

The background of the cover features three distinct fossil images. The top left shows a dark, branching plant fossil on a light-colored rock matrix. The top right shows a large, white, teardrop-shaped fossil, possibly a seed or fruit, with reddish-brown veins. The bottom half of the cover is dominated by a large, detailed fossil of a plant stem with a prominent vascular network, showing circular and polygonal cells.

# TRANSFORMATIVE PALEOBOTANY

PAPERS TO COMMEMORATE THE LIFE AND LEGACY OF THOMAS N. TAYLOR

EDITED BY MICHAEL KRINGS, CARLA J. HARPER, NÉSTOR RUBÉN CÚNEO, AND GAR W. ROTHWELL



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# Transformative Paleobotany

## Papers to Commemorate the Life and Legacy of Thomas N. Taylor

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# Polar Regions of the Mesozoic–Paleogene Greenhouse World as Refugia for Relict Plant Groups

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## 1. INTRODUCTION

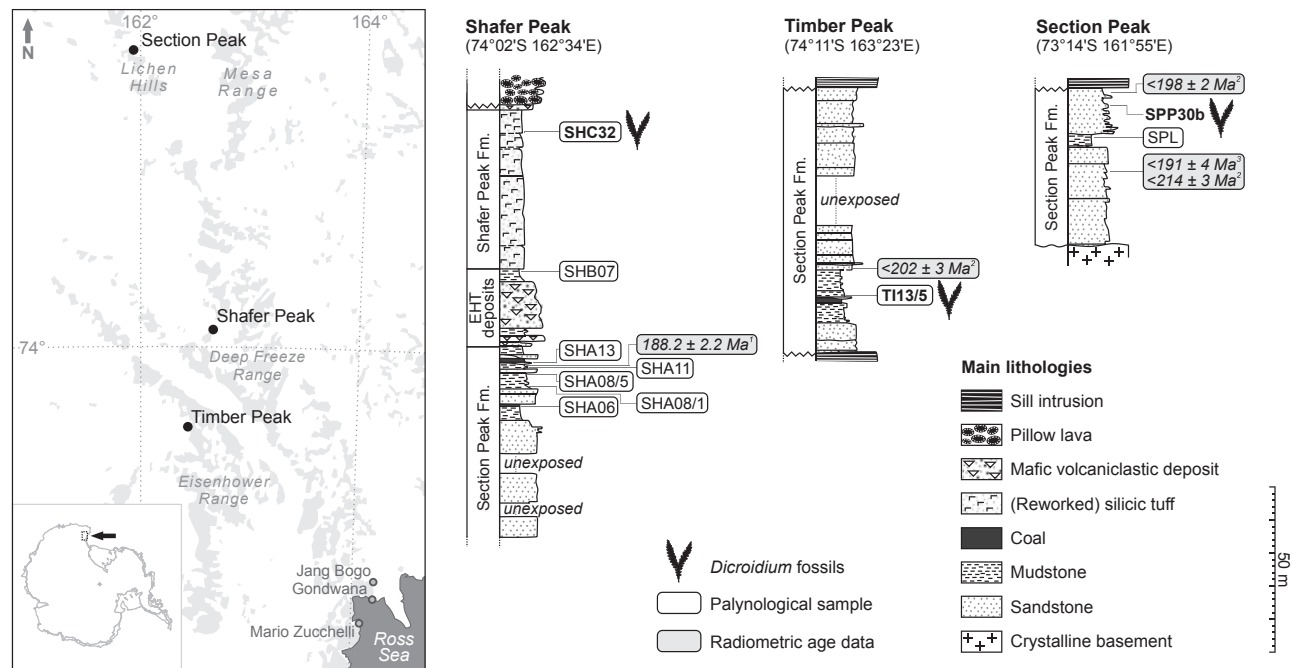
Today, a prominent effect of the decreasing amount and increasing seasonality of solar energy input with increasing latitude is the latitudinal gradient in species richness; that is, the general decrease in biodiversity from the equator toward the poles (Hillebrand, 2004; Gaston, 2000, 2007). Although this phenomenon has long been recognized and has fascinated some of the most celebrated minds of ecology and evolutionary theory (Von Humboldt, 1806; Darwin, 1859; Wallace, 1878), its underpinning mechanisms remain poorly understood (Rohde, 1992; Gaston, 2000; Willig et al., 2003; Hillebrand, 2004). In recent decades, it has become increasingly clear that the latitudinal gradient concept can be transposed to a much greater evolutionary scale and projected deep into geological time, revealing biogeographical patterns in the origination and extinction of clades (Crane and Lidgard, 1989; Jablonski, 1993; Jablonski et al., 2006; Mittelbach et al., 2007; Fig. 24.1). The cold deserts of the polar regions today are among the most inhospitable places on Earth. Global climates, however, have been changing throughout Earth history, and during warmer periods of the Phanerozoic, large parts of landmasses in high northern and southern latitudes were covered in lush vegetation (e.g., Heer, 1868; Halle, 1913; Taylor and Taylor, 1990; Cantrill and Poole, 2012). These past high-latitude terrestrial ecosystems have repeatedly been shown to host the youngest occurrences of plant taxa that had long disappeared from lower-latitude basins (e.g., McLoughlin et al., 2008, 2011).

Here, we present *Dicroidium* cuticles from Jurassic strata of East Antarctica that significantly postdate the

presumed extinction of this iconic plant group of the Gondwanan Triassic. It appears that contrary to current assertions (Pattemore et al., 2015; Pattemore, 2016), *Dicroidium* did not perish in the course of the end-Triassic biotic crisis, but survived with relictual populations in polar refugia well into the Jurassic. On this basis, we provide a review of case studies outlining the changing geographical distributions of both austral and boreal plant groups to highlight a common pattern among archaic plant groups—that of retreat to the poles in the wake of biotic crises.

## 1.1 The *Dicroidium* Plants

Plants with *Dicroidium*-type foliage are the best-known representatives of Umkomasiaceae (=Corystospermaceae), a group of extinct gymnosperms that were common elements in many early and mid-Mesozoic floras worldwide. *Dicroidium* plants constituted medium-sized to tall canopy trees producing distinctive forked fronds (the name-bringing *Dicroidium*) and leafless fertile branching systems, either with terminal, recurved cupules (*Umkomasia*) or with short-stalked, leafy microsporophylls with abaxial clusters of free pollen sacs (*Pteruchus*) containing non-taeniate bisaccate pollen (*Falcisporites*) (Taylor et al., 2006, 2009). *Dicroidium* foliage is highly variable in size, architecture (simple to tripinnate), leaflet morphology (needle-like, entire, to variably lobed or dissected), and venation (e.g., simple, taeniopteroid, odontopteroid, or alethopteroid; see Archangelsky, 1968; Retallack, 1977; Anderson and Anderson, 1983). All frond forms, however, possess the characteristic basal bifurcation (see Anderson and Anderson, 1983), share



**FIGURE 24.1** Geographic and stratigraphic setting of the studied material. Modified from Bomfleur et al. (2014); radiometric age data adopted from Elsner (2010), Elsner et al. (2013), and Goodge and Fanning (2010).

distinctive epidermal and cuticular features (e.g., Gothan, 1912; Thomas, 1933; Jacob and Jacob, 1950; Townrow, 1957; Archangelsky, 1968; Bomfleur and Kerp, 2010), and are associated with similar reproductive organs (e.g., Thomas, 1933; Anderson and Anderson, 1983). The *Dicroidium* seed ferns were the dominant gymnosperm group in temperate forest and wetland environments across most of the Southern Hemisphere during the Middle and Late Triassic (e.g., Anderson et al., 1999; McLoughlin, 2001). Owing to their ubiquitous occurrence and sheer abundance in the Gondwanan Triassic, the informal term “*Dicroidium* flora” is commonly used to describe their main geographic and biostratigraphic realm (e.g., Hirmer, 1936; Townrow, 1957; Barnard, 1973; Gould, 1975; McLoughlin, 2001; Artabe et al., 2003).

