelsky, 1968; Holmes, 1982). Thus, *X. elongata* is here discussed as *D. elongatum*.

### Fossil Preparation and Imaging

Fossil plant specimens detailed here occur in different states of preservation (i.e., impressions, compressions, and permineralizations) that require the use of different preparation techniques. Standard techniques have been applied in the study of the compression-impression specimens (e.g., Jones and Rowe, 1999). In permineralizations (i.e., silicified peat) anatomical details were analyzed using the acetate peel technique after etching in hydrofluoric acid (Galtier and Phillips, 1999). In some instances, anatomical details of compression specimens were studied using a modified transfer technique (Escapa et al., 2010a). Compression-impression specimens were photographed with a Nikon FinePix Si Pro digital camera, using polarized light to increase the contrast and definition of details for some compression specimens. For low-magnification images of silicified plants, acetate peels were scanned directly using an Epson Perfection V750 Pro Scanner at 1200 dpi. For higher magnification, specimens were photographed using a Leica MZ16 stereomicroscope with both reflected or transmitted light and a Leica DM500 B compound microscope with transmitted light. Where necessary, digital images were minimally processed using Adobe Photoshop CS, version 8.0 (Adobe Systems).

### Geological Setting

The Transantarctic Basin persisted behind the active continental margin of the East Antarctic craton from the Devonian to the Jurassic (Collinson et al., 1994). Its entire sedimentary record is referred to as the Beacon Supergroup (Barrett et al., 1972). Plant-bearing Triassic deposits form part of the Victoria Group and were laid down in two main depocenters of the basin: (1) a retroarc foreland basin, preserved in part in the CTM, and (2) the epicratonic Victoria subbasin exposed in southern (SVL) and northern Victoria Land (NVL) (Collinson et al., 1994). In the CTM (Fig. 1), Triassic rocks are included in the Fremouw and Falla Formations (Fig. 2) (Barrett, 1969). In SVL two Triassic units are recognized, the Feather Conglomerate and Lashly Formation (Barrett et al., 1971), whereas the Triassic in NVL is represented only by the Section Peak Formation, a supposed equivalent of the upper Lashly Formation in SVL (Collinson et al., 1986).

The Fremouw Formation in the CTM is a very well-known unit of undeformed sedimentary strata ~650 m thick deposited by low-sinuosity braided streams on an extensive alluvial plain (Barrett et al., 1986; Collinson et al., 1994). Three informal members were established based on lithology (Barrett, 1969; Barrett et al., 1986); the lower and middle members have larger proportions of fine-grained facies due to higher subsidence rates, whereas the upper is characterized by cliff-forming sandstones. The whole unit has yielded typical Gondwanan Triassic faunas (*Lystrosaurus* and *Cynognathus*) and floras (the seed fern *Dicroidium*) (Hammer, 1990; Krull and Retallack, 2000; Taylor et al., 2000). Based on this megafossil record and associated palynomorph content (Kyle and Schopf, 1982; Farabee et al., 1990) the Fremouw Formation is considered to be Lower–Middle Triassic. It is conformably overlain by the Falla Formation (Barrett, 1969; Barrett et al., 1986), which encompasses a ~300 m thick series of siliciclastic fining-upward cycles (Elliott, 1996). The Falla Formation is interpreted as deposits of a low-sinuosity braided stream system with a high proportion of preserved lacustrine and paludal floodplain deposits (Barrett et al., 1986), and is assigned to the Upper Triassic based on its paleobotanical and palynological content (Kyle, 1977; Farabee et al., 1989; Boucher et al., 1993). As originally defined by Barrett (1969), the Falla Formation included Lower Jurassic rocks, but this part of the section was renamed the Hanson Formation (Elliot, 1996) in recognition of its increased volcaniclastic content when compared to the underlying Falla Formation.

In SVL the Feather Conglomerate is an ~250 m sequence of mostly sandy and less conglomeratic facies deposited by braided streams (Barrett et al., 1971; Barrett and Kohn, 1975; Barrett and Fitzgerald, 1985). The sandier lower part is considered to be Permian based on its stratigraphic position and paleocurrent pattern (Barrett and Fitzgerald, 1985), whereas the upper, more fine-grained part (Fleming Member) is assigned an Early–early Middle Triassic age based on palynology (Kyle, 1977). This unit is overlain by the Lashly Formation, which is ~520 m thick at its type locality (Mount Bastion; Barrett et al., 1971). The Lashly has been divided into four members based on the proportion of sandy sediments. Members B and D show higher proportions of sand, indicating sedimentation from low-sinuosity braided streams and lower subsidence rates in the basin, whereas members A and C are characterized by a high proportion of fine-grained sediments and coal. Members A and C were probably deposited by meandering streams under higher subsidence rates and have yielded well-preserved plant fossil assemblages (e.g., Collinson, 1990; Phipps et al., 1998). The megafossil and palynomorph content of the Lashly Formation indicates a Middle Triassic age for members A and B, and Late Triassic for members C and D (Kyle and Schopf, 1982; Farabee et al., 1990; Retallack and Alonso-Zarza, 1998).

In NVL, Triassic rocks are included in the ≤200-m-thick Section Peak Formation (Gair et al., 1965; Collinson et al., 1986; Schöner et al., 2007). In southern NVL the formation rests directly on the crystalline basement, but unconformably overlies the Permian Takrouna Formation in northern NVL (Collinson et al., 1986). The Section Peak Formation is mainly composed of medium- to coarse-grained, typically trough cross-bedded sandstones deposited by braided streams (Collinson et al., 1986). A basal conglomeratic series of variable thickness may occur locally (Schöner et al., 2007, 2011). Intercalations of overbank fines, including plant-bearing siltstones, mudstones, and coal, occur in the upper part of the formation (Tessensohn and Mädler, 1987; Schöner et al., 2007, 2011). Mega- and microfloras indicate a Late Triassic age at least for the upper part of the sequence (Gair et al., 1965; Norris, 1965; Tessensohn and Mädler, 1987; Bomfleur et al., 2007, 2011a, 2011b), which likely corresponds to the Falla and upper Lashly Formations in the CTM and SVL, respectively (Schöner et al., 2007, 2011). Palynological and lithologic data place the top of the formation in the Lower Jurassic (Norris, 1965; Pertusati et al., 2006; Schöner et al., 2007, 2011).

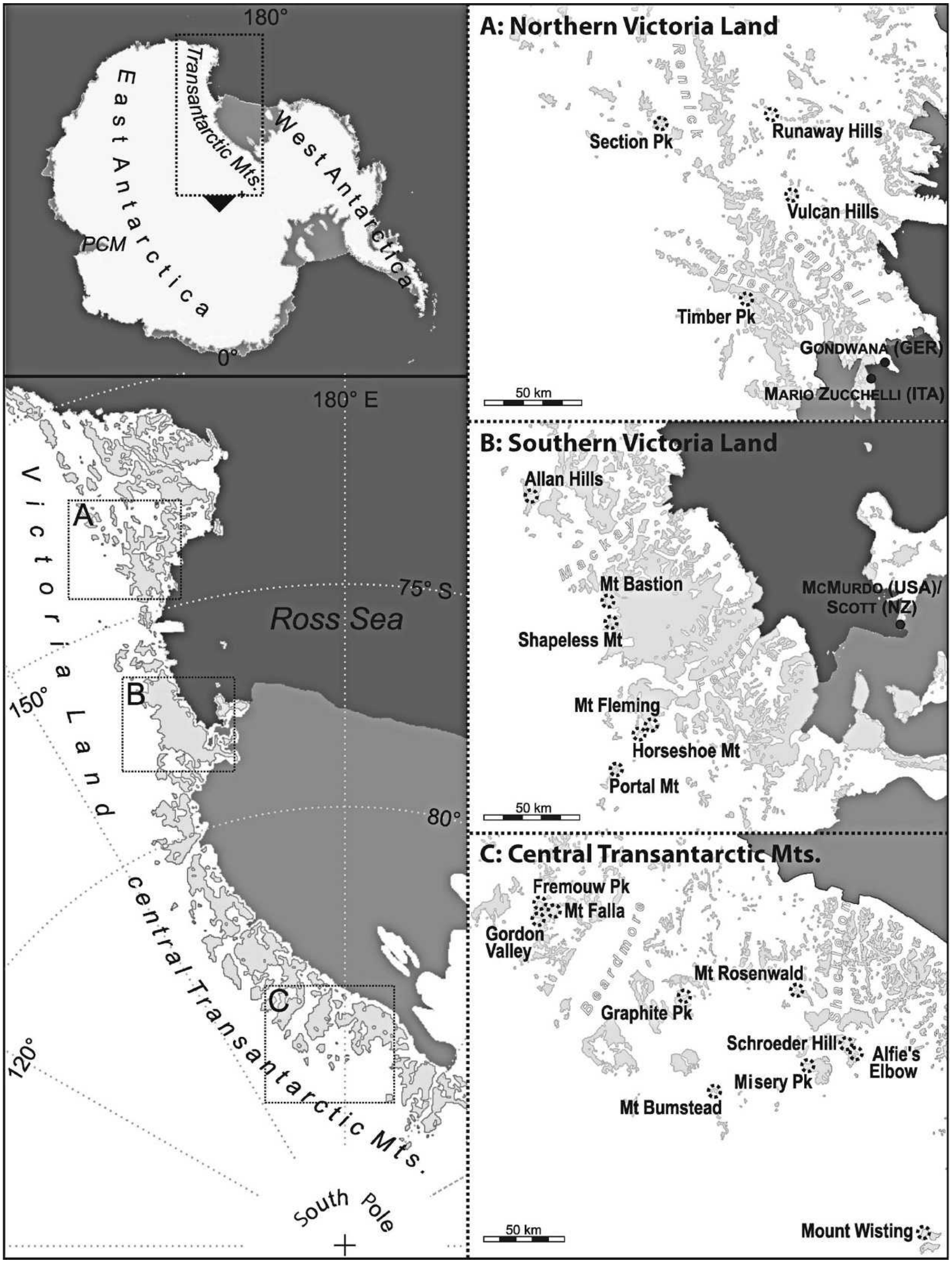


**FIGURE 1**—Geographic locations of plant fossil localities in the Transantarctic Mountains (SVL, NVL, and CTM); PCM = Prince Charles Mountains.

## Triassic Plant Localities

For the present contribution we use a combined geographic (Fig. 1) and stratigraphic (Fig. 2) locality concept. In this context, one locality may include several plant-bearing sections or horizons of a lithostratigraphic unit in a designated area. The confidence of the stratigraphic position varies among the different localities included in this contribution; stratigraphic uncertainty for individual localities is represented in Figure 2. Three groups of localities were defined in order and according to their proximity in the stratigraphic column.