It has generally been assumed that the *Dicroidium* flora first appeared during the Early Triassic and perished in the course of the end-Triassic biotic crisis (Anderson and Anderson, 1983; Pattemore et al., 2015). However, there have also been early clues that the *Dicroidium* seed ferns may not have been restricted exclusively to the Triassic of Gondwana. Unexpected co-occurrences of supposed *Dicroidium* fronds together with *Glossopteris*—the iconic Permian plant fossil of Gondwana—in Madagascar (Carpentier, 1936), India (e.g., Pant and Pant, 1987), and Antarctica (e.g., Rigby and Schopf, 1969) cast doubt about the abrupt replacement of the Permian *Glossopteris* flora with the Triassic *Dicroidium* flora. Whereas there is now evidence that most of these unusual mixed assemblages

contain the latest *Glossopteris* survivors rather than precocious *Dicroidium* occurrences (see Section 4.3.2), well-preserved *Dicroidium* fronds occur in reliably dated Permian deposits of Jordan (Kerp et al., 2006; Abu Hamad et al., 2008, 2017). Conversely, the possible occurrence of *Dicroidium* in the Jurassic of Antarctica has also been reported (Rees and Cleal, 2004), but the fragments are incomplete and assignment has been considered tentative.

## 2. MATERIAL AND METHODS

This study is based primarily on new occurrences of *Dicroidium* fossils in Jurassic deposits of the Victoria Group at two localities in North Victoria Land, Transantarctic Mountains: Section Peak and Shafer Peak (Bomfleur et al., 2011c; Fig. 24.1). Well-preserved cuticle-bearing compression fossils of *Dicroidium* fronds from Triassic deposits at Timber Peak, North Victoria Land (Bomfleur and Kerp, 2010) are illustrated for comparison (Fig. 24.1). The material was collected during the austral summer 2005/2006 in the course of the Ninth German Antarctic North Victorialand Expedition (GANOVEX IX). Rock samples for analysis of cuticle and other mesofossil content were treated using 48% hydrofluoric for up to 2 months until sufficient amounts of organic residues were obtained, depending on sample material. The organic residues were then carefully neutralized via repeated steps of decanting and adding distilled water, then macerated using Schulze’s reagent (40%  $\text{HNO}_3$  + a few crystals of  $\text{KClO}_3$ ) for up to 3 h, rinsed

thoroughly in water, and then cleaned and bleached by immersion in a mild potassium hydroxide solution (2% KOH) for a few seconds. The residues were washed in water again until neutral, dehydrated in pure glycerol, and mounted on permanent slides using glycerol jelly. The material is stored in the collection of the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität Münster (Münster, Germany).

## 2.1 Dispersed Cuticles From Section Peak

Cuticles were recovered from a bulk-macerated sample of a carbonaceous fine-grained sandstone bed (SPP30b) from the upper part of the Section Peak Formation at Section Peak, Lichen Hills (Fig. 24.1; see also left part of Schöner et al., 2011, Fig. 6a). The bed contains mass accumulations of organic debris smaller than 1 cm, most of which represent fragments of coalified wood or of conifer needles (Bomfleur et al., 2011c; see Pertusati et al., 2006 and Kerp and Bomfleur, 2011, Plate 12). A combination of radiometric and palynological age data (see Bomfleur et al., 2014) indicates a Sinemurian (most likely late early or middle Sinemurian) age for the host deposit.

## 2.2 Dispersed Cuticles From Shafer Peak

Cuticles were recovered from an up to 1.4-m-thick bed of tuffaceous siltstone to fine-grained sandstone (SHC32) in the upper part of the Shafer Peak Formation at the type section on the northern flank of Shafer Peak, Deep Freeze Range (Fig. 24.1; see also Fig. 5a of Bomfleur et al., 2011b). The SHC32 bed is a fluviially reworked silicic tuff, and is rich in clay-gall rip-up clasts, charcoal debris, and variably sized other plant remains, including large fronds and frond fragments of bennettitaleans (*Otozamites* spp., *Zamites* sp.) and dipterid ferns (*Clathropteris meniscioides*) (Bomfleur et al., 2011b,c). Bulk macerations have yielded various additional plant remains, including conifer twigs and leaves (Bomfleur et al., 2011b) and the single cuticle fragment described here. Palynostratigraphy (Bomfleur et al., 2014) and radiometric age data from correlative deposits of reworked silicic tuff in the central Transantarctic Mountains ( $182.7 \pm 1.8$  Ma: Elliot et al., 2007;  $186.2 \pm 1.7$  Ma: Elliot et al., 2017) and Tasmania ( $182 \pm 4$  Ma: Bromfield et al., 2007) provide strong evidence to suggest a middle or late Pliensbachian age ( $\sim 185$  Ma) for the plant-bearing SHC32 bed at Shafer Peak.

## 2.3 The *Dicroidium* Assemblage From Timber Peak

The upper portion of a crevasse-splay deposit (TI13/5) capping a coal seam in the middle part of the Section Peak Formation at Timber Peak, northern Eisenhower

Range, yielded a well-preserved and remarkably diverse *Dicroidium* assemblage (Bomfleur and Kerp, 2010) that we use here for comparison with the dispersed cuticles. The deposit also yielded a rich palynomorph assemblage (Norris, 1965; Bomfleur et al., 2014). Based on the dominance of non-taeniate bisaccate pollen grains and on the co-occurrence of the stratigraphically significant palynomorphs *Craterisporites rotundus*, *Polycingulatisporites crenulatus*, *Polycingulatisporites radiatus*, *Antulsporites varigranulatus*, and *Cadargasporites reticulatus*, the flora has been assigned a Rhaetian age (Bomfleur et al., 2014), making this one of the most diverse and youngest securely dated *Dicroidium* assemblages known.

## 3. RESULTS

### Family Umkomasiaceae Petriella, 1981

#### Genus *Dicroidium* Gothan, 1912

#### *Dicroidium odontopteroides* (Morris) Gothan, 1912

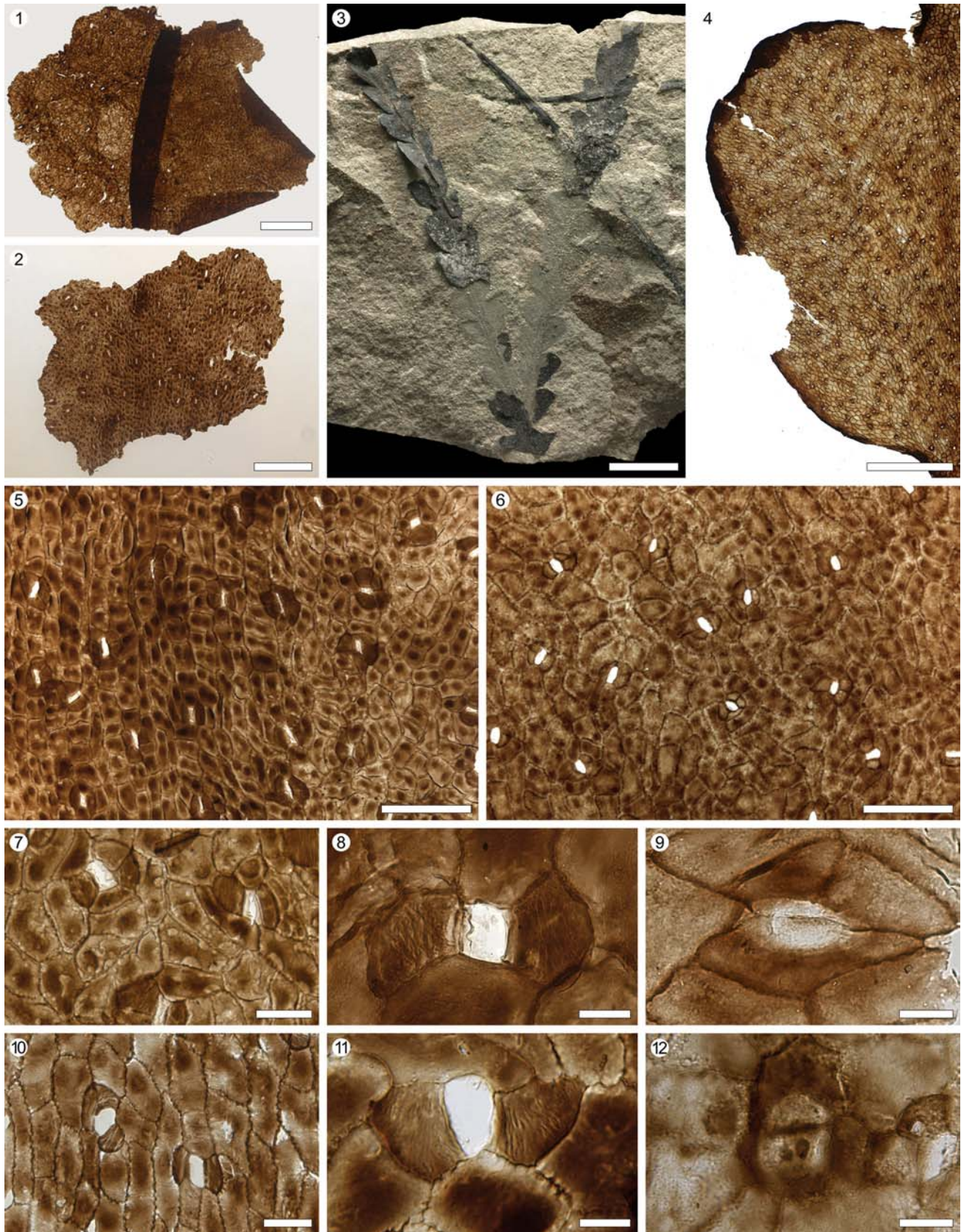
(Plate I, 1, 2, 5, and 7–9)