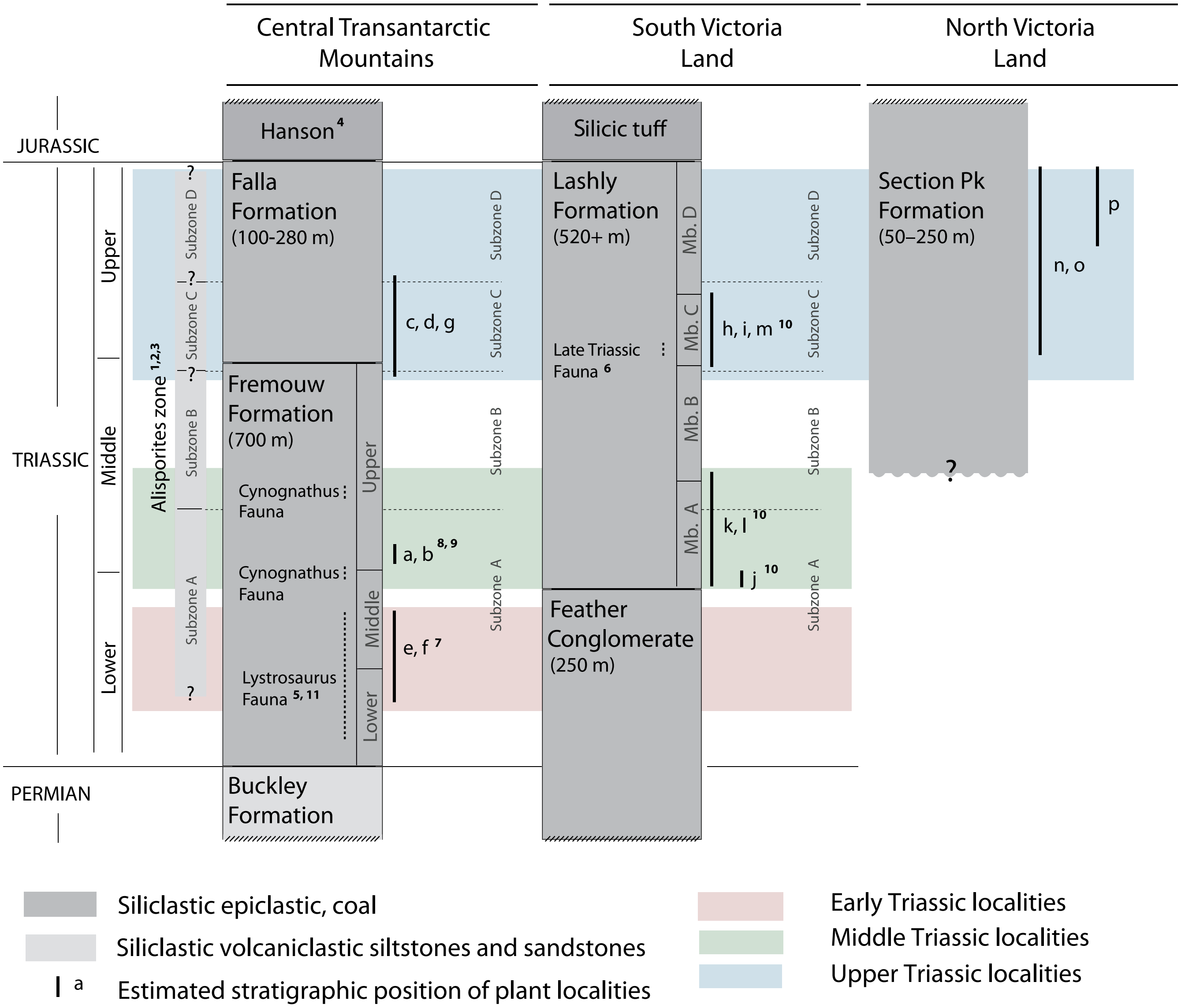
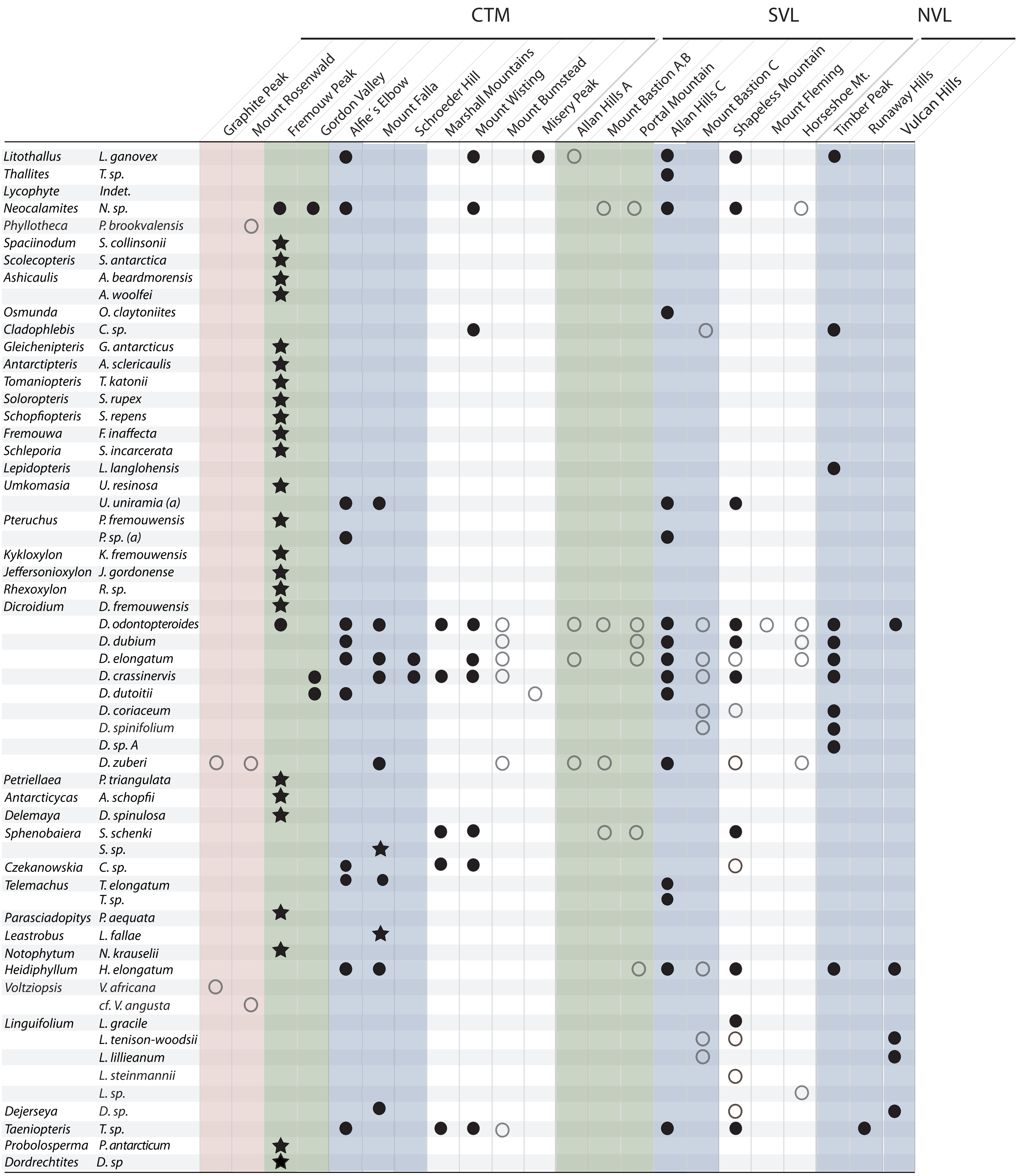


**FIGURE 2**—General stratigraphic distribution of Triassic megafloras in different regions of the Transantarctic Mountains. Age, chronostratigraphic, and lithostratigraphic columns not to scale. Lines on the left of plant localities (lower case letters a–p) show uncertainty in the chronostratigraphic position of plant horizons. Red box = stratigraphic distribution of Lower Triassic plant localities; green box = Middle Triassic sites (probably including part of the upper Lower Triassic); and blue box = Upper Triassic localities (probably including part of the upper Middle Triassic). Plant localities include from the CTM (Fig. 1C): a = Fremouw Peak and base of Mount Falla, b = Gordon Valley, c = Mount Falla, d = Alfie's Elbow, e = Graphite Peak, f = Mount Rosenwald, g = Schroeder Hill, from SVL (Fig. 1B): h = Allan Hills, Lashly Formation, Member C, i = Shapeless Mountain, j = Allan Hills, Lashly Formation, Member A, k = Portal Mountain, l = Mount Bastion, Lashly, Member A–B, m = Mount Bastion, Lashly, Member C; and from NVL (Fig. 1A): n = Timber Peak, o = Runaway Hills, p = Vulcan Hills. References for fossil sites, palynological zones, and lithostratigraphic units include: 1 = Kyle, 1977; 2 = Farabee et al., 1989; 3 = Farabee et al., 1990; 4 = Elliot, 1996; 5 = Collinson et al., 2006; 6 = Hammer et al., 2004; 7 = Retallack et al., 2005; 8 = Cúneo et al., 2003; 9 = Taylor et al., 1989; 10 = Gabites, 1985.

The first group (Fig. 2) includes Lower Triassic localities of the lower and middle Fremouw Formation in the CTM. At Graphite Peak and Mount Rosenwald, plant-bearing horizons occur between 50 and 300 m above the uppermost coal seam of the Permian Buckley Formation (Townrow, 1967b; Retallack et al., 2005). The second group (Fig. 2) includes localities in the upper Fremouw Formation (CTM) or in members A and B of the Lashly Formation (SVL). The age of these floras was estimated as Middle Triassic (Anisian–Ladinian) based on microfloras that have been assigned to subzones A and B of the informal Triassic *Alisporites* palynological zone of Kyle and Schopf (1982). The lower plant horizons from Member A of the Lashly Formation, however, may extend into the upper Lower Triassic (Kyle and Schopf, 1982; Gabites, 1985).

Most plant localities from the third group can be confidently placed into the Upper Triassic or the uppermost Middle Triassic, represented by the upper Fremouw Formation in the CTM, Members C and D of the Lashly Formation in SVL, and the Section Peak Formation in NVL. The suggested late Middle–Late Triassic age for these assemblages is based on the record of subzones C and D of the *Alisporites* Zone recognized for Antarctica (Kyle and Schopf, 1982).

Some additional localities cannot unambiguously be placed into any of these groups due to poor stratigraphic control; however, since the fossil content can be referred to the Triassic, they were considered herein as evidence for plant distribution in the Triassic of Antarctica (Fig. 3). For example, Townrow (1967a) described a flora from erratic boulders in the CTM that probably derived from the Falla Formation (Cantrill et al., 1995). This flora includes four species of *Dicroidium,* one ginkgoalean, and one species of *Taeniopteris,* and is considered to be no older that Middle Triassic (Townrow, 1967a). From Horseshoe Mountain and Shapeless Mountain in SVL, Rigby (1985) reported



| | | CTM | | | | | | | | | | | SVL | | | | | | | | NVL | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Graphite Peak | Mount Rosenwald | Fremouw Peak | Gordon Valley | Alfie´s Elbow | Mount Falla | Schroeder Hill | Marshall Mountains | Mount Wisting | Mount Bumstead | Misery Peak | Allan Hills A | Mount Bastion A,B | Portal Mountain | Allan Hills C | Mount Bastion C | Shapeless Mountain | Mount Fleming | Horseshoe Mt. | Timber Peak | Runaway Hills | Vulcan Hills |
| *Litothallus* | *L. ganovex* | | | | | ● | | | | ● | | ● | ○ | | | ● | | ● | | | ● | | |
| *Thallites* | *T. sp.* | | | | | | | | | | | | | | | ● | | | | | | | |
| *Lycophyte* | *Indet.* | | | | | | | | | | | | | | | | | | | | | | |
| *Neocalamites* | *N. sp.* | | | ● | ● | ● | | | | ● | | | | ○ | ○ | ● | | ● | | ○ | | | |
| *Phyllotheca* | *P. brookvalensis* | | ○ | | | | | | | | | | | | | | | | | | | | |
| *Spaciinodum* | *S. collinsonii* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Scolecopteris* | *S. antarctica* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Ashicaulis* | *A. beardmorensis* | | | ★ | | | | | | | | | | | | | | | | | | | |
| | *A. woolfei* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Osmunda* | *O. claytoniites* | | | | | | | | | | | | | | | ● | | | | | | | |
| *Cladophlebis* | *C. sp.* | | | | | | | | | ● | | | | | | | ○ | | | | ● | | |
| *Gleichenipteris* | *G. antarcticus* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Antarctipteris* | *A. sclericaulis* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Tomaniopteris* | *T. katonii* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Soloropteris* | *S. rupex* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Schopfiopteris* | *S. repens* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Fremouwa* | *F. inaffecta* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Schleporia* | *S. incarcerata* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Lepidopteris* | *L. langlohensis* | | | | | | | | | | | | | | | | | | | | ● | | |
| *Umkomasia* | *U. resinosa* | | | ★ | | | | | | | | | | | | | | | | | | | |
| | *U. uniramia (a)* | | | | | ● | ● | | | | | | | | | ● | | ● | | | | | |
| *Pteruchus* | *P. fremouwensis* | | | ★ | | | | | | | | | | | | | | | | | | | |
| | *P. sp. (a)* | | | | | ● | | | | | | | | | | ● | | | | | | | |
| *Kykloxylon* | *K. fremouwensis* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Jeffersonioxylon* | *J. gordonense* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Rhexoxylon* | *R. sp.* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Dicroidium* | *D. fremouwensis* | | | ★ | | | | | | | | | | | | | | | | | | | |
| | *D. odontopteroides* | | | ● | | ● | ● | | ● | ● | ○ | | ○ | ○ | ○ | ● | ○ | ● | ○ | ○ | ● | | ● |
| | *D. dubium* | | | | | ● | | | | | ○ | | | | ○ | ● | | ● | | ○ | ● | | |
| | *D. elongatum* | | | | | ● | ● | ● | | ● | ○ | | ○ | | ○ | ● | ○ | ○ | | ○ | ● | | |
| | *D. crassinervis* | | | | ● | | ● | ● | ● | ● | ○ | | | | | ● | ○ | ● | | | ● | | |
| | *D. dutoitii* | | | | ● | ● | | | | | | ○ | | | | ● | | | | | | | |
| | *D. coriaceum* | | | | | | | | | | | | | | | | ○ | ○ | | | ● | | |
| | *D. spinifolium* | | | | | | | | | | | | | | | | ○ | | | | ● | | |
| | *D. sp. A* | | | | | | | | | | | | | | | | | | | | ● | | |
| | *D. zuberi* | ○ | ○ | | | | ● | | | | ○ | | ○ | ○ | | ● | | ○ | | ○ | | | |
| *Petriellaea* | *P. triangulata* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Antarcticycas* | *A. schopfii* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Delemaya* | *D. spinulosa* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Sphenobaiera* | *S. schenki* | | | | | | | | ● | ● | | | | ○ | ○ | | | ● | | | | | |
| | *S. sp.* | | | | | | ★ | | | | | | | | | | | | | | | | |
| *Czekanowskia* | *C. sp.* | | | | | ● | | | ● | ● | | | | | | | | ○ | | | | | |
| *Telemachus* | *T. elongatum* | | | | | ● | ● | | | | | | | | | ● | | | | | | | |
| | *T. sp.* | | | | | | | | | | | | | | | ● | | | | | | | |
| *Parasciadopitys* | *P. aequata* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Leastrobus* | *L. fallae* | | | | | | ★ | | | | | | | | | | | | | | | | |
| *Notophytum* | *N. krauselii* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Heidiphyllum* | *H. elongatum* | | | | | ● | ● | | | | | | | | ○ | ● | ○ | ● | | | ● | | ● |
| *Voltziopsis* | *V. africana* | ○ | | | | | | | | | | | | | | | | | | | | | |
| | *cf. V. angusta* | | ○ | | | | | | | | | | | | | | | | | | | | |
| *Linguifolium* | *L. gracile* | | | | | | | | | | | | | | | | | ● | | | | | |
| | *L. tenison-woodsii* | | | | | | | | | | | | | | | | ○ | ○ | | | | | ● |
| | *L. lillieanum* | | | | | | | | | | | | | | | | ○ | | | | | | ● |
| | *L. steinmannii* | | | | | | | | | | | | | | | | | ○ | | | | | |
| | *L. sp.* | | | | | | | | | | | | | | | | | | | ○ | | | |
| *Dejerseya* | *D. sp.* | | | | | | ● | | | | | | | | | | | ○ | | | | | ● |
| *Taeniopteris* | *T. sp.* | | | | | ● | | | ● | ● | ○ | | | | | ● | | ● | | | | ● | |
| *Probolosperma* | *P. antarcticum* | | | ★ | | | | | | | | | | | | | | | | | | | |
| *Dordrechtites* | *D. sp* | | | ★ | | | | | | | | | | | | | | | | | | | |

**FIGURE 3**—Distribution of fossil species among the different Triassic localities from Antarctica. Circles = impression-compression assemblages; stars = sites with permineralized plants; filled circles = species in KUPB or GIX collections; open circles = references from the literature. Stratigraphic position of each locality is represented by colors (see Fig. 2). Uncolored localities are those of uncertain stratigraphic position.

*Neocalamites*, several species of *Dicroidium*, *Linguifolium*, and *Baiera*, as well as *Heidiphyllum elongatum*, *Dejerseya* sp., and *Czekanowskia*. No detailed information for these collections has been given; however, the fossils were probably collected from the Middle and Upper Triassic of Members B and C of the Lashly Formation. In NVL, *Taeniopteris* sp. occurs in siltstone blocks among slope debris at Runaway Hills (Bomfleur et al., 2007, 2011a). Micro- and megafloras from other localities in NVL indicate that the plant-bearing Beacon deposits in this region are no older than Middle Triassic (e.g., Tessensohn and Mädler, 1987).

## NATURAL PLANT GROUPS IN THE TRIASSIC OF ANTARCTICA

The distribution of species from the various localities is summarized in Figure 3. A major focus of this contribution is evaluating the distribution of (morpho)species as evidence to support the presence of natural groups in the Triassic of Antarctica. The systematic classification follows that proposed by Taylor et al. (2009).

### Thalloid Fossils

*Litothallus ganovex* (Bomfleur et al., 2009) is an enigmatic thalloid organism that appears to be relatively common in the Middle and Upper Triassic of the Transantarctic Mountains, as it is currently known from NVL, SVL, and the Shackleton Glacier area (Fig. 3). This plant is preserved in the form of compression fossils (Fig. 4A) and isolated sheets of cells (Fig. 4B). The simple, rosettelike thalli are up to 10 cm across and usually show a distinctive, homogeneous cell pattern composed of isodiametric, rounded polygonal cells (Fig. 4B). *Litothallus ganovex* has been suggested to represent a crustose freshwater macroalga (Bomfleur et al., 2009), because it resembles certain extant members of the red algal order Hildenbrandiales in macromorphology and cellular details. Other thallophyte fossils are exceedingly rare in the Triassic of the Transantarctic Mountains and represented only by poorly preserved compressions of putative liverworts. These occur in the form of dichotomously dividing, strap-shaped thalli with a more or less pronounced midrib. These fossils are assigned to broadly defined morphotaxa such as *Thallites* due to the poor preservation and lack of features indicating the biological affinities. Dispersed cuticle fragments tentatively assigned to bryophytes have recently been described from Timber Peak (Bomfleur and Kerp, 2010a).

### Lycopsids

Although only one lycopsid megafossil has been reported to date, several independent lines of evidence document the presence of the group in the Triassic plant communities of Antarctica. Lycopsid spores, e.g., *Aratrisporites* spp. and *Uvaesporites verrucosus*, were identified in the Fremouw and Falla Formations (Farabee et al., 1990; Askin and Cully, 1996) in the Beardmore and Shackleton Glacier areas in the CTM. Triassic strata of the Amery Group, Prince Charles Mountains, yielded a large diversity of isoetalean or selaginellalean micro- and megaspores as well as isolated lycopsid sporangia (Cantrill and Drinnan, 1994; McLoughlin et al., 1997; Lindström and McLoughlin, 2007). More recently, Bomfleur et al. (2011c) described strap-shaped leaves of *Mesenteriophyllum serratum* from the so-called Alfie's Elbow locality (Axsmith et al., 2000) near the head of the Shackleton Glacier (CTM). The leaves are associated with sporophylls and sporangia on the same slab. The plant parts are assigned to the Pleuromeiales, but all are poorly preserved impressions and coalified compressions (Fig. 4F).

### Equisetales

After the peak of equisetalean diversity and distribution during the late Paleozoic (including the arborescent Calamitaceae), the Mesozoic is characterized by a decrease in the diversity of this group. Equisetales in the Triassic of Antarctica are known from well-preserved permineralizations and compressions included in the family Equisetaceae (Osborn and Taylor, 1989; Osborn et al., 2000; Ryberg et al., 2008, Schwendemann et al., 2010a). The permineralized equisetophyte, *Spaciinodum collinsonii* Osborn and Taylor emend. Schwendemann et al. (2010a), is known from stems, leaves, buds, and reproductive structures. Compression fossils of equisetaleans include stems and leaves of *Neocalamites* (Figs. 4C–D). Poorly preserved leafy axes of *Phyllotheca brookvalensis* have also been noted from Lower Triassic rocks of Mount Rosenwald, Shackleton Glacier area, CTM (Retallack, 2005); these were later transferred to the newly erected genus *Townroviamites* (Holmes, 2001). There are several similarities in morphology and organization of stems and leaves between *Spaciinodum* and *Neocalamites*, and further research may indicate that they are related or perhaps represent different preservational states of organs produced by the same plant. Recently described permineralized fertile specimens of *Spaciinodum* (Fig. 4E; Schwendemann et al., 2010a) show in general terms the classic organization (e.g., terminal cones with whorls of peltate sporangiophores, absence of intercalated bracts) of fertile *Neocalamites* species (Vladimirovicz, 1958; Kon'no, 1962; Escapa and Cúneo, 2006).

### Ferns

Ferns were an important and diverse component of high-latitude plant communities during the Triassic (Millay and Taylor, 1990; Skog, 2001). On continental Antarctica, this group shows a high diversity with several families represented by both compression-impressions and permineralizations. Although some of these ferns are almost identical to extant species, others cannot be assigned to any modern family.

Eusporangiate ferns are represented by a single marattialean species (Delevoryas et al., 1992). *Scolecopteris antarctica* is known from permineralized fertile remains showing typical marattialean characters (Fig. 5A), i.e., radial synangia borne on *Pecopteris*-like pinnules. In contrast, leptosporangiate ferns are very diverse and abundant, with representatives of the Osmundaceae, Gleicheniaceae, Matoniaceae, Dipteridaceae, and additional remains tentatively assigned to the Cyatheaceae (Millay and Taylor, 1990). The Osmundaceae (Osmundales) is represented in the Middle Triassic permineralized peat by stems of *Ashicaulis beardmorensis* (Schopf) Tidwell (originally *Osmundacaulis*; Schopf, 1978), and stems and fronds of *A. woolfei* (Fig. 5B; Rothwell et al., 2002). Several characters in the latter species suggest close affinities with *Osmunda*, one of the four living genera of the family (Rothwell et al., 2002). Another osmundaceous fern is *Osmunda claytoniites* from the Middle Triassic of southern Victoria Land (Figs. 5C–E). This species is known from very well-preserved compression-impressions of both vegetative and fertile fronds, representing one of the oldest records of foliar-borne *Osmunda* sporangia (Phipps et al., 1998). The fossil species is remarkably similar to extant *O. claytoniana*, showing an interesting case of evolutionary stasis (Phipps et al., 1998) that forms an important constraint for studies of fern diversification (e.g., Schuettpelz and Pryer, 2007).

The Gleicheniaceae (Filicales) is represented by the Middle Triassic *Gleichenipteris antarcticus* from the Fremouw Peak permineralized peat (Phipps et al., 2000). This taxon includes permineralized sporangia attached to poorly preserved foliar units (Fig. 5G). Although fragmented, the combination of fertile characters in *G. antarcticus* unequivocally places this fossil fern within the Gleicheniaceae. The sporangia of *G. antarcticus* were found closely associated with the stem *Antarctipteris sclericaulis* (Fig. 5F), which has been tentatively assigned to the Gleicheniaceae (Millay and Taylor, 1990).

The record of the Matoniaceae (Filicales) in the Triassic permineralized peat consists of two species of anatomically preserved organs. *Tomaniopteris katonii* (Fig. 6A) is known from permineralized sori and sporangia (Klavins et al., 2004). Stems of *Soloropteris rupex* (Fig. 6B; Millay and Taylor, 1990) were tentatively included in this family as well. This monotypic genus shows a combination of characters strongly suggesting affinities with the Matoniaceae, including peltate sori, an indusium composed of multiseriate segments, and sporangia with vertical and incomplete annuli. Weber (2008) considered that *Soloropteris* may even represent better evidence for the presence of Matoniaceae in the early Mesozoic than *Tomaniopteris*. Along with the Gleicheniaceae, the Matoniaceae is considered one of the most

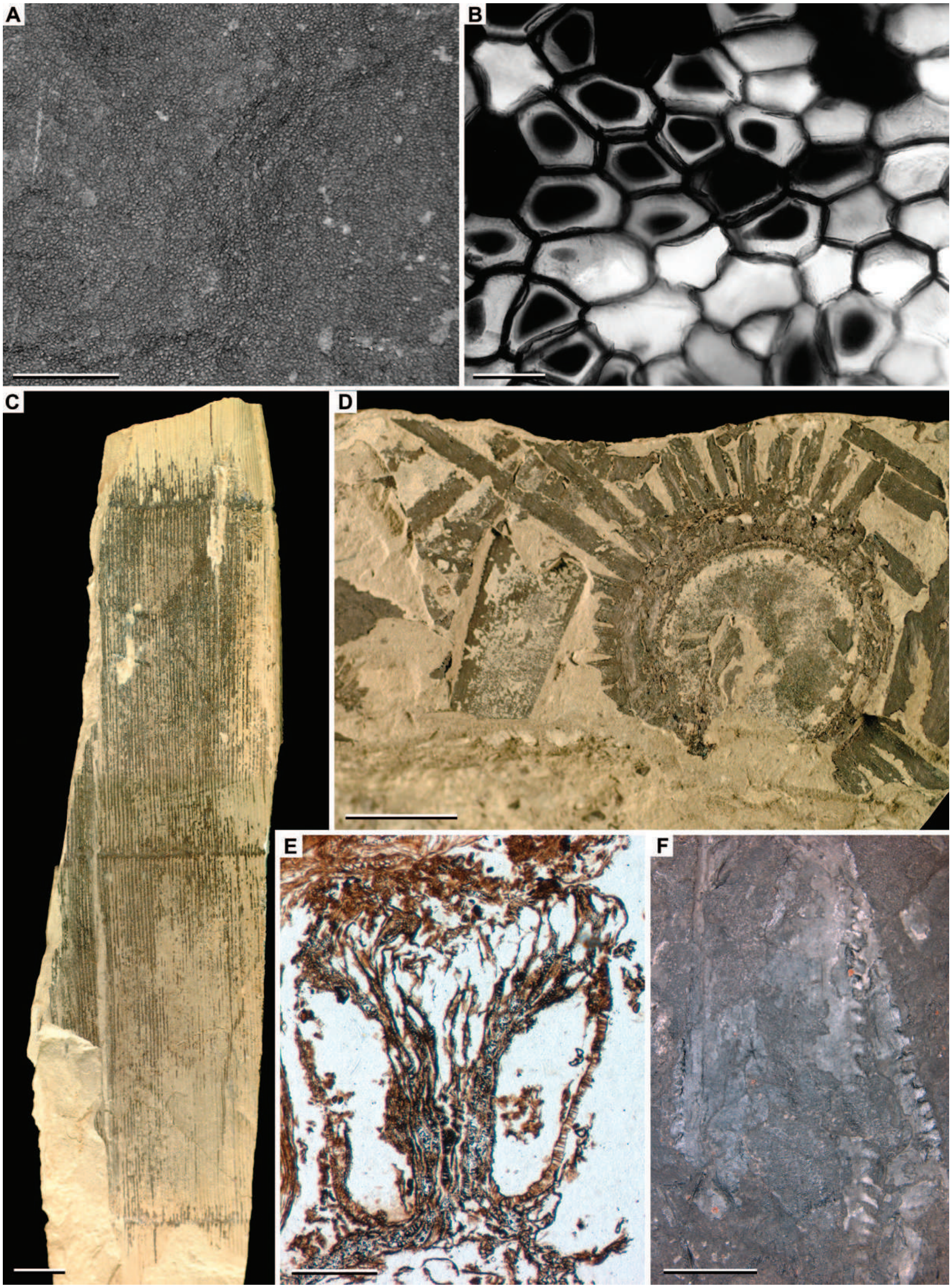


**FIGURE 4**—Thalloid fossils (A–B), Equisetaceae (C–E), and lycopsid (F) from the Triassic of Antarctica. All are compression fossils, except for E, a permineralization. A) Thallus of *Lithothallus ganovex*. Timber Peak, GIX-TI13/5-071a(001-slide 1); scale = 50 μm. B) Detail of *L. ganovex* thallus showing homogeneous cell pattern. Alfie's Elbow, T11-720a; scale = 1 mm. C) *Neocalamites* sp. axis showing articulate organization with nodes and internodes. Misery Peak T 6079A; scale = 1 cm. D) *Neocalamites* sp. nodal diaphragm showing a whorl of linear leaves. Allan Hills, Member C, T11-657A; scale = 1 cm. E) *Spaciinodum collinsonii* transverse section of a cone showing a single peltate sporangiophore (cone axis at the bottom). Fremouw Peak, slide 23,017; scale = 250 μm. F) Poorly preserved *Mesenteriophyllum serratum* leaf showing characteristic serrate margin (right). Alfie's Elbow, T 5568c; scale = 5 mm.