**Material:** Four cuticle fragments GIX-SPP30b-001(001–004).

**Locality, unit, and age:** Section Peak, Lichen Hills (North Victoria Land, East Antarctica); Section Peak Formation, late early or middle Sinemurian (Early Jurassic).

**Description:** Cuticle on one leaf surface slightly thicker than on the other (Plate I, 1). Epidermal cells usually elongate, rounded-rectangular and up to three times longer than wide, rarely longer or square to isodiametric polygonal; venation weakly discernible with cells above and below vein courses slightly more strongly cutinized and mainly arranged parallel or transverse to vein course (Plate I, 5 center left); cells in intercostal fields more irregularly oriented (Plate I, 5 right). Cuticle surface of each regular epidermal cell with one to four (typically two) even-sized, dome- or lens-shaped thickenings of about 25  $\mu$ m diameter; numbers, shapes, and arrangements of these thickenings variable among cells depending on cell size and shape, but thickenings altogether evenly and regularly distributed over the cuticle surface excluding the stomata. Intercellular flanges uneven, commonly buttressed, or nodose (Plate I, 5 and 7). Leaves unevenly amphistomatic with stomata more common on one leaf surface than the other (Plate I, 1). Stomata irregularly distributed over leaf surfaces, oriented mainly parallel or transverse to vein courses in costal fields and oriented inconsistently in intercostal fields (Plate I, 5); most of the longitudinally or transversely oriented stomata asymmetrically bowtie- or hourglass-shaped with two undifferentiated polar cells similar to surrounding regular epidermal cells and with two to four lateral subsidiary cells that are much more thickly cutinized, lacking dome-shaped thickenings but bearing a series of longitudinal wrinkles (Plate I, 5, 7, and 8); some stomata surrounded by an incomplete ring of up to five similarly, differentiated subsidiary cells (Plate I, 5).





**PLATE 1** *Dicroidium odontopteroides* from the Lower Jurassic (1, 2, 5, and 7–9) and Upper Triassic (3, 4, 6, and 10–12) of North Victoria Land, East Antarctica. (1 and 2) Overviews of dispersed cuticle fragments GIX-SPP30b-001(003) (1) and GIX-SPP30b-001(001) (2); (3) Cuticle-bearing frond compression (GIX-TI13/5-001a); (4) Cuticle of complete pinna (GIX-TI13/5-001a-sl-1); (5 and 6) Comparison of cuticle overviews from Early Jurassic (5: GIX-SPP30b-001(001)) and Late Triassic (6: GIX-TI13/5) specimens; (7 and 10) Comparison of groups of stomata on cuticles of Early Jurassic (7: GIX-SPP30b-001(003)) and Late Triassic (10: GIX-TI13/5-) specimens; (8 and 11) Comparison of details of individual stomata on cuticles of Early Jurassic (8) and Late Triassic (11) specimens; (9 and 12) Comparison of hair bases on cuticles of Early Jurassic (9) and Late Triassic (12) specimens. Specimen numbers: (1) = GIX-SPP30b-001(003); (2, 5, 7, and 8) = GIX-SPP30b-001(001); (3, 4, and 6) = GIX-TI13/5-001a; (9) = GIX-SPP30b-001(004); (10) = GIX-TI13/5-026; (11) = GIX-TI13/5-011a(66); (12) = GIX-TI13/5-011a(47). Scale bars: (1 and 2) = 500  $\mu$ m; (3) = 1 cm; (4) = 1 mm; (5 and 6) = 200  $\mu$ m; (7 and 10) = 50  $\mu$ m; (8, 9, 11, and 12) = 20  $\mu$ m.



Stomatal pit rounded rectangular to elliptic, typically 20–30  $\mu\text{m}$  long and three times longer than wide; guard cells apparently only slightly sunken; guard-cell cutinizations thin and membranaceous (Plate I, 7 and 8), commonly lacking (Plate I, 11). Hair bases present but rare, circular to oval in outline, up to  $\sim 50 \mu\text{m}$  in diameter, with very thin cuticle in the center surrounded by a thickened rim with sharp edges; hairs biseriate at least basally.

**Comparison and remarks:** The diagnostic epidermal and cuticular features of these fragments match precisely those of the cuticles obtained from *Dicroidium odontopteroides* from Timber Peak (Plate I, 3, 4, 6, and 10–12). Slight differences include the overall somewhat thicker cutinization of the Section Peak cuticles and their more pristine preservational quality as evident in, for example, attached remnants of the delicate guard-cell cutinizations (Plate I, 7 and 8 vs. Plate I, 10 and 11) and the much smoother appearance of the cuticle under low magnification (Plate I, 5 vs. Plate I, 6). We consider these differences to result either from contrasting taphonomic contexts or to fall into the expected range of natural variation.

***Dicroidium elongatum* (Carruth.) S. Archang., 1968**

(Plate II, 1, 5, and 7)

**Material:** One cuticle fragment GIX-SPP30b-001(005).

**Locality, unit, and age:** Section Peak, Lichen Hills (North Victoria Land, East Antarctica); Section Peak Formation, late early or middle Sinemurian (Early Jurassic).

**Description:** Cuticle fragment moderately thick compared to co-occurring gymnosperm cuticles. Regular epidermal cells rounded rectangular, fusiform, or irregularly elongate, longitudinally oriented and aligned forming irregular, discontinuous rows throughout the preserved cuticle portion; no differentiation into costal and intercostal fields discernible (Plate II, 1). Anticlinal walls straight or gently curving with even, relatively thick intercellular flanges; outer cuticle surface smooth (Plate II, 5). Stomata evenly distributed over leaf surface; most stomata oriented longitudinally, characteristically butterfly-shaped with a rounded-rectangular stomatal pit flanked by two or three differentiated lateral subsidiary cells; lateral subsidiary cells much smaller than surrounding regular epidermal cells and of rounded-to curved-trapeziform shape, commonly flanked lengthwise by an encircling cell; subsidiary-cell cuticle not or slightly thinner than that of adjacent regular epidermal cells (including encircling cells); walls forming the stomatal pit heavily cutinized (Plate II, 5 and 7).

**Comparison and remarks:** The fragment is essentially identical to the cuticles of the leaf margins of *D. elongatum* from Timber Peak (Plate II, 2–4, 6, and 8) based on (1) the conspicuous longitudinal elongation and (2) alignment of epidermal cells throughout the preserved cuticle portion; (3) the lengthwise orientation and (4) the characteristic butterfly shapes of stomata resulting from (5) usually two

opposite, small, rounded to curved trapeziform lateral subsidiary cells that are (6) about as thickly cutinized as surrounding regular epidermal cells; (7) the gently curving anticlinal walls with smooth and evenly cutinized intercellular flanges; and (8) the smooth outer cuticle surface (see Bomfleur and Kerp, 2010). Although the specimen is just a small fragment, the remarkable similarity to *D. elongatum* cuticles from Timber Peak in all diagnostic epidermal and cuticular features warrants assignment to this species.

***Dicroidium* sp.**

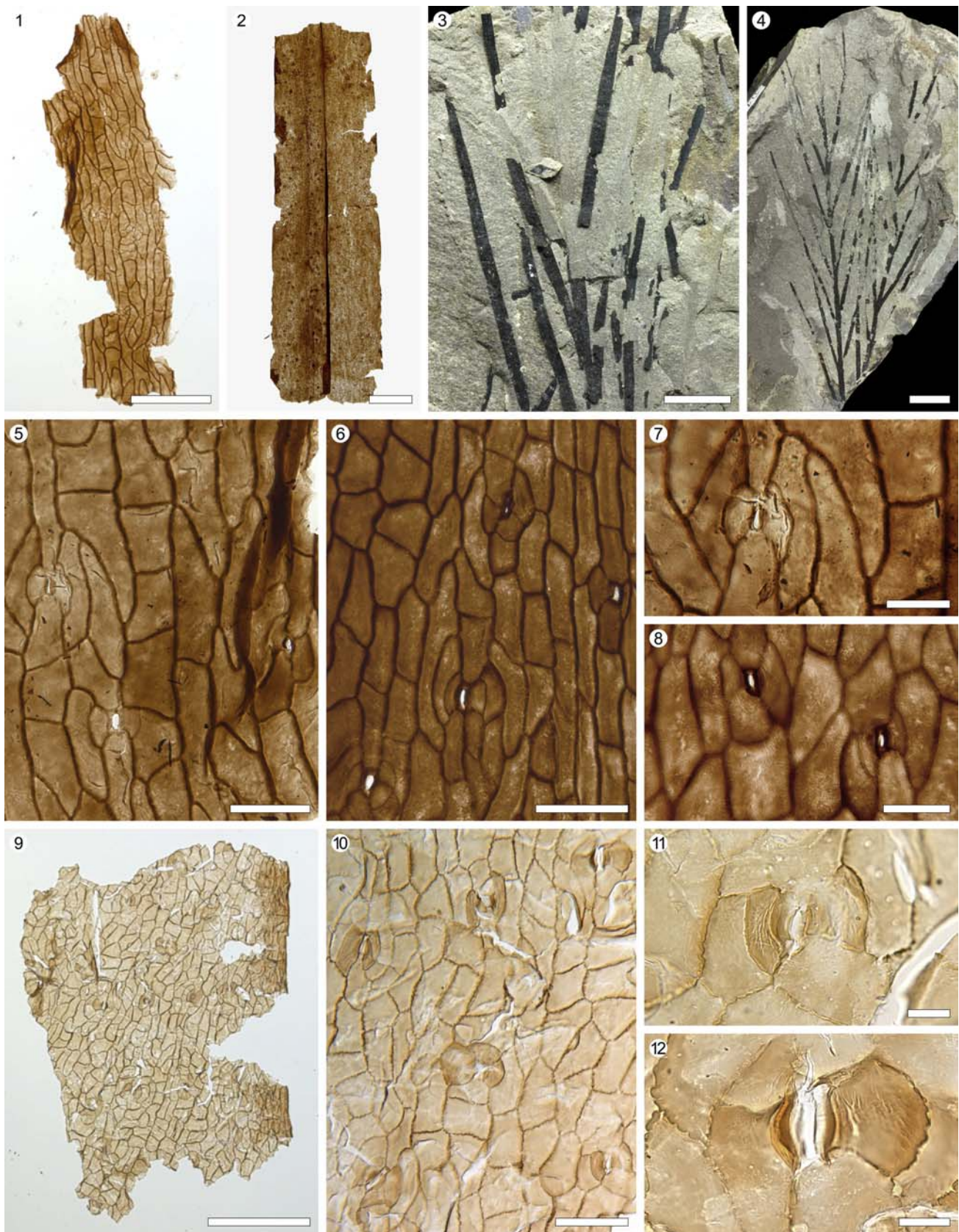
(Plate II, 9–12)

**Material:** One cuticle fragment on slide GIX-SHC32-000(36).

**Locality, unit, and age:** Shafer Peak, Deep Freeze Range (North Victoria Land, East Antarctica); Shafer Peak Formation, middle or late Pliensbachian (Early Jurassic).

**Description:** Cuticle moderately thick compared to co-occurring cuticles of other gymnosperm taxa. Ultimate veins reaching the margin at an acute angle (Plate II, 9). Epidermal cell pattern weakly differentiated into costal fields with more slender cells that are longitudinally aligned and oriented mainly parallel or transverse to vein course, and into intercostal fields with larger, broader cells that are oriented less consistently (Plate II, 9). Anticlinal walls generally straight or only slightly curving, with uneven, nodose to buttressed intercellular flanges; outer cuticle surface smooth (Plate II, 10–12). Most cells stout rectangular (usually less than two times longer than wide) or about isodiametric polygonal. Stomata evenly distributed over leaf surface (Plate II, 9 and 10); most stomatal complexes oriented longitudinally or transversely to adjacent vein courses, butterfly- or bowtie-shaped (Plate II, 10–12) with a rectangular pit flanked by two or three differentiated lateral subsidiary cells; some stomata surrounded by an incomplete ring of three or four differentiated subsidiary cells; subsidiary cells smaller and more slender than surrounding regular epidermal cells, sporadically flanked lengthwise by an encircling cell; subsidiary-cell cuticle with curved wrinkles and furrows concentric around the stomatal pit, overall thicker than that of adjacent regular epidermal cells including encircling cells; guard cells only slightly sunken; inner guard-cell walls with membranous, curved-trapeziform cutinizations bearing indistinct radial striae (Plate II, 11 and 12).

**Comparison and remarks:** The sum of characteristic epidermal and cuticular features, notably, the differentiation and the arrangement of subsidiary cells in relation to the orientation of the stoma (see Jacob and Jacob, 1950; Bomfleur and Kerp, 2010), enables assignment of this fragment to *Dicroidium*. Other individual features typical of *Dicroidium* cuticles are the uneven, nodose, or buttressed cutinization of intercellular flanges



**PLATE II** Additional *Dicroidium* cuticles from the Lower Jurassic (1, 5, 7, and 9–12) and Upper Triassic (2–4, 6, and 8) of North Victoria Land, East Antarctica. (1 and 2) Dispersed cuticle fragments of *Dicroidium elongatum* from the Lower Jurassic (1) and Upper Triassic (2); (3 and 4) Cuticle-bearing frond compressions of *D. elongatum*; (5 and 6) Comparison of cuticle overviews from Early Jurassic (5) and Late Triassic (6) specimens of *D. elongatum*; (7 and 8) Comparison showing details of stomata from Early Jurassic (7) and Late Triassic (8) specimens of *D. elongatum*; (9) Overview of dispersed cuticle fragment of *Dicroidium* sp. from the Pliensbachian Shafer Peak Formation at Shafer Peak; (10) detail of (9) showing epidermal cell pattern and distribution, orientation, and organization of stomatal complexes; (11 and 12) details of (9) showing well-preserved stomata with preserved guard-cell cutinizations (12). Specimen numbers: (1, 5, and 7) = GIX-SPP30b-001(005); (2) = GIX-TI13/5-011a(38); (3) = GIX-TI13/5-010a; (4) = GIX-TI13/5-008a; (6 and 8) = GIX-TI13/5-011a(25); (9–12) = GIX-SHC32-000(36). Scale bars: (1 and 9) = 500  $\mu$ m; (2) = 1 mm; (3 and 4) = 1 cm; (5, 6, and 10) = 100  $\mu$ m; (7 and 8) = 50  $\mu$ m; (11 and 12) = 20  $\mu$ m.