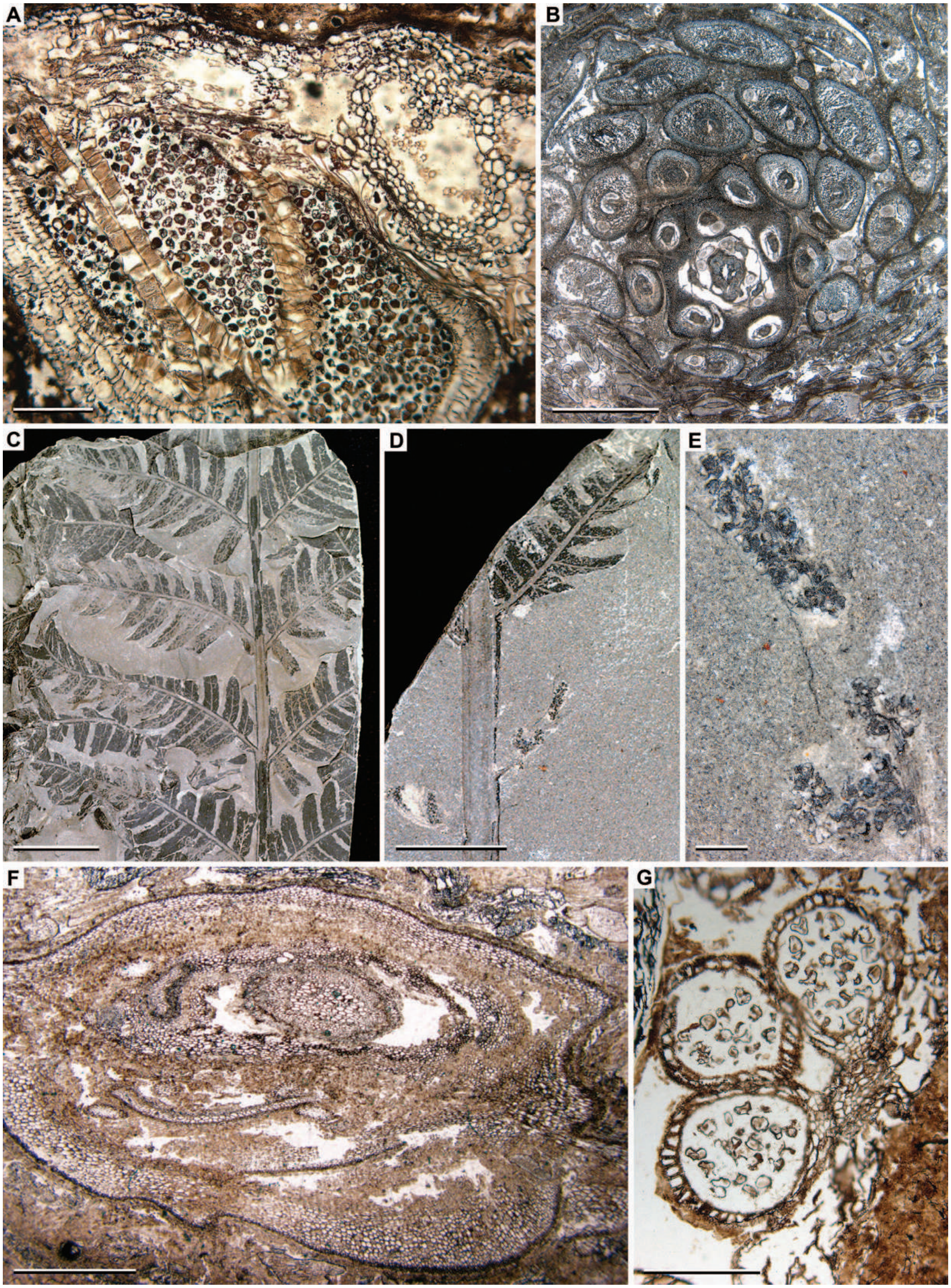


**FIGURE 5**—Fern fossils from the Triassic of Antarctica; Marattiaceae (A), Osmundaceae (B–E), and Gleicheniaceae (F–G). Fremouw Peak permineralizations (A–B; F–G); compressions from the Allan Hills (C–E). A) Oblique section of permineralized *Scolecopteris antarctica* with thick-walled synangia filled with spores. 15,711 A #24; scale = 2 mm. B) Transverse section through stem (center) and numerous surrounding petioles of *Ashicaulis woolfei*. 12,825 C top; scale = 5 mm. C) *Osmunda claytoniites* sterile frond. T 11 412; scale = 2 cm. D) *Osmunda claytoniites* showing part of sterile pinna above and two alternate fertile pinnae below. T 8 246d; scale = 1 cm. E) Higher magnification of fertile pinna of *O. claytoniites* showing clusters of sporangia. T 11 246; scale = 1 mm. F) Stem of *Antarctipteris sclericaulis* in transverse section showing central protostele. 10,424 G bot #2θ; scale = 2 mm. G) Sporangia of *Gleichenipteris antarcticus*. 11,233 A bot #1; scale = 250 µm.

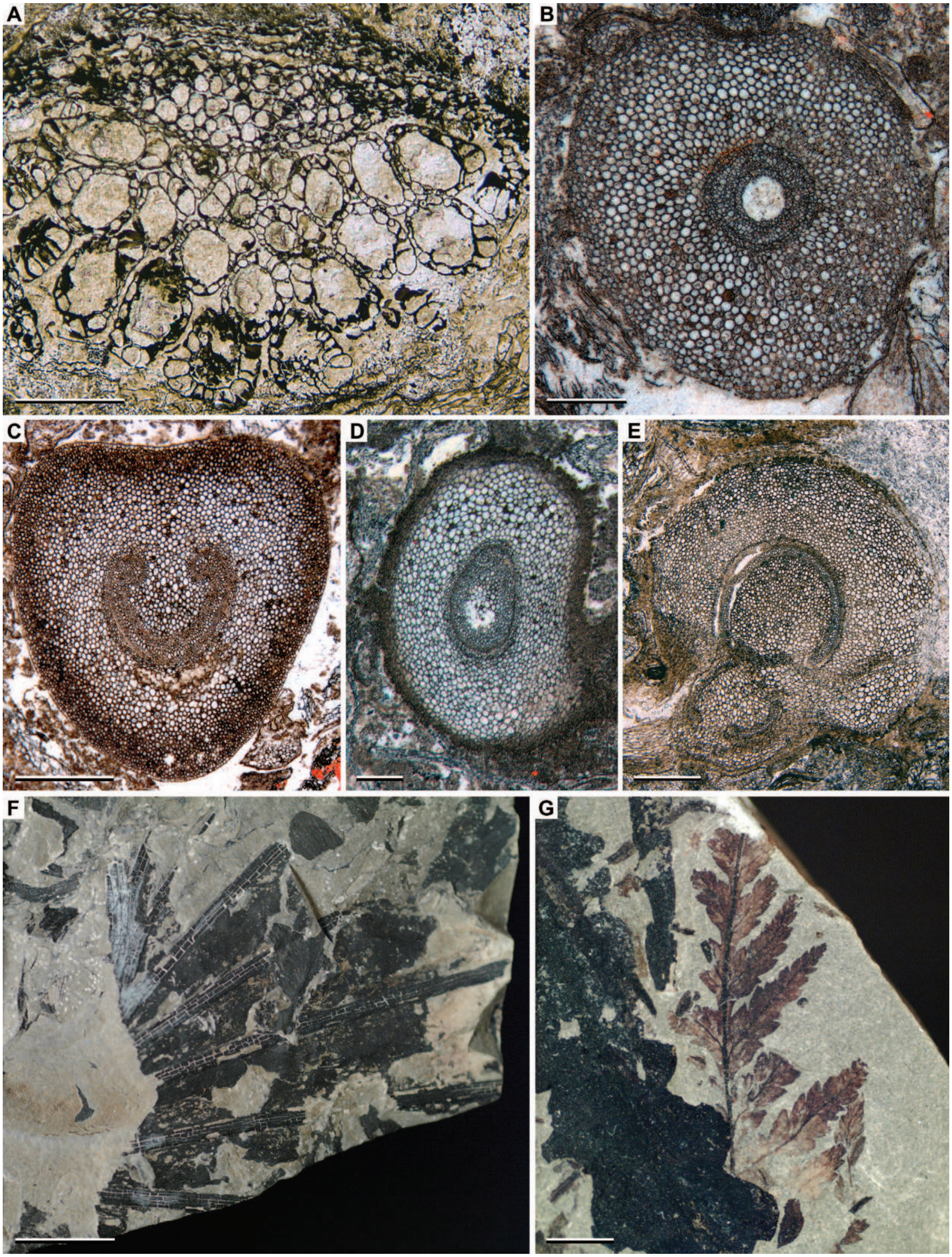


**FIGURE 6**—Matoniaceae (A, possibly B), Cyatheaceae (C), and ferns *incertae sedis* (D–G) from the Triassic of Antarctica. A) A sorus of *Tomaniopteris katonii* showing sporangia attached in rows to a receptacle (above). 11,248 B #4; scale = 250 µm. B) Transverse section through siphonostelic stem of *Soloropteris rupex*. 13,762 B top; scale = 0.5 mm. C) Transverse section of petiole of *Schopfiopteris repens*. 10,424 G bot #2β; scale = 50 µm. D) Stem of *Fremouwa inaffecta* in transverse section. 10,103 B1, #2α; scale = 50 µm. E) Stem of *Schleporia incarcerata* in transverse section with departing branch trace (lower left). 10,119 D bot #16β; scale = 1 mm. F) *Dictyophyllum* sp. partial frond. Alfie's Elbow, T 1205; scale = 1 cm. G) *Sphenopteris* sp. foliage. Mount Falla, T 7 175; scale = 5 mm. A–E = permineralizations from Fremouw Peak.

ancient clades of leptosporangiate ferns, which is confirmed by the early occurrence of the family in the lower Middle Triassic of Antarctica. *Tomaniopteris katonii* has been also used as a minimum age constraint for the stem of the Matoniaceae clade in a study of epiphytic fern diversification (Schuettpelz and Pryer, 2007).

The Dipteridaceae (Filicales) was only briefly mentioned as being represented by *Dictyophyllum* sp. at the Upper Triassic Alfie's Elbow locality, in the Shackleton Glacier region, CTM (Axsmith et al., 2000). This fossil (Fig. 6F) shows characters consistent with the genus, such as the pinnate leaf and reticulate venation. Three subgenera were proposed for *Dictyophyllum* (Herbst, 1992), but the fragmentary nature of the Antarctic specimen precludes a more detailed determination. *Dictyophyllum* constitutes an important component of several Northern Hemisphere Late Triassic floras (Corsin and Waterlot, 1979) but is less common in the Triassic of the Southern Hemisphere. In this region, *Dictyophyllum* is one of the most conspicuous taxa in the Early Jurassic, probably indicating wet and warm climatic conditions. On the Antarctic Peninsula, the Dipteridaceae is represented by several taxa in the Jurassic, e.g., *Goeppertella*, which has been used for biostratigraphy (Rees, 1993; Rees and Cleal, 2004).

Additional permineralized fern remains from the Triassic of Antarctica show more ambiguous systematic positions. For instance, the stems of *Schopfiopteris repens* (Fig. 6C) were tentatively assigned to the Cyatheaceae (Millay and Taylor, 1990), although the absence of fertile organs hampers more detailed comparisons. In addition, *Fremouwa inaffecta* and *Schleporia incarcerata* (Figs. 6D–E) were originally described as ferns *incertae sedis*. Stems with ectophloic siphonosteles characterize all three species. Finally, compressed fern foliage assigned to different morphogenera has been collected from several Triassic sites (e.g., *Sphenopteris* sp., Fig. 6G). Even though all of these plant fossils cannot be positively assigned to any natural family at present, they add to the diversity of leptosporangiate fern communities in the Triassic of Antarctica.

## Pteridosperms (Seed Ferns)

Seed ferns are common and in many cases dominant elements in Triassic plant fossil assemblages of the CTM. Although they can be assigned to a variety of natural groups, the vast majority of pteridosperm fossils can be attributed to the Corystospermales, a group that dominated floras in this region and throughout Gondwana during the Middle and Late Triassic (Anderson et al., 1999).

The corystosperm leaf morphogenus *Dicroidium* ranks among the most common Triassic compression-impression fossils in Antarctica (Figs. 7A–G) and adjacent regions of Gondwana. The fronds are small to medium size and characterized by an acute-angled bifurcation occurring within the lower half of the rachis (Gothan, 1912). Leaf architecture and pinnule shapes in *Dicroidium* are highly variable (Figs. 7A–G), which renders a systematic classification difficult (Anderson and Anderson, 1983). Fronds may be simple and entire margined (*D. dutoitii*, *D. coriaceum*) or once-to-several-times pinnate. Pinnate fronds may bear linear, straight, and single-veined pinnules (*D. elongatum*), rhomboidal pinnules with predominantly odontopteroid venation (e.g., *D. odontopteroides*, *D. crassinervis*), or elongated tongue-shaped pinnules with alethopteroid venation (e.g., *D. dubium*). The largest Antarctic *Dicroidium* species, *D. zuberi* (Fig. 7B), has bipinnate fronds reaching up to 40 cm long. Corystosperm reproductive organs occur frequently and commonly on the same bedding planes with *Dicroidium* foliage.