(see, e.g., [Anderson and Anderson, 1983](#), Figs. 6.3 and 6.4, Plates 107, 3,4,8 and 108, 3,5; [Cantrill et al., 1995](#), Fig. 3e and f; [Barale et al., 2005](#), Figs. 24–28); the thicker cutinization but lack of papillae on differentiated subsidiary cells (see [Anderson and Anderson, 1983](#), Figs. 6.2 and 6.4; [Bomfleur and Kerp, 2010](#)); the stomata scattered irregularly over the lamina irrespective of vein courses (see [Anderson and Anderson, 1983](#); [Abu Hamad et al., 2008](#); [Bomfleur and Kerp, 2010](#)); and the relatively little-sunken guard cells (see [Anderson and Anderson, 1983](#); [Bomfleur and Kerp, 2010](#)). The particular combination of features in the present specimen is, however, unknown among the *Dicroidium* cuticles studied so far ([Jacob and Jacob, 1950](#); [Archangelsky, 1968](#); [Anderson and Anderson, 1983](#); [Cantrill et al., 1995](#); [Abu Hamad et al., 2008](#); [Bomfleur and Kerp, 2010](#)). We suggest it represents probably a distinct species, but refrain from a formal systematic treatment because of the fragmentary nature and limited sample size of the material.

## 4. DISCUSSION

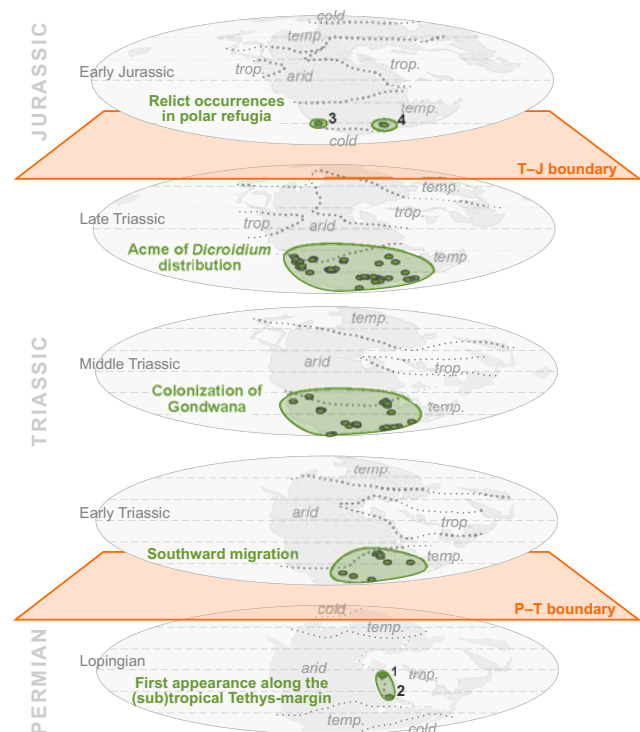
### 4.1 Relictual *Dicroidium* Occurrences in the Jurassic of Antarctica

The apparent occurrence of *Dicroidium* in Jurassic deposits warrants particular scrutiny regarding the proper identification of the material, the age determination of the host deposits, and the possibility of reworking or sample contamination. First, *Dicroidium* cuticles and epidermal morphologies are very well known and have early on been recognized as distinctive for the group ([Thomas, 1933](#); [Jacob and Jacob, 1950](#); [Townrow, 1957](#); [Archangelsky, 1968](#); [Bomfleur and Kerp, 2010](#)). Hence, even though the sample material includes only small cuticle fragments, the striking similarity in all observable features of these fragments compared to the cuticles obtained from the Triassic *Dicroidium* compressions is so significant that we consider their systematic affiliation beyond doubt. Second, the age assignments for the host deposits are robust, being constrained via a combination of palynostratigraphy ([Norris, 1965](#); [Pertusati et al., 2006](#); [Bomfleur et al., 2014](#)), radiometric ages of detrital and juvenile volcanic zircons ([Elsner, 2010](#); [Goodge and Fanning, 2010](#); [Elsner et al., 2013](#)), lithostratigraphic correlation, and biostratigraphic ranges of co-occurring plant macrofossils ([Bomfleur et al., 2011b,c](#)). Third, any significant effect of reworking is unlikely because the dispersed *Dicroidium* cuticles have a similar state of preservation compared to those of co-occurring (characteristically Jurassic) gymnosperm taxa. Moreover, the *Dicroidium* cuticles—though fragmented—appear well preserved, and the fine details preserved on some of the fragments (e.g., the delicate guard-cell cutinizations on the cuticles of *D. odontopteroides*) would

not have survived repeated erosion and transport. Finally, the dispersed Jurassic cuticles of *D. odontopteroides* and of *D. elongatum* do differ noticeably from the Triassic *in situ* cuticles in overall preservational aspect (e.g., in having deformations caused by the much larger grain size of the sedimentary matrix) and in those cuticle features that we consider to fall into the range of intraspecific variability (e.g., absolute cuticle thickness). Taken together, the cuticle fragments presented here provide the first robust evidence of *Dicroidium* seed ferns in the Jurassic, and may provide further circumstantial evidence to support earlier identifications of *Dicroidium* fragments in the Lower Jurassic of the Antarctic Peninsula ([Rees and Cleal, 2004](#)).

### 4.2 Distribution of *Dicroidium* Through Space and Time

These youngest occurrences of *Dicroidium* in Antarctica complement a remarkable pattern in the distribution of *Dicroidium* plants through space and time ([Fig. 24.2](#)). The group apparently originated some time during the late Palaeozoic in seasonally dry and disturbance-prone environments of the palaeoequatorial regions, with the



**FIGURE 24.2** Distribution of *Dicroidium* through space and time. Base maps and climates based on the Paleomap Project ([Scotese, 2002](#)); *Dicroidium* occurrences compiled primarily from [Anderson and Anderson \(1983\)](#) with additional data from [Artabe et al. \(2003\)](#), (3) [Rees and Cleal \(2004\)](#), (1) [Abu Hamad et al. \(2008\)](#), [Bomfleur and Kerp \(2010\)](#), [Pal et al. \(2014\)](#), [Pattimore et al. \(2015\)](#), (2) [Schneebeil-Hermann et al. \(2015\)](#), and (4) this study.



oldest reliable fossil records from the Lopingian (Upper Permian) of Jordan (Kerp et al., 2006; Abu Hamad et al., 2008) and Pakistan (Schneebeil-Hermann et al., 2015). As global temperatures rose toward the end of the Palaeozoic, *Dicroidium* migrated southward along the Tethys margin and began to invade the extensive lowlands of the Gondwanan high latitudes that were vacated by the gradual demise of the once dominant, cool-adapted glossopterid swamp forests (McLoughlin, 2001). By the later Early Triassic, *Dicroidium* vegetation had extended across most of eastern Gondwana, reaching far into polar latitudes beyond 80°S, and then made its first appearance in western Gondwana at the beginning of the Middle Triassic (Artabe et al., 2001). *Dicroidium* distribution reached its heyday with increasingly humid climates during the early Late Triassic (Simms and Ruffel, 1990), when the characteristic leaf type had become the most dominant macrofloral element across the entire extratropical regions of Gondwana (Anderson and Anderson, 1983). Regional climates during that time were humid and warm temperate, with high rainfall throughout the year and without extended periods of frost even at high latitudes (Escapa et al., 2011). Nevertheless, even without low-temperature environmental stresses in these ancient high-latitude habitats, the annual phases of continuous summer daylight and continuous winter darkness may have lasted for up to several months. The *Dicroidium* plants were apparently well adapted to cope with this extreme seasonality: they were seasonally deciduous and entered dormancy to endure the long, warm winter darkness (Meyer-Berthaud et al., 1992; Cúneo et al., 2003; Bomfleur and Kerp, 2010); modified, early leaf-ontogenetic foliar outgrowths of the fronds may have served to boost the restoration of metabolic activity during spring flush (Bomfleur et al., 2012); and a specialized leaf physiology with short-lived “high-performance foliage” maximized assimilation rates during the growth season (Bomfleur and Kerp, 2010), which is also reflected in the remarkable thickness of growth rings in corresponding fossil wood (Decombeix et al., 2014). Altogether, life mode and ecological characteristics rendered the *Dicroidium* plants remarkably successful competitors in the mesic high-latitude environments of Gondwana, where they formed the dominant canopy elements in old-growth forest, woodland, and forested mire vegetation.