Corystosperm pollen organs are assigned to the genus *Pteruchus* (Figs. 8B, D); they consist of naked axes with suboppositely to alternately arranged, short-stalked microsporophylls that bear abaxial clusters of spindle-shaped pollen sacs (e.g., Yao et al., 1995; Taylor and Taylor, 2009). Pollen grains are bisaccate, nontaeniate, and have reticulate saccus ornamentation (Osborn and Taylor, 1993). They are assigned to the dispersed pollen genera *Alisporites*, *Falcisporites*, and *Pteruchipollenites* (e.g., Balme, 1995; Taylor et al., 2006). The genus *Umkomasia* is used for the ovulate organs of the corystosperms (Figs. 8A, E) and consists of a three-dimensional branching system (Thomas, 1933; Klavins et al., 2002). A recurved cupule on a short stalk is attached at the end of each ultimate branchlet. Ovules are borne singly or in pairs and are almost fully enclosed by the cupule. The micropylar end of the ovule bears a curved, bifid protrusion of the integument that usually extends beyond the cupule margin in compression specimens (Thomas, 1933).

Plant fossil localities from the CTM have yielded a wealth of information about the paleobiology of the Corystospermales. Of special interest are the permineralized peat deposits from Middle Triassic rocks of Fremouw Peak, from which anatomically preserved leaves (*D. fremouwensis*; Pigg, 1990), pollen organs (*Pteruchus fremouwensis*; Yao et al., 1995), ovulate organs (*U. resinosa*; Klavins et al., 2002), and stems (*Kykloxylon fremouwensis*; Meyer-Berthaud et al., 1992, 1993) have been described. The presence of a particular type of secretory cavity in all of these organs enabled a whole-plant reconstruction of the corystosperm plant from Fremouw Peak, based on a line of anatomical evidence following Oliver and Scott (1904). The *D. fremouwensis* plant is reconstructed as a forest tree (Taylor, 1996) up to 30 m tall with a *Ginkgo*-like growth habit, which contrasts with the tree-fern- and liana-like reconstructions of *Dicroidium* plants from South America (Petriella, 1978), and underscores the wide morphological variability in the group (Taylor et al., 2006). In addition, the Upper Triassic Alfie's Elbow site (Shackleton Glacier area, CTM) has yielded a corystosperm stem fragment with attached leaves (*D. odontopteroides*) and short shoots bearing ovulate organs assigned to *U. uniramia* (Fig. 7E; Axsmith et al., 2000). The specimen represents the first evidence of different corystosperm organs in actual organic connection (Taylor et al., 2006). A remarkably diverse *Dicroidium* flora containing seven species, all with well-preserved cuticles, has been described from the Upper Triassic of Timber Peak in NVL (Bomfleur and Kerp, 2010a). This material promises to enable a clearer delimitation of the genus and some of its individual species, based on a combination of morphology and epidermal anatomy.

Further seed fern groups are represented in Antarctica by sporadic occurrences. The Petriellales are an enigmatic group of pteridosperms that was erected based on anatomically preserved ovuliferous organs from the Middle Triassic permineralized peat of Fremouw Peak, CTM (Taylor et al., 1994). The isolated fructifications consist of once-bifurcated fertile axes that each bear a terminal leaflike cupule containing two to six ovules (Fig. 8C). Ovules and seeds are small and triangular in cross section (Taylor et al., 1994). Other petriellalean organs are so far lacking in Antarctic assemblages, but are known from other regions of Gondwana. The petriellalean foliage *Rochipteris* (including *Kannaskoppifolia*) is currently known from South America, South Africa, Australia, and New Zealand; it consists of wedge- to fan-shaped, entire to deeply dissected leaves with spreading venation that shows characteristic anastomoses (Herbst et al., 2001; Anderson and Anderson, 2003; Barone-Nugent et al., 2003). Compressed ovulate organs (*Kannaskoppia*) and pollen organs (*Kannaskoppianthus*) have been described from the Molteno Formation of South Africa; some of these occur in organic connection to stems bearing *Rochipteris* foliage (Anderson and Anderson, 2003).

Although known from other parts of Gondwana (and Pangea), peltasperms are rarer in the Triassic of Antarctica and represented by fragments of *Lepidopteris* (Fig. 7H). A previously undescribed frond fragment from the Upper Triassic of Mount Wisting is here identified as the peltasperm foliage *Lepidopteris stormbergensis*. Fragmented but well-preserved dispersed cuticles of *L. langlohensis* have recently been described from the Upper Triassic of Timber Peak (Bomfleur and Kerp, 2010a), and McLoughlin et al. (1997) illustrated *Lepidopteris* leaf fragments and dispersed cuticles from Lower Triassic strata of the Prince Charles Mountains.

**FIGURE 7**—Corystospermales (vegetative, A–G) and Peltaspermales (vegetative, H) from the Triassic of Antarctica. A, D–E from Alfie's Elbow site; B–C, F–G from the Allan Hills. A) *Dicroidium odontopteroides* frond. T 12 1048a; scale = 1 cm. B) *Dicroidium zuberi.* T 11 855A; scale = 5 cm. C) *Dicroidium elongatum.* T 11 451B; scale = 1 cm. D) *Dicroidium odontopteroides.* T 12 1002; scale = 1 cm. E) *Dicroidium dubium*. T 1270; scale = 1 cm. F) *Dicroidium dutoitii.* T 11 604; scale = 1 cm. G) *Dicroidium spinifolium.* T 11 454b; scale = 1 cm. H) *Lepidopteris* sp. Mount Wisting, T 1891; scale = 1 cm.

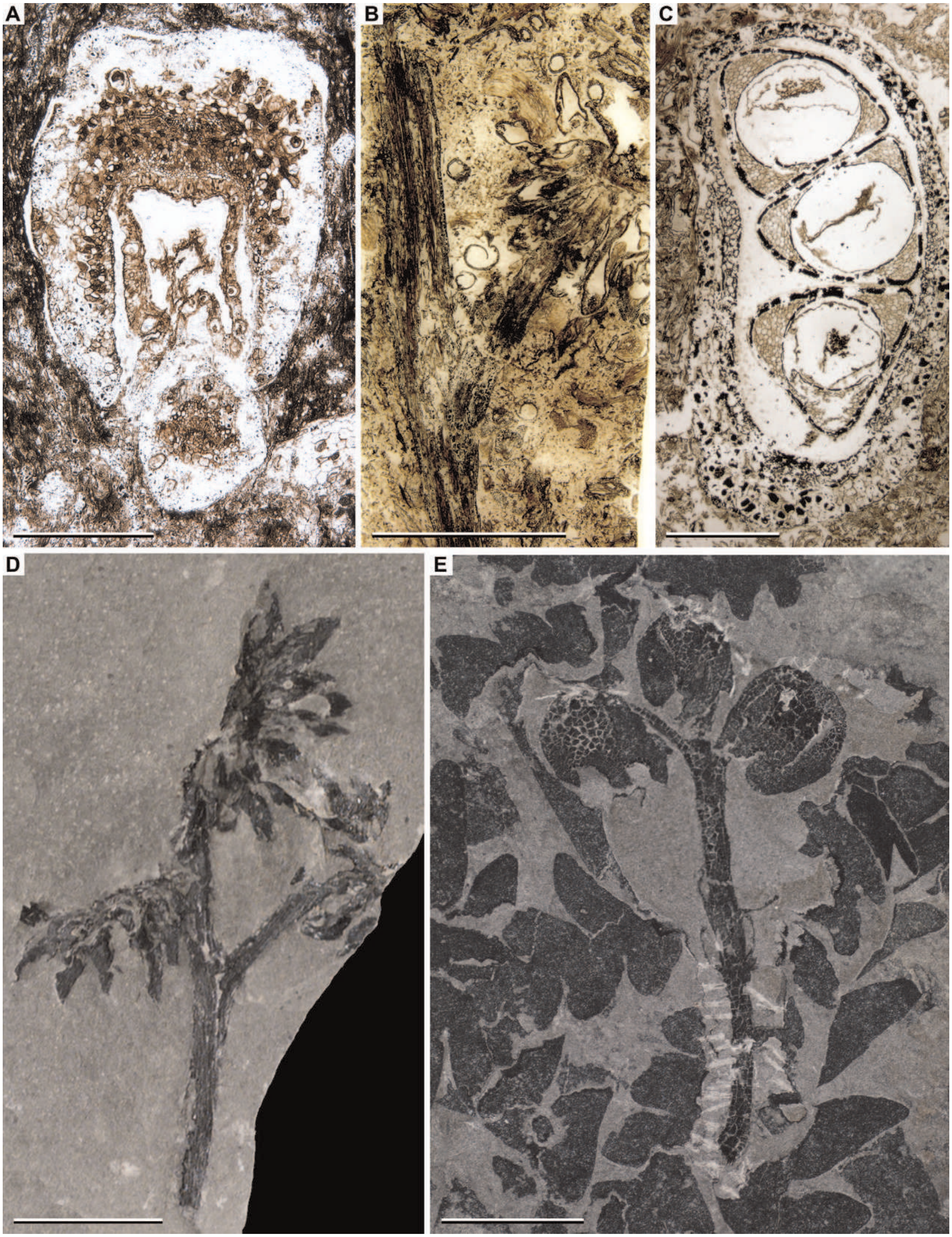


**FIGURE 8**—Petriellales (C) and Corystospermales (reproductive, A–B; D–E) from the Triassic of Antarctica. A–C = permineralizations from Fremouw Peak. A) Transverse section of permineralized cupule of *Umkomasia resinosa* with a single ovule inside and cupule stalk (below). 11,323 DE #88; scale = 1 mm. B) *Pteruchus fremouwensis.* Longitudinal section through an axis (left) with attached, stalked microsporophyll-bearing pollen sacs. 10,145 D side 5a; scale = 4 mm. C) *Petriellaea triangulata*. Transverse section of cupule showing three ovules. 10,023 A #17; scale = 0.5 mm. D) *Pteruchus* sp. showing three microsporophylls. Allan Hills, T 11 330A; scale = 5 mm. E) *Umkomasia uniramia* stalk bearing three cupules; pieces of *Dicroidium* foliage. Alfie's Elbow, T 12 1033; scale = 1 cm.

Further foliage morphotypes, which cannot yet be assigned with certainty to any particular group of seed ferns, occur in the Triassic of Antarctica. *Linguifolium* is a presumed seed-fern leaf that was widespread in southern Gondwana during the Middle and Late Triassic (e.g., Retallack, 1977; Artabe et al., 2001; Anderson and Anderson, 2003). In Antarctica, *Linguifolium* has been described from localities in North and South Victoria Land (Gabites, 1985; Rigby, 1985; Tessensohn and Mädler, 1987). The simple, narrow elliptic to lanceolate leaves are entire margined and have a strong midvein. Secondary veins arise at acute angles, curve toward the margin, and dichotomize up to two times (Retallack, 1981). Individual species of *Linguifolium* are distinguished only by differences in gross morphology, e.g., leaf width and shape, and it has been suggested that future studies will prove at least some of the species to be synonymous (Anderson and Anderson, 2003). Species recorded from Antarctica include *L. gracile*, *L. tenison-woodsii*, *L. arctum*, and *L. steinmannii* (Rigby, 1985; Gabites, 1985). A similar leaf morphotype is *Dejerseya*, which is discussed below under *incertae sedis*).

### Cycadales

At present, the Cycadales is represented in the Triassic of Antarctica by a single plant, *Antarcticycas schopfii*, which occurs in the permineralized peat from Fremouw Peak, CTM, and is probably the most completely known fossil cycad of any age (Hermsen et al., 2009). The plant is known from stems (Fig. 9A; Smoot et al., 1985), cataphylls (scale-like leaves; Hermsen et al., 2006), and roots with mycorrhizal fungi (Millay et al., 1987; Stubblefield et al., 1987; Phipps and Taylor, 1996) assigned to the genus *Antarcticycas*, probable pollen cones of *Delemaya spinulosa* (Fig. 9B; Klavins et al., 2003, 2005; Schwendemann et al., 2009), and detached leaves assigned to *Yelchophyllum omegapetiolaris* (Fig. 9C; Hermsen et al., 2007a). The various parts were reconstructed based on anatomical features as a single natural species (Hermsen et al., 2009), which is interpreted to have been a small plant, possibly with a subterranean stem. There is some evidence that *Antarcticycas schopfii* may have been insect pollinated (Klavins et al., 2005).

In compression floras, by contrast, sparse occurrences of the morphogenus *Taeniopteris* constitute the only remains with possible cycadalean affinities (Fig. 9D; Townrow, 1967a). Since leaves with *Taeniopteris*-like morphology are known to occur in several other plant groups, i.e., Bennettitales and Pentoxylales (e.g., Drinnan and Chambers, 1985), the natural affinities of the Antarctic *Taeniopteris* remain unclear.

### Ginkgophyta

Fossil remains assigned to the Ginkgoales are widely distributed on all the Gondwanan continents during the Triassic (Anderson and Anderson, 2003 and references therein). The most common leaf morphotaxa of this group are *Baiera*, *Sphenobaiera*, *Ginkgophyllum*, and *Ginkgo*. In contrast to the high diversity of this group in other regions of Gondwana (e.g., Argentina, Zamuner et al., 2001), the only previous records of Ginkgoales in the Triassic of Antarctica are three species of *Baiera* reported from Shapeless Mountain and Horseshoe Mountain in SVL (Gabites, 1985; Rigby, 1985). Unfortunately, no stratigraphic specifications or fossil illustrations were included in the latter contribution.

There are several ginkgoalean-like leaves from different localities in the collections of the University of Kansas. Numerous specimens of *Sphenobaiera schenkii* occur in shales of the Upper Triassic Lashly Formation at Shapeless Mountain (SVL, Fig. 9F), and additional remains were recovered from the Falla Formation (also Upper Triassic) in the Marshall Mountains. The absence of a distinctive petiole, in addition to the highly dissected and wedge-shaped leaves (Fig. 9F), are criteria for inclusion in the morphogenus *Sphenobaiera* (Anderson and Anderson, 1989). A second species was recovered from the Falla Formation at Mount Falla in the CTM (Fig. 9E; *Sphenobaiera* sp.). In addition, a single specimen of the genus *Hamshawvia* Anderson and Anderson (2003), an ovuliferous reproductive organ, was recovered from the Alfie's Elbow site (Axsmith et al., 2000). In the Upper Triassic Molteno Formation, *Hamshawvia* occurs in association with *Sphenobaiera*-like leaves, and these specimens were assigned to the newly proposed order Hamshawviales (Anderson and Anderson, 2003). A similar association was also noted in the Middle Triassic of Australia (Holmes and Anderson, 2007); however, leaves of ginkgoalean appearance may represent the vegetative parts of different natural groups. Thus, Antarctic *Sphenobaiera* leaves may not represent foliage of true Ginkgoales.

### Conifers

Compared to the Permian diversity and especially to their explosive radiation during the Early Jurassic, the diversity of Southern Hemisphere conifers in the Triassic is rather low. In the present collections, conifers are represented by such isolated organs as permineralized branches and leaves of *Notophytum* (Meyer-Berthaud and Taylor, 1991; Axsmith et al., 1998), compressed strap-shaped leaves of *Heidiphyllum* (Fig. 10D), the permineralized pollen cone *Leastrobus* (Fig. 10E; Hermsen et al., 2007b), permineralized seed cones assigned to *Parasciadopitys* (Fig. 10C; Yao et al., 1997), and compressed seed cones of *Telemachus* (Figs. 10A–B; Yao et al., 1993). Although some of these organs were originally assigned to different conifer families, i.e., Podocarpaceae, Voltziaceae, and Cupressaceae *sensu lato* (as Taxodiaceae, see discussion in Axsmith et al., 1998), all of them may be affiliated to the same conifer lineage, representing a widely distributed Southern Hemisphere transitional conifer (Escapa et al., 2010b). Fragmentary small-leaved conifers have been mentioned from the Lower Triassic of the CTM (*Voltziopsis africana* and *Pagiophyllum* sp. cf. *V. angusta*) collected at Graphite Peak and Mount Rosenwald, respectively (Retallack et al., 2005). *Pagiophyllum* also occurs in the Norian of the PCM (Cantrill et al., 1995; McLoughlin et al., 1997).

### Gymnosperms *Incertae Sedis*

The large diversity of gymnosperms in the Triassic of Antarctica is complemented by occurrences of isolated organs of uncertain higher taxonomic affinities. *Probolosperma antarcticum* (Fig. 11A; Decombeix et al., 2010) and *Ignotospermum monilii* (Perovich and Taylor, 1989) are isolated permineralized ovules from Fremouw Peak with combinations of features that do not allow unambiguous assignment to a particular natural group. Further enigmatic fructifications present in the Triassic of Antarctica include *Matatiella* and *Dordrechtites*, both ovulate organs that were originally described from the Upper Triassic Molteno Formation of South Africa (Anderson and Anderson, 2003). *Matatiella* has a loose cone-like appearance and consists of a straight central axis with helically arranged megasporophylls that are palmately divided into four to six lobes, each bearing a single, enclosed ovule. A cluster of compressed megasporophylls very similar to those of *Matatiella* has been collected from the Falla Formation in the Queen Alexandra Range, CTM, and has recently been assigned to the peltasperms (Bomfleur et al., 2011d). *Dordrechtites* was previously classified in a new order of coniferophytes (Anderson and Anderson, 2003); based on the present evidence, however, the systematic position remains unclear. The record of this genus in the Triassic of Antarctica is exclusively based on isolated compressed and permineralized ovuliferous complexes recovered from the base of Mount Falla (?Fremouw Formation) (Fig. 11D; Bergene et al., 2011).

Another leaf morphotype, *Dejerseya*, has been described as a probable seed fern. *Dejerseya* exhibits a variously lobed margin and dense, frequently forking secondary veins that form fan-shaped groups

**FIGURE 9**—Cycadales (A–D, Fremouw Peak) and Ginkgophyta (E–F) from the Triassic of Antarctica. A) *Antarcticycas schopfii* stem in transverse section showing large pith (center) with narrow ring of wood and numerous mucilage canals. 10,119, I1 side (surface scan); scale = 1 cm. B) *Delemaya spinulosa.* Longitudinal section of pollen cone. 10,424 M bot, 115, slide 21434; scale = 2 mm. C) Transverse section of leaf, *Yelchophyllum omegapetiolaris*. 10,424 G1 side 1 #28, slide 22523; scale = 0.1 mm. D) *Taeniopteris* sp. (Cycadales ?). Shapeless Mountain, SVL. T 1546; scale = 1 cm. E) *Sphenobaiera* sp. (Ginkgophyta). Mount Falla T 5654B; scale = 1 cm. F) *Sphenobaiera schenkii.* Shapeless Mountain. T 1619a; scale = 1 cm.

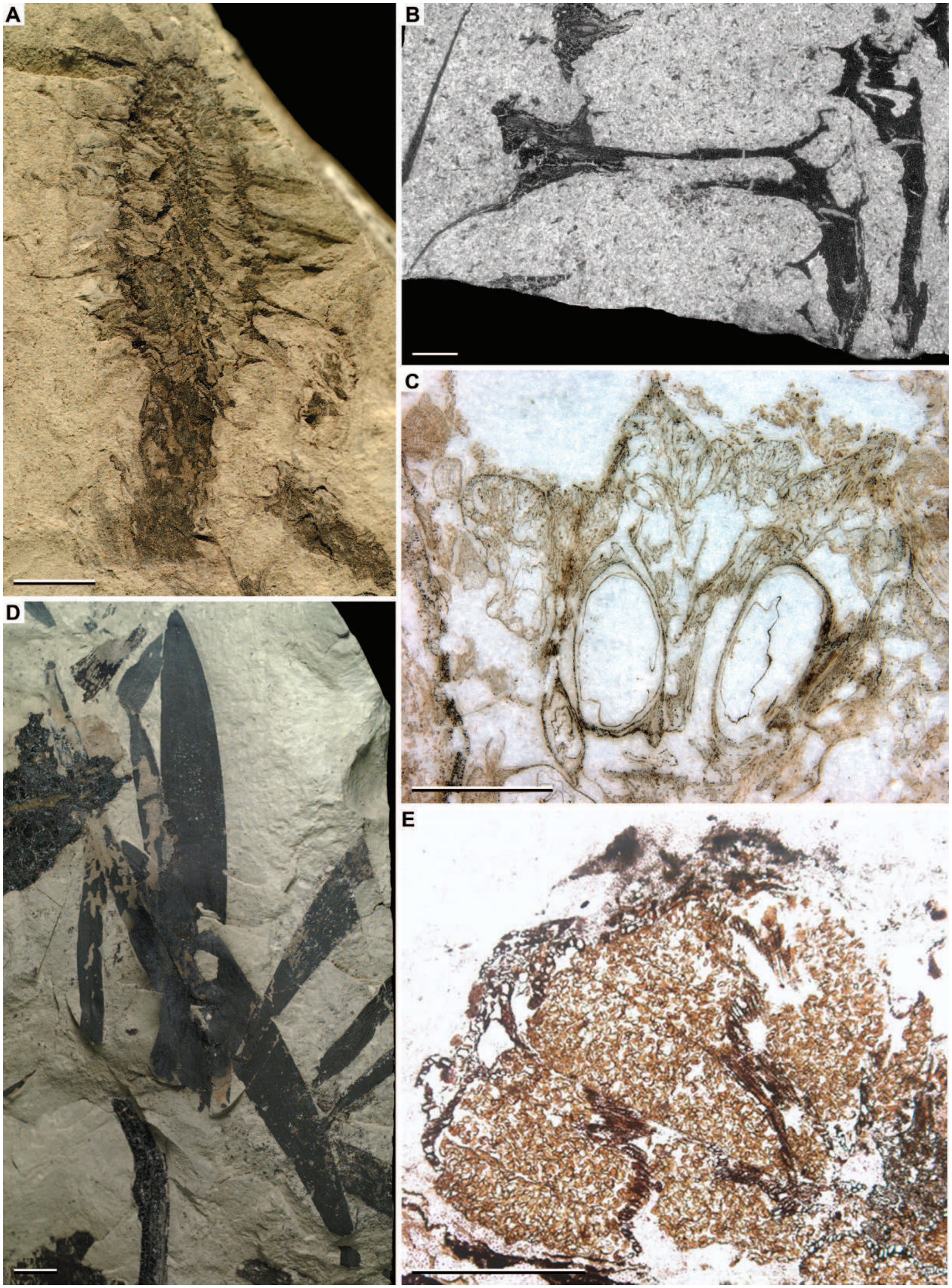


**FIGURE 10**—Conifers from the Triassic of Antarctica. A) *Telemachus elongatus* cone (Voltziales). Allan Hills Level C, T 202A; scale = 1 cm. B) Longitudinal section through part of a *Telemachus elongatus* cone, showing cone axis (right) with an attached single cone-scale complex. Note elongated bract (far left). Alfie's Elbow T 5594A; scale = 1 mm. C) Transverse section through *Parasciadopitys aequata* cone showing oblique section of permineralized ovuliferous scale bearing two ovules; scale tips above. Fremouw Peak, 10,852 B top; scale = 5 mm. D) Compressed *Heidiphyllum elongatum* leaves. Allan Hills T 11 652; scale = 1 cm. E) Transverse section of pollen cone *Leastrobus fallae* (Voltziales) showing pollen sacs with pollen. Mount Falla, 15,454 E, slide 22473; scale = 1 mm.

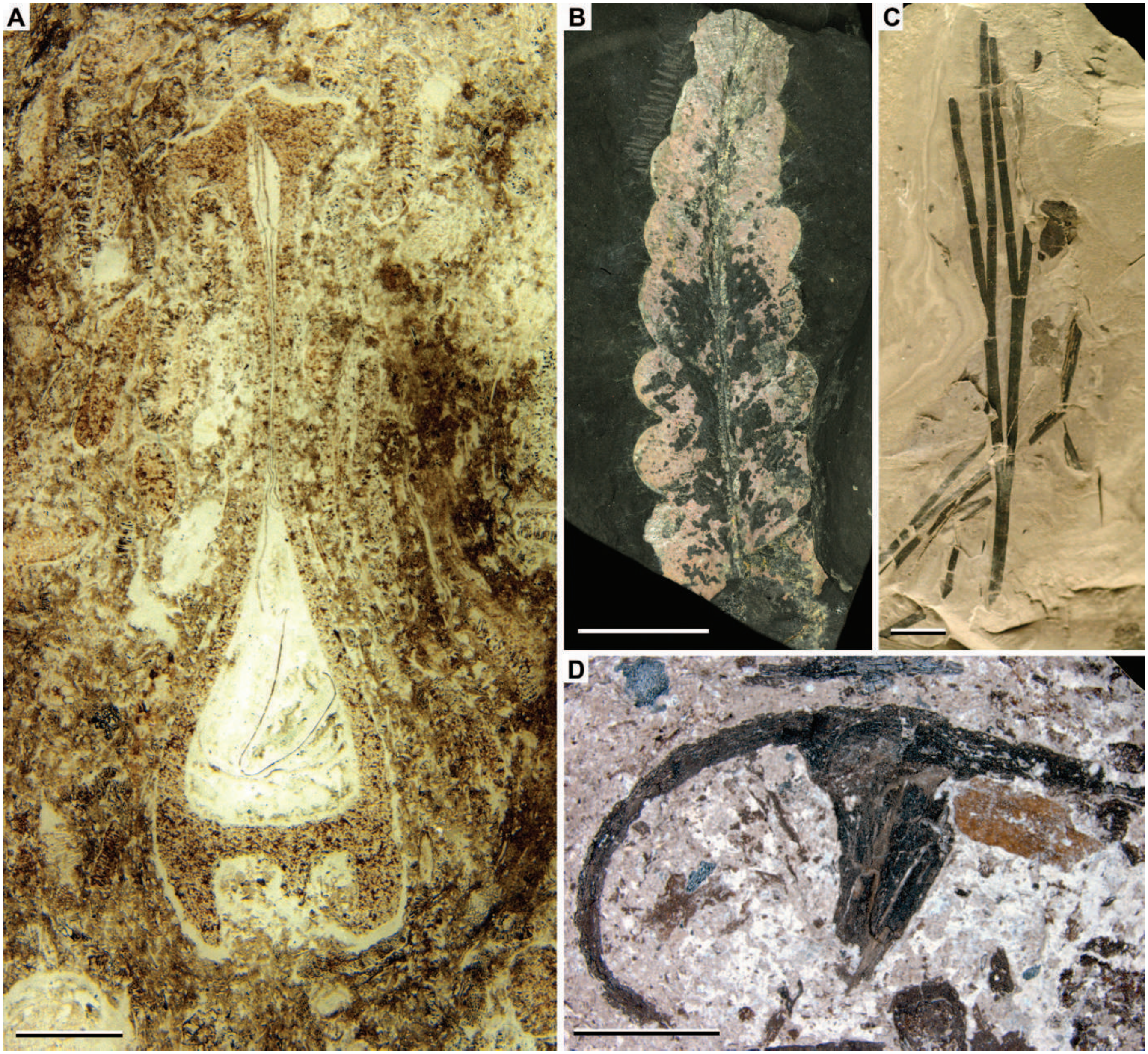


**FIGURE 11**—Gymnosperms *incertae sedis* from the Triassic of Antarctica. A) Permineralized ovule of *Probolosperma antarcticum.* Fremouw Peak, 12,597 D bot #60, slide 23773; scale = 1 mm. B) *Dejerseya* sp. Vulcan Hills, NVL, GIX-VH09-10; scale = 1 cm. C) *Czekanowskia*-like foliage. Alfie's Elbow, T 5532; scale = 1 cm. D) *Dordrechtites* sp. base of Mount Falla, T 5949; scale = 5 mm.