Our results indicate that toward the end of the Triassic, *Dicroidium* plants only gradually began to disappear and lingered on in Jurassic floras as minor relictual elements in more modern vegetation communities dominated by conifers, Bennettitales, and various ferns. It remains difficult to resolve the precise mechanisms for this gradual demise of the *Dicroidium* seed ferns. Certainly, the immense magmatism of the Central Atlantic Magmatic Province around the Triassic–Jurassic boundary and of the Ferrar-Karoo Large Igneous Province around the

Pliensbachian–Toarcian boundary must have triggered complex cascades of effects on the Earth System and the biosphere (see Bond and Grasby, 2017). Massive release of greenhouse gases during these magmatic episodes, for instance, is argued to have increased seasonal aridity in the continental interior of Pangaeian landmasses (Bonis and Kürschner, 2012). In the face of such changing environmental conditions, more stress-tolerant conifer groups and Bennettitales may have eventually gained adaptational advantages over the *Dicroidium* plants, which gradually declined as other gymnosperms rose to dominance (see McLoughlin, 2001).

### 4.3 Plant Relictualism in the High Latitudes of a Greenhouse World

These youngest relictual occurrences of *Dicroidium* in polar habitats provide an important further contribution to the emerging picture that during times of global warmth, high-latitude regions may have provided climatically stable last refugia for relict populations of plant groups in the wake of biotic crises. Here we summarize key examples of plant groups that show such younger-than-expected high-latitude occurrences including isoëtalean lycopsids, various groups of extinct seed ferns, Bennettitales, and conifers.

#### 4.3.1 Isoëtales

Herbaceous Isoëtales have a long fossil record extending back to the Devonian (Pigg, 1992, 2001), and they were probably related closely to the arborescent Lepidodendrales of the late Palaeozoic coal-forming mires. *Paurodendron* was an early herbaceous isoëtalean plant that grew widely in the Pennsylvanian equatorial coal swamps of North America and Europe (Fry, 1954; Schlanker and Leisman, 1969; Phillips and Leisman, 1966; Rothwell and Erwin, 1985). McLoughlin et al. (2015a) extended the stratigraphic and geographic range of *Paurodendron* to ~70° south palaeolatitude in Wordian strata of the Lambert Graben, Antarctica (Plate III, 1 and 2). *Paurodendron* apparently disappeared from the palaeotropics around the end of the Carboniferous as the western equatorial regions of Pangaea transitioned from humid (peat-forming) to semi-arid conditions. Peat accumulation persisted in high southern latitudes until the close of the Permian, and *Paurodendron* appears to have tracked southward with the poleward contraction of glossopterid-dominated peat-forming environments toward the end of the Palaeozoic. There is a 35 million year gap between the youngest equatorial records and the southern high-latitude records of *Paurodendron*, but McLoughlin et al. (2015a) noted that this may be a function of strong preservational biases—the genus only being recognized from three-dimensionally preserved (permineralized) fossils.





**PLATE III** Selected examples for plant taxa with relictual occurrences in high palaeolatitudes. (1 and 2) Longitudinal (1) and transverse (2) sections through stems of *Paurodendron stellatum* (Isoëtales) from the Guadalupian of the Prince Charles Mountains, East Antarctica (McLoughlin et al., 2015a); (3) Mat of notably small *Glossopteris* leaves from the Lopingian Newcastle Coal Measures of the Sydney Basin, New South Wales, Australia (AMF 124224S); (4) probable *Peltaspermales* from the Upper Jurassic or lowermost Cretaceous of Clack Island, Queensland, Australia; note intercalary pinnules on the frond (arrows) and *Peltaspermum*-like ovuliferous disk in the lower right of the image; (5 and 6) frond compression (5) and cuticle with stoma (6) of *Komlopteris eocenica*, and Eocene seed fern from Tasmania (McLoughlin et al., 2008); (7) *Sagenopteris* leaf (Caytoniales) from the Triassic of Kyrgyzstan; (8 and 9) *Ptilophyllum muelleri* (Bennettitales) from the Oligocene of Emmaville, New South Wales, Australia (McLoughlin et al., 2008). Scale bars: (1) = 1 mm; (2) = 250 µm; (3 and 4) = 1 cm; (5 and 7–9) = 5 mm; (6) = 25 µm.



Notably, also the youngest occurrences of pleuromeian lycophytes—the dominant plants of many Lower and lower Middle Triassic plant assemblages worldwide (Retallack, 1997)—are from Norian–Rhaetian (Late Triassic) deposits of the central Transantarctic Mountains (Bomfleur et al., 2011a). Although the fossils are incomplete fragments, fertile features and a characteristic internal leaf structure indicate affinities with *Pleuromeia*. The unusual occurrence of these fossils in carbonaceous flood-basin deposits has been interpreted to indicate that Pleuromeiales migrated far south during the Middle Triassic and adapted to peat-swamp environments, where they persisted well into the Late Triassic when they had long disappeared from their typical lower-latitude habitats (Bomfleur et al., 2011a).

#### 4.3.2 *Glossopteridales*

Glossopterids were a distinctive group of gymnosperms that occupied southern middle to high latitudes in the Permian. They are most typically represented in the fossil record by their spatulate, reticulate-veined leaves, uniquely segmented roots, taeniate bisaccate pollen, and axillary or leaf-borne, winged, multiovulate reproductive organs. During the early Permian (Cisuralian) glossopterids rapidly occupied lowland habitats vacated by the retreating ice sheets of the Late Palaeozoic Ice Age. The group reached its acme in the Guadalupian to Lopingian at which time it overwhelmingly dominated mire environments from middle to near-polar southern latitudes. *Glossopteris* and its allies were clearly adapted to cool temperate, strongly seasonal climates, evidenced by the group's restriction to palaeolatitudes greater than 30°S (McLoughlin, 2001), the deciduous nature of the plants (McLoughlin, 2011), adaptations to consistently humid mire habitats (Balme et al., 1995; McLoughlin, 1993), and association with marine sediments bearing cold-water sedimentary indices, such as glendonites and ice-rafted dropstones (Retallack, 1980; Shi and McLoughlin, 1997). Glossopterids appear to have persisted to the end of the Permian. It is unclear whether they survived locally into the earliest Triassic. It is notable that the stratigraphic spacing of coals and coal bed thickness declines in the uppermost Permian of the Amery Group, East Antarctica (McLoughlin and Drinnan, 1997a,b), and this appears to signal a general decline in the conditions suitable for supporting the mire-dominating *Glossopteris* flora. Remarkably, the youngest Permian assemblages in the Parana Basin, Brazil (Rio do Rasto Formation: Rohn and Rösler, 1992), the Karoo Basin, South Africa (Normandien Formation: Anderson and Anderson, 1985), and the Bowen Basin, Australia (Blackwater Group: McLoughlin, 1993, 1994a,b) all host large numbers of small-leaved species (Plate III, 3). A few large-leaved forms are still present but typically restricted to local deposits that may have characterized nutrient-rich

and/or very moist habitats. By the Changhsingian, coal-forming environments had disappeared from the northern sectors of Gondwana and are best represented in the southernmost palaeolatitudes, then occupied by eastern Australia and Antarctica. This suggests a general poleward contraction of the core domain dominated by glossopterids as the supercontinent experienced dramatic warming and marked seasonal drying with the intensification of the Gondwanan monsoon around the Permian–Triassic boundary (McLoughlin et al., 1997).

The youngest records of glossopterid leaves are from putative basal Triassic strata in East Antarctica (Rigby and Schopf, 1969; McManus et al., 2002; see Elliot et al., 2016) and South Africa (Gastaldo et al., 2015) and from the Nidpur beds in central India (Pant and Pant, 1987). Moreover, some dispersed fossil pollen typically attributed to glossopterids persists into Lower Triassic strata (Lindström and McLoughlin, 2007; Gastaldo et al., 2015). However, many of these records have been considered equivocal. The Nidpur beds have been subject to faulting juxtaposing Permian and Triassic strata such that the source rocks of past sampling are uncertain; dispersed palynomorphs are subject to considerable reworking making the last appearance datum for any one pollen type unreliable for dating the disappearance of the parent plants; some putative *Glossopteris* leaves may have been misidentified, and instead potentially belong to other tongue-shaped leaves with reticulate venation, for example, *Gontriglossa* (see Holmes et al., 2010); and the placement of the Permian–Triassic boundary, especially in the Transantarctic Mountains and the Karoo Basin successions, is uncertain. Nevertheless, recent high-resolution radiometric dating of a volcanoclastic sandstone bed 37 m below the stratigraphically highest *Glossopteris* assemblages at a section in Antarctica yielded a maximum depositional age of  $250.3 \pm 2.2$  Ma (Elliot et al., 2016), indicating that at least some of the Antarctic *Glossopteris* records may indeed be earliest Triassic in age. Moreover, detailed analysis of fossil assemblages across the Permian–Triassic transition in the Eastern Cape Province (Gastaldo et al., 2017) appear to confirm that *Glossopteris* may have also persisted there into the earliest Triassic.

#### 4.3.3 *Peltaspermales*

Peltaspermales originated during the Late Carboniferous and are well represented in some Northern Hemisphere, particularly Angaran, Permian floras (Taylor et al., 2006). In Gondwana, they made their appearance around the end of the Permian and were prominently represented by *Scytophyllum* and the *Lepidopteris*–*Peltaspermum*–*Antevsia* association of organs throughout the Triassic (Anderson and Anderson, 1989, 2003). The group appears to have become extinct in most areas, together with a broad range

of other seed plants, at the end of the Triassic (McElwain and Punyasena, 2007; Kustatscher et al., 2018). However, *Lepidopteris* foliage, together with *Peltaspermum*-like ovuliferous disks and *Antevsia*-like pollen organs, have recently been found in Lower to Middle Jurassic deposits of the Cañadon Asfalto Formation at the Pomelo locality in Chubut, southern Argentina (Elgorriaga et al., 2016). Moreover, Rozefelds (1988) and McLoughlin et al. (2015b) illustrated latest Jurassic or earliest Cretaceous *Pachypteris* leaves from eastern Australia that are possibly peltaspermean. Although dismissed by Pattemore et al. (2015) as fern fronds, the leaves bear conspicuous *zwischenfiedern* (intercalary pinnules or rachis leaflets) and apparently had a blistery rachis and a thick lamina, facilitating complex lepidopteran-like leaf-mining attack typical of seed plants (Plate III, 4); moreover, the dispersed umbrella-shaped structures (fern croziers according to Pattemore et al., 2015) occurring immediately adjacent to the foliage remains are very similar to typical *Peltaspermum* ovuliferous discs (Plate III, 4). Together, these records indicate persistence of this group well beyond the Triassic in southern high latitudes.

#### 4.3.4 Caytoniales

In the Northern Hemisphere, some similar patterns of contraction to high latitudes are apparent among Mesozoic gymnosperm groups. Among the most remarkable examples is the Caytoniales, an extinct group of gymnosperms most commonly represented by their distinctive, palmately compound leaves (*Sagenopteris*; Plate III, 5) with two pairs of mesh-veined leaflets (Taylor et al., 2006). Their main stratigraphic distribution extends from the Middle Triassic to the Early Cretaceous. However, Hollick (1930) and Herman (2013) noted the persistence but progressive decline of Caytoniales together with Ginkgoales and Nilssoniales (a group superficially similar and possibly related to Cycadales) in floras of the Bering Strait region, reaching palaeolatitudes beyond 80°N, through the Late Cretaceous as angiosperm dominance increased in the region. Krassilov (1978) also recorded Caytoniales and Nilssoniales extending to at least the Santonian and Bennettitales to the latest Maastrichtian on Sakhalin. Boyd (1992) recognized the similar persistence of Caytoniales together with Bennettitales well into the Late Cretaceous of Greenland, long after these groups had declined at lower latitudes. Notably, more continuous landmasses at high latitudes of the Northern Hemisphere enabled movement of ancient gymnosperm groups with fewer constraints from open sea barriers compared to the fragmented Gondwanan terranes. Continuous landmasses in the north also facilitated movement of newly evolved plant groups (e.g., angiosperms) such that it might be expected that if intergroup competition were an important factor in the

contraction of some seed plants, then such decline might have occurred earlier and been more abrupt in the Northern Hemisphere compared to the Southern Hemisphere.

#### 4.3.5 Bennettitales

Bennettitales was a group of seed plants with complex flower-like reproductive structures and either stocky cycad-like or thin divaricate-branching stems (Pott and McLoughlin, 2014). Their origins and phylogenetic relationships remain obscure. They were clearly present in Gondwana by the Middle Triassic (McLoughlin et al., 2018) and were relatively common and cosmopolitan by the Carnian (Kustatscher et al., 2018). After the disappearance of the *Dicroidium*-dominated mire communities at the end of the Triassic, Bennettitales became one of the chief plant groups of lowland ecosystems across Gondwana from the Early Jurassic to mid-Cretaceous. Following the Aptian cool phase and the appearance of angiosperms, bennettitalean foliage becomes sparse in the fossil record. The youngest Cretaceous examples are again from southeastern Gondwana (New Zealand and eastern Australia; Daniel et al., 1990; McLoughlin et al., 2010) and from the Russian Far East (Gnilovskaya and Golovneva, 2018), all then positioned at relatively high latitudes. This group also appears to have survived the end-Cretaceous mass extinction and is represented in Oligocene deposits of northern Tasmania and northern New South Wales (Australia) by the single species *Ptilozamites muelleri* (Plate III, 8 and 9; McLoughlin et al., 2011).

#### 4.3.6 Cheirolepidiaceae

Cheirolepidiaceae was a group of scale-leaved shrub- to tree-sized conifers that appeared in the Late Triassic, underwent a surge in relative abundance (based on the records of their distinctive *Classopollis* pollen) around the Triassic–Jurassic boundary, and were consistent elements of global floras through the Jurassic and Early Cretaceous. Although some representatives (e.g., frenalopsids) probably typified low-latitude semi-arid and saline coastal settings (Alvin, 1982), some members of the family with *Brachyphyllum*-type foliage were apparently adapted to cooler and wetter environments of higher latitudes (Tosolini et al., 2015). Cheirolepidiaceae were consistent (although steadily declining in importance) elements of dispersed cuticle and pollen floras in Gondwana until the Maastrichtian (Helby et al., 1987; Pole, 2000), but the group appears to have disappeared from most regions of the world by the close of the Cretaceous. Significantly, Barreda et al. (2012) noted a short-lived resurgence of this group (represented by a *Classopollis* pollen spike) in lowermost Paleocene strata of Patagonia (then at ~50°S) before their eventual demise in the Danian (Alvin, 1982).



#### 4.3.7 *Komlopteris*

Whereas the *Dicroidium* seed ferns apparently vanished some time during the Jurassic, other foliage genera tentatively assigned to Umkomasiales (=Corystospermales; e.g., *Rintoulia*, *Komlopteris*, *Pachypteris*, *Pachydermophyllum*, and *Archangelskya*) persisted in Gondwanan vegetation in modest numbers and diversity through the Jurassic and Early Cretaceous (McLoughlin et al., 2002; Rees and Cleal, 2004; Turner et al., 2009). Following the Aptian cool phase, corystosperm foliage is generally absent from Albian–Late Cretaceous floras. Most remarkably, however, a final representative of this group (*Komlopteris eocenica*; Plate III, 5 and 6) is recorded from Eocene strata of Tasmania based on foliage with well-preserved cuticle (McLoughlin et al., 2008). *Alisporites*-type bisaccate pollen of putative corystospermalean affinity is also known elsewhere in Eocene strata of southeastern Australia (Harris, 1965).