in the lobes (Fig. 11B). The genus occurs only sporadically in the Middle and Upper Triassic of Australia (e.g., Jones and de Jersey, 1947), South Africa (Anderson and Anderson, 2003), and South America (Gnaedinger and Herbst, 1998, 2004), and is also known from the Vulcan Hills, NVL (Fig. 11B). A further tentative Antarctic occurrence of the genus comes from Shapeless Mountain (Rigby, 1985), but this material has never been figured or formally described. In the Molteno Formation (South Africa) and the Ipswich Coal Measures (eastern Australia) *Dejerseya* foliage is closely associated with the assumed pollen cone *Switzianthus* and with yet-undescribed, *Matatiella*-like ovuliferous organs (Anderson and Anderson, 2003). Recently, Bomfleur et al. (2011d) described the same association of these three taxa from the Upper Triassic of Mount Falla in the CTM and proposed that the plant represents a new family of peltasperms in Gondwana.

In addition, several gymnospermous leaf compressions from Antarctica are doubtful in terms of their taxonomic position. Elongated and highly dissected leaves were recovered from several localities in Antarctica and resemble the morphogenus *Czekanowskia* Heer (Harris and Millington, 1974) (Fig. 11C); however, since neither short shoots nor cuticle characters are preserved, any final assignation to the genus remains uncertain. *Czekanowskia*, together with such leaf morphogenera as *Solenites*, are generally assigned to the order Czekanowskiales (Taylor et al., 2009) and represent common components in the Northern Hemisphere Mesozoic, especially in Angaran and Cathaysian floras (e.g., Samylina and Kiritchkova, 1993; Sun et al., 2009). Major differences between czekanowskialeans and other gymnosperms are based on the ovulate structures (Harris, 1951; Zhou, 2009), and preclude the inclusion of the Antarctic leaves in this Mesozoic order.

## Other Antarctic Triassic Floras

Most of our knowledge of Triassic floras of Antarctica is based on material from the CTM and Victoria Land on the margin of the East Antarctic craton. Triassic floras have also been described, however, from the Prince Charles Mountains (PCM) (see Geological Setting) on the opposite side of the craton (Cantrill and Drinnan, 1994; Cantrill et al., 1995; McLoughlin et al., 1997). These megafloras were recovered from the Flagstone Bench Formation, which rests immediately above the Bainmedart Coal Measures containing a mid- to Late Permian *Glossopteris* flora (both units are assigned to the Amery Group; McLoughlin and Drinnan, 1997a). The Flagstone Bench Formation spans the interval from the base of the Triassic to at least the Norian (McLoughlin and Drinnan, 1997b) and is subdivided into three members: the Ritchie, Jetty, and McKelvey Members in ascending stratigraphic order. Fragments of *Lepidopteris* leaves, lycophyte sporangia, and a range of other plant mesofossils occur in the sparse siltstone beds of the Lower Triassic (Induan?) Ritchie Member, spanning an interval of at least 200 m above the Permian-Triassic boundary (McLoughlin et al., 1997). Lycophyte microspores, megaspores, and sporangial remains are particularly abundant in these beds (Lindström and McLoughlin, 2007; Vajda and McLoughlin, 2007).

The best-preserved Triassic macrofloras in the PCM derive from the sparse siltstone beds between major channel sandstone cross-bed sets in the McKelvey Member. These assemblages include the corystosperm remains *Dicroidium zuberi*, *D. crassinervis* forma *stelznerianum*, and *Pteruchus dubius*; the conifers *Pagiophyllum papillatus*, *Heidiphyllum elongatum*, and dispersed cone fragments; and unidentified taeniopterid leaves and circular scale leaves (Webb and Fielding, 1993; Cantrill et al., 1995; McLoughlin et al., 1997). Palynological studies have confirmed a Norian (Late Triassic) age for these fossiliferous strata (Foster et al., 1994; McLoughlin et al., 1997).

As in most of the Triassic Gondwanan plant assemblages, those from the PCM appear to be dominated by corystosperms (*Dicroidium* foliage). Different paleogeographic and paleoenvironmental settings of these floras may explain the lower diversity and different species composition compared to other Antarctic *Dicroidium* floras (Cantrill et al., 1995). The presence of coniferous leafy twigs assigned to *Pagiophyllum* is an interesting occurrence, since the evidence suggests the presence of just one natural conifer group (family) in the Triassic of the CTM (Escapa et al., 2010b). Cantrill et al. (1995) explained the occurrence of *Pagiophyllum* in the PCM by the proximity of this East Antarctic locality to the Indian landmass during the Triassic, where this morphotaxon, which could belong to a different family, is well known.

Another flora that had been classically considered as Triassic is that from Williams Point on Livingston Island, off the Antarctic Peninsula (e.g., Orlando, 1968; Lacey and Lucas, 1981). Later studies based on more extensive collections, however, demonstrated an Albian–Cenomanian (Early Cretaceous) age for this taphoflora (Rees and Smellie, 1989), on the basis of a rich angiosperm record. They considered that the previous interpretations of this flora were based on poor preservation and ambiguously identified specimens.

The anatomically preserved flora from Collinson Ridge, in the Shackleton Glacier area, CTM (McManus et al., 2002) contains silicified ovules, leaves, and wood. The fossils were collected from basal levels of the Fremouw Formation (Collinson et al., 2006), in strata below the lowest Triassic vertebrate horizon (*Lystrosaurus* Zone) and thought to be Triassic in age based on lithology. Even though the plants occur in levels previously referred to the Lower Triassic (lower Fremouw Formation), the flora, which includes *Glossopteris*, *Vertebraria*, and *Araucarioxylon*-type wood, clearly indicates a Late Permian age for this silicified peat (McManus et al., 2002).

## DISCUSSION

Most of the Triassic floras in Gondwana are preserved as impression-compression fossils, in some cases bearing well-preserved cuticles (e.g., Bomfleur and Kerp, 2010a). Our systematic knowledge of these floras has been improved during the last few decades due to dedicated efforts in particular areas of eastern and western Gondwana (e.g., Anderson and Anderson, 1983; Holmes and Anderson, 2005, 2007; Artabe et al., 2007a and references therein). Antarctica, however, is one of the few places where permineralized fossils (aside from wood) are present in addition to the impression-compression record, and this preservational type provides additional data on the morphology and anatomy of plants from these high paleolatitude communities. Here, reproductive and vegetative structures of several plant groups have been described, affording a better understanding of these groups not only in Antarctica, but also throughout their ranges (e.g., Taylor, 1996; Hermsen et al., 2009). On the other hand, to compare anatomically preserved plants with those preserved as compressions or impressions is not an easy task, so a detailed comparison with surrounding floras in the Triassic of Gondwana cannot be based on permineralizations alone. In some cases, these difficulties affect the interpretation of the distribution of particular natural groups, which in turn has consequences for any further hypotheses regarding, e.g., biostratigraphy, paleoecology, and phytogeography.

### Temporal Distribution and Composition of the Floras

The Triassic is one of the most interesting periods in the evolution of the plant kingdom with several groups (e.g., sphenopsids, ferns, conifers) undergoing morphological changes from primitive late Paleozoic forms to the first representatives of modern, derived morphologies. One interesting aspect of the Antarctic paleofloras is that the CTM preserve an almost continuous Triassic terrestrial sedimentary record, with megafloras known in the Upper Permian (Cúneo et al., 1993; Schwendemann et al., 2010b and references therein) through to the overlying Lower Jurassic (e.g., Plumstead, 1962; Townrow, 1967c; Yao et al., 1991).

In general, the Triassic floras of Antarctica, as elsewhere in Gondwana, are characterized by the disappearance of the glossopterid seed ferns around the Permian-Triassic boundary (McLoughlin et al., 1997; Lindström and McLoughlin, 2007) and the appearance of other groups of gymnosperms, especially corystosperms. *Dicroidium* foliage has been used in the past as an index fossil for the Triassic in Gondwana, but this approach represents an oversimplification of our current understanding of the stratigraphic distribution of these fossils (e.g., Kerp et al., 2006). By the Middle Triassic at the latest, corystosperm seed ferns are dominant, not only in the CTM, but in the PCM as well (McLoughlin et al., 1997). They are represented by several species of leaves, stems, and reproductive organs (both ovule- and pollen-producing structures) and this dominance continues until the end of the Triassic. Although conifers are present in the Triassic of Antarctica, only a single group is represented. By contrast, in the Jurassic of Antarctica, conifers appear to become the dominant group, although our knowledge of the Jurassic floral record from East Antarctica is very sparse (but see Plumstead, 1962; Truswell, 1991; Yao et al., 1991; Bomfleur et al., 2007, 2011a). The former Early Jurassic floras from West Antarctica, now considered of early Middle Jurassic age (Hunter et al., 2005), have been extensively studied (Rees and Cleal, 2004 and references therein) and the plant diversity there is much higher. At present, differences due to preservational and collection biases, to differences in paleolatitudes, or to the deposition of volcanics in the CTM, resulting in unsuitable environmental conditions for plant growth and preservation, are difficult to decipher.

Utilizing the distribution or evolution of Triassic megafloras in Antarctica for biostratigraphic purposes is possible only to a limited degree at the present time. The main reason is the lack of a stratigraphic record of plant megafossils that is complete enough to identify detailed changes in floral composition. Furthermore, the overall paucity of biostratigraphically significant plant macrofossil taxa in Triassic floras worldwide makes a detailed biostratigraphic zonation based on macrofossils difficult. As a result, a reliable biostratigraphy for now will be based on associated sources, in particular palynological data from the Middle–Late Triassic (e.g., Farabee et al., 1989, 1991) and fossil vertebrates, as is the case for the Early Triassic in the CTM (e.g., Hammer, 1990). By taking into account the presence or absence of megaplant morphotaxa at each reported locality (Fig. 3) and the stratigraphic position of every locality along with suggested ages (Fig. 2), a general biostratigraphic scheme through the Triassic succession in continental Antarctica can be proposed, however. In this context, compressed and permineralized Triassic floras are grouped into three informal stages (Fig. 2). An Early Triassic, low-diversity floral stage principally recorded from the CTM (Figs. 2–3, pink boxes) can be characterized by the presence of bipinnate *Dicroidium* fragments (*D. zuberi*) and transitional voltzialean conifers with other minor components (Retallack et al., 2005). It is important to note, however, that Early Triassic floras from the CTM have been very poorly studied and the only megafossils illlustrated are very poorly preserved and fragmentary (Retallack, 2005; Retallack et al., 2005). In the Prince Charles Mountain succession, on the other hand, the Early Triassic interval is dominated by *Lepidopteris* and lycophyte remains (McLoughlin et al., 1997). This initial stage can be correlated with the *Lystrosaurus* and *Cynognathus* faunas recorded from the CTM (Collinson et al., 2006).

The poorly known Early Triassic floras are followed stratigraphically by a Middle Triassic floral stage (Figs. 2–3, green boxes) recognized mostly from localities in the CTM and SVL and characterized by considerable plant diversity, as represented by all the natural groups mentioned in this paper. The plant record in the CTM, however, comes mainly from two localities, i.e., Fremouw Peak and a site at the base of Mount Falla (Hermsen et al., 2007b) in which plants are preserved as permineralizations; however, the Mount Falla site cannot be traced laterally to outline its extent for biochronostratigraphic purposes. Finally, a late Middle–Late Triassic plant stage is represented by several localities in the CTM, NVL, and SVL basins (Figs. 2–3, blue boxes). During this time, the flora of continental Antarctica is represented by most of the recognized plant groups from the Triassic of Antarctica that have been recorded from compressions and impressions (Fig. 3), and shows the dominance of the corystosperm seed ferns typical of the rest of Gondwana.

Although much less diverse at the generic level, the chronostratigraphic plant succession from Antarctica can be compared with that suggested for southwestern Gondwana, where Spalletti et al. (1999) recognized three plant stages (five zones) that they named Barrealian, Cortaderitian, and Florian. These were based principally on Argentinean floras and defined in general terms by the appearance, maximum diversification, and declination of the *Dicroidium* flora (Artabe et al., 2007a); stratigraphically, they approximately match the Lower, Middle, and Upper Triassic series. The earliest of these floral stages is characterized by the first appearance of so-called mesophytic plant elements (Spalletti et al., 1999) and climatically by a strong global monsoonal system, which has been related to the presence of Pangea (Preto et al., 2010). Note that the terms mesophytic and paleophytic have been variously defined and are now regarded as oversimplications of floral change (DiMichele et al., 2008). Nevertheless, in Gondwana (with a few possible exceptions), there was complete floral turnover in the transition from Paleozoic to Mesozoic. This dramatic floristic replacement seems to have been a more gradual process in pantropical areas (Dobruskina, 1993; DiMichele et al., 2008), but rapid in extratropical Gondwana. This event is present in Antarctica at CTM localities, where Permian Glossopteridales are abruptly replaced by the first appearance of *Dicroidium* (McManus et al., 2002; Retallack et al., 2005; Collinson et al., 2006). To date the only megafloral records from this time in the CTM are poorly documented examples of two conifers and the bipinnate *Dicroidium zuberi* (Retallack et al., 2005). The better-preserved Early Triassic megaplants of easternmost Antarctica (PCM) include pinnae of *Lepidopteris* and lycopsid megaspores (McLoughlin et al., 1997), and palynomorphs show an increase in nontaeniate bisaccate gymnosperm pollen and lycophyte microspores at this time (Lindström and McLoughlin, 2007).

The second southwestern Gondwana stage, known as Cortaderitian (Spalletti et al., 1999), is characterized by a maximum diversification of *Dicroidium*, which is also observed in Antarctic floras (Fig. 3). Small-leaved conifers are completely absent, but the multiveined leaf morphotype *Heidiphyllum* is present. Intensive sampling in these localities in Argentina has provided a qualitative improvement in the knowledge of the floras, which are composed of lycopsids, equisetaleans, ferns (e.g., Osmundaceae), seed ferns, cycads, ginkgophytes, conifers, and other gymnosperms (Artabe et al., 2007a and references therein). Most localities assigned to the Middle and Late Triassic in Antarctica can be related to this group and the main differences among them can be better explained by preservational and sample biases than by real biotic changes. This is also concordant with the proposed ages for the Cortaderitian stage in southwestern Gondwana, which started in the Middle Triassic and extended into the early Late Triassic (Spalletti et al., 2003).

The third southwestern Gondwana stage is usually defined by the partial replacement of typical Triassic species by morphotypes with Early Jurassic affinities (Artabe et al., 2007a). Although *Dicroidium* is still present in Argentina, the corystosperms are most commonly confined to the understory (Artabe et al., 2001). There appears to be no clear equivalent of this stage in Antarctica, but this may be due to floral provincialism (Bomfleur and Kerp, 2010a). In NVL, diverse *Dicroidium* floras from the Upper Triassic Section Peak Formation become replaced in the overlying Lower Jurassic Shafer Peak Formation by floras dominated by cycadophytes (Bennettitales) and various ferns (Bomfleur et al., 2007, 2011b). Interestingly, one of the latter floras is anatomically preserved and contains *Polyphacelus stormensis* (Bomfleur and Kerp, 2010b), a dipterid fern initially described from the Lower Jurassic of the CTM (Yao et al., 1991).

## Community Structure and Paleoclimatic Setting

The Permian–Triassic transition in Antarctica shows a major shift in the plant community structure and paleoenvironmental-paleoclimatic conditions at the beginning of the Mesozoic. Perhaps the most visible and dramatic changes are those related to the disappearance of peat-forming conditions that characterized the end of the Permian in Antarctica (Collinson, 1997; Collinson et al., 2006). Even though alluvial systems generally dominated the scene in the entire Transantarctic Basin across the P-T boundary, the extensive peat-swamp environments associated with braided or meandering fluvial systems disappeared by the beginning of the Triassic, not only in Antarctica but also elsewhere in Gondwana (sometimes called the coal gap; Veevers, 1994; Retallack et al., 1996). This sedimentological shift in Antarctica was associated with tectonic events related to the growth of a fold belt west-southwest of the Antarctic craton (Cúneo et al., 1991, 2003; Collinson et al., 1994), which certainly contributed to the sudden and extreme change in the structure and composition of the plant communities. The very successful Permian glossopterid seed ferns (Cúneo et al., 1993) were replaced by different elements, including lycopsids (in wetter habitats) and other groups of seed plants elsewhere. Although the equisetophytes appear in Australia during this time (e.g., Holmes, 2001), to date there is little evidence for them in Antarctica and they are not widespread in Argentina until the Middle Triassic (Spalletti et al., 2003). Collinson (1997) has suggested that the climate of the Early Triassic in the CTM was more seasonal than in the Permian, based on the lack of coal and the presence of stream deposits that suggest seasonal water input. Based on general circulation models and sedimentological data, the Triassic macroclimate has been characterized as dominated by a megamonsoonal circulation, with seasonal rainfall and a lack of zonal differentiation (e.g., Parrish, 1993). As Preto et al. (2010) noted more recently, however, little detailed work has been done on Triassic paleoclimate overall. Paleoclimate around the Tethys is characterized as warm and humid (e.g., Kustatscher et al., 2010), whereas in Gondwana it is interpreted to have been warm temperate all the way to the poles, but perhaps characterized by more seasonality than the tropics (Parrish, 1993), an idea that is supported by tree-ring data (e.g., Pires et al., 2005; Artabe et al., 2007b; Taylor and Ryberg, 2007).

The community organization of the Early Triassic seems to have persisted in the Middle Triassic according to evidence from the upper Fremouw Formation (CTM) and Members A and B of the Lashly Formation (SVL). Cúneo et al. (2003) described a standing fossil forest from Gordon Valley in the CTM (Fremouw Formation) and demonstrated a relatively dense stand composed of trees ≤30 m high that produced *Dicroidium* foliage. The forest occupied levee and proximal floodplain environments of braided fluvial systems, whereas the backswamps nearby were inhabited by stands of *Neocalamites*. Interestingly, much denser and more diversified but smaller tree communities have been described from coeval examples in Argentina (Brea et al., 2008). At the same time, a diverse surrounding plant community represented by different ferns, cycads, and other gymnosperms is evidenced from the Fremouw Peak permineralized peat (see above). The presence of peat accumulations and coal seams marks a return to moist conditions under a warmer, temperate regime. Tree rings indicate adequate water availability and temperatures conducive to extensive plant growth (Ryberg and Taylor, 2007; Taylor and Ryberg, 2007), which contrasts with estimated semiarid conditions recorded from the Middle Triassic interval in the PCM (McLoughlin et al., 1997).

During the Late Triassic, the structure of the vegetation appears to be similar, although less is known about the fossils of this period. The principal canopy (tree layer) was probably composed of corystosperms with some conifers (i.e., *Telemachus, Heidiphyllum*) making an appearance. As has been suggested for the Middle Triassic forests (Taylor, 1996), these arborescent corystosperms were probably also deciduous (Bomfleur and Kerp, 2010a). Ginkgophytes were also probably part of this canopy. Due to the presumably humid conditions, the understory, at least in SVL, was composed mostly of osmundaceous ferns. Taphocoenoses from the Falla and uppermost Fremouw Formations in the CTM, as well as the Lashly (Member C) in SVL and Section Peak Formations (NVL) represent the best relicts of the suggested Late Triassic plant community organization. Similar conditions were apparently present in the PCM as well (McLoughlin et al., 1997).

### Paleophytogeographic Considerations

Antarctica, with its position in the center of Gondwana, plays an important role in reconstructing paleogeographic changes during the time of Pangea. Research is, however, in its most basic stages of comparing Antarctic taxa distributions with those from other Gondwana continents. The Triassic megafloras of Gondwana have been traditionally referred to as the *Dicroidium* flora, and this floristic assemblage is formally considered a phytogeographic realm (McLoughlin, 2001; Artabe et al., 2003; Spalletti et al., 2003). Although dominated by the corystosperm pteridosperms, a large number of other groups of Mesozoic seed plants are present in smaller numbers and less diversity (e.g., conifers, cycadophytes, and other seed ferns).

During the late Paleozoic and early Mesozoic, fossil floras in Gondwana show clear signs of provinciality. Two main phytogeographic areas were postulated for the Middle–Late Triassic Gondwana realm. Originally recognized from Western Australian palynofloras and termed Ipswich- and Onslow-type microfloras (Dolby and Balme, 1976, de Jersey and Raine, 1990), these have been considered to represent latitudinal floral belts (e.g., Artabe et al., 2003; Spalletti et al., 2003). Other authors, however, suggest that the different compositions of Ipswich and Onslow microfloras rather reflect maritime influence in the peri-Tethyan realm, probably due to warming oceanic currents (e.g., Cirilli and Eshet, 1991; Foster et al., 1994; Buratti and Cirilli, 2007).

Artabe et al. (2003) proposed to further subdivide the southern Gondwanan floral realm (extratropical region of these authors) into two provinces based on different species composition and a few endemic genera: the Southwest province, including floras from Brazil, Chile, Argentina, and South Africa, and the Southeast province, with floras from Australasia and Antarctica. The definition of phytogeographic units for the Triassic of Gondwana based on plant megafossils, however, presents a number of subjectivities that certainly affect the resultant hypotheses. The use of species-related endemism (Artabe et al., 2003) as the main evidence to delimit phytogeographic provinces is hampered by the artificial biases inherent to species taxonomy in fossil plants (e.g., Cúneo, 1996). The high degree of homoplasy present in particular plant organs is one of the first biases affecting the taxonomy of species. Examples include species of the fern foliage morphogenus *Cladophlebis,* which occurs in several localities and thus apparently has a broad geographic distribution; however, detailed studies show that this morphotaxon can actually represent foliage of different natural families, such as Osmundaceae (e.g., Phipps et al., 1998), or Schizaeaceae and Cyatheaceae (Halle, 1913). Similar examples occur for many other plant groups in the fossil record, especially when isolated vegetative structures are included in the analysis. Particularly in the Triassic of Gondwana, most of the taxa are known from isolated organs and only a few reconstructions based on several organs (whole plants) have been proposed (Petriella, 1978; Taylor, 1996; Hermsen et al., 2009; Escapa et al., 2010b).

Taphonomic and preservational biases can also affect phytogeographic theories based on morphotaxa. For instance, the permineralized conifer leaves and branches of *Notophytum krauselii* (Meyer-Berthaud and Taylor, 1991; Axsmith et al., 1998) and the permineralized ovulate cones *Parasciadopitys aequata* (Yao et al., 1997) were considered as independent evidence supporting a distinct Southeast province (Artabe et al., 2003), whereas the compressed leaf taxon *Heidiphyllum elongatum* was a shared species with the Southwest province. A more recent study (Escapa et al., 2010b), however, provides evidence that all of these species formed part of the same plant and that *Parasciadopitys* represents a different preservational state of the compressed ovulate cone *Telemachus* (Escapa et al., 2010b), which is widely distributed in both the Southwest and Southeast provinces. Finally, the use of reliable biochronostratigraphic control is of fundamental importance before attempting phytogeographic proposals. In this regard, the suggested species endemism that characterizes the phytogeographic differentiation proposed by Artabe et al. (2003) was developed considering the Triassic as an undivided time slice, a fact that introduces a strong bias in terms of evolutionary lineages, climatic dynamics, and paleogeographic changes that clearly affect the distribution of Triassic biotas (Spalletti et al., 2003). Nonetheless, the detailed scheme of Artabe et al. (2003) was an important and pioneering step that showed interesting regionalisms in the distribution and diversity of particular plant groups, and also pointed out the essential need for an improved non-marine Gondwanan chronostratigraphic scheme.

## CONCLUSIONS

Almost every major plant clade that had evolved by this time period is represented in the Triassic megaplant record in Antarctica, even though there is a pattern of low generic diversity when compared with adjacent regions of Gondwana. Each group within the gymnosperms is represented, but usually only by a single member, with the exception of *Dicroidium*. The pattern is particularly apparent in such clades as the lycophytes, cycads, and ginkgophytes. Reasons for this lower diversity could be related to less sampling in the continental Antarctic, although phytogeographic and paleoclimatic conditions at these high paleolatitudes could affect the distribution (including immigration) of Antarctic biotas during the floral replacement process following the end-Permian biotic crisis. When compared with the Gondwana realm, the lack of any bennettitalean record is probably the most relevant absence of a major clade in the Triassic floras of Antarctica.

Even though there has been a substantial increase in our knowledge of Triassic plants from Antarctica in recent decades, this compilation highlights how much is still to be accomplished. There are still many unanswered questions from a systematic and taxonomic viewpoint and only a loose biostratigraphic framework based on plant megafossil occurrences can be envisaged for Antarctica during the Triassic. In this regard, the use of alternative approaches in order to develop a more accurate and detailed geochronology becomes essential. Thus, a major effort should be undertaken to develop combined magnetostratigraphic and radiometric studies, and the widespread presence of volcaniclastics in the Triassic succession represents an initial ground on which these studies could be attempted.

Paleoecological settings are apparently not so different from those known from other Gondwana areas. The structure and composition of the vegetation shows a well-developed tree canopy mostly composed of corystosperms, conifers, and possibly ginkgophytes, and a lower stratum (understory) dominated by ferns, particularly osmundaceous ferns, and cycads in more open community patches.

The phytogeographic arrangement of Antarctic floras during the Triassic seems to have been controlled largely by light seasonality in the high-latitude paleogeographic location (>70° S), which probably precluded more intense plant migration from mid-temperate belts. To date, no endemics have been identified, except for those due to preservation bias.

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