#### 4.3.8 *Podozamitaceae*

*Podozamites* encompasses broad multiveined conifer foliage with thin cuticle and unique, transversely oriented paracytic stomata. The leaves were commonly shed attached to whole short shoots and the plant is interpreted to have been seasonally deciduous (Pole et al., 2016). *Podozamites* has been linked tentatively to the reproductive structures *Cycadocarpidium* and *Swedenborgia* (Harris, 1979; Bugdaeva, 1995) and placed within a distinct family: Podozamitaceae Nemejc (1950). A recent survey of *Podozamites* distributions in Asia carried out by Pole et al. (2016) noted that the genus appeared in the Early Triassic and ranged from 15° to over 80°N during the later part of that period with particularly strong representation in middle latitudes. In the Early Jurassic, the genus maintained a broad latitudinal range (at least 30–70°N). It slightly contracted in the Middle Jurassic to a range of around 30–60°N, and persisted predominantly in maritime settings at around 20–60°N in the Late Jurassic (with a center of representation around 35°N) in tandem with drying of the continental interior. The group's range extended to 15–75°N in the Early Cretaceous, retaining a predominantly maritime distribution but with a center of representation around 50°N. During the Late Cretaceous, however, the distribution of the last remaining *Podozamites* in East Asia contracted rapidly northward into polar latitudes with the onset of angiosperm dominance in the regional vegetation. The genus disappeared from the region some time after the Santonian–Campanian (Pole et al., 2016). Pole et al. (2016) noted that the demise of *Podozamites* was contemporaneous with, and potentially linked to, the poleward expansion of angiosperms and scale-leaved conifers, but that additional factors, such as regional

climatic shifts and intensifying herbivory on broad-leaved plants, may have also contributed to the group's extinction.

#### 4.3.9 *Palissyaceae*

Palissyaceae is an enigmatic conifer family that includes cones attributed to *Palissya* (and the synonymous *Knezourocarpon*), *Stachyotaxus*, and *Metridiostrobus*. Foliage similar to *Elatocladus* has been inferred to be affiliated with these organs. As yet, it cannot be confirmed whether the cones of this group represent ovuliferous or polleniferous organs since ovules have been interpreted to be associated with some specimens (Florin, 1951; Delevoryas and Hope, 1981) but pollen sacs and monosulcate pollen grains have been identified on other material (Schweitzer and Kirchner, 1996; Van Konijnenburg-van Cittert, 2008). It is likely that *Palissya* has been employed for two distinctly different cone types and a thorough review of the group is needed. Nevertheless, palissyacean cones with distinctive cup-shaped structures on the adaxial surface of the sporophylls have a peculiar geographic and stratigraphic range. They appear in the low to middle latitudes of the Northern Hemisphere in the Late Triassic (Delevoryas and Hope, 1981) and spread rapidly through Laurasia. They persisted in Europe in the Early Jurassic (Nathorst, 1908; Florin, 1958) but also make their first appearance in Australia at that time. Thereafter, Palissyaceae appears to have become predominantly a high-latitude Gondwanan clade, with common representation of cones in Early Jurassic to Aptian strata of New Zealand, Australia, and Antarctica (Von Ettingshausen, 1891; Edwards, 1934; Parris et al., 1995; Cantrill, 2000; McLoughlin et al., 2002; Jansson et al., 2008; Pattemore et al., 2014). The youngest occurrences of the group appear to be in Aptian strata of the Antarctic Peninsula region (Cantrill, 2000) and in the Koonwarra Fossil Bed of the Gippsland Basin, southeastern Australia (Driinnan and Chambers, 1986), the latter unit hosting the earliest angiosperms in the region. Putative younger examples are based on fossil foliage of uncertain affinity.

#### 4.3.10 *Gondwanan Equisetales*

Equisetaleans (horsetails) have a long stratigraphic record extending from the Devonian to present (Taylor et al., 2009), and occurred on Gondwanan landmasses from at least the Carboniferous (Gutiérrez, 1995; Morris, 1985). The group was diverse through the late Palaeozoic, incorporating some arborescent forms (Rössler and Noll, 2002, 2006), but steadily declined in diversity and abundance through the Mesozoic, at which time it was represented by mainly herbaceous taxa. Today, the group is represented by *Equisetum*—an almost cosmopolitan genus

of about 15 extant species and several extinct forms (Hauke, 1963, 1978). Indigenous *Equisetum* is notably absent from New Zealand, Australia, Antarctica, and some Pacific islands, although some species thrive in these regions today as exotic weeds (Clifford and Constantine, 1980; Brownsie and Perrie, 2015). Pole and McLoughlin (2017) proposed that a combination of substantial environmental change (particularly drying and abrupt warming/cooling) and competition from diversifying angiosperm groups probably contributed to the demise of equisetaleans across the New Zealand–Australian–Antarctic region through the late Mesozoic and Paleogene. Until recently, the youngest equisetaleans reported from Australasia were from Cenomanian to Maastrichtian strata (see McLoughlin et al., 2010). However, Pole and McLoughlin (2017) illustrated *Equisetum* fossils from two Miocene deposits in New Zealand indicating that the group survived the end-Cretaceous mass extinction and persisted in wetter parts of this region until its probable demise from late Cenozoic warming and drying (in Australia) and cooling (in New Zealand).

#### 4.3.11 Gondwanan Ginkgoales

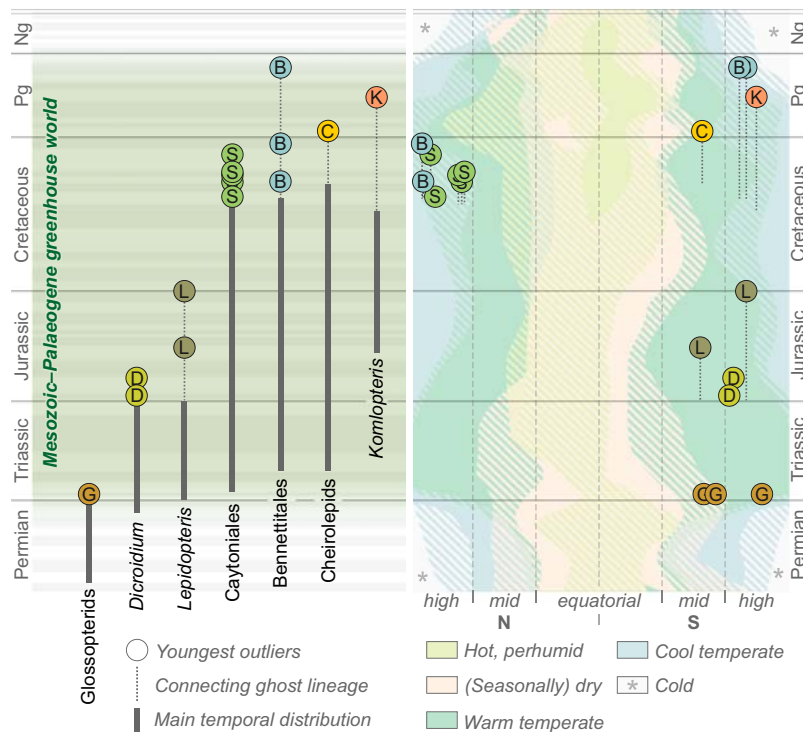
Ginkgoales have a long fossil record in Gondwana, initiating at least as early as the Cisuralian (Early Permian: Cúneo, 1987), although some *Ginkgo*-like flabellate leaves are known from even older (Carboniferous) strata (Archangelsky and Leguizamón, 1980). They were widespread and abundant during the Middle and Late Triassic (Anderson and Anderson, 1989, 2003; Holmes and Anderson, 2007) but disappeared from some regions (e.g., Australia) during the Jurassic, apparently in conjunction with a prolonged interval of global warmth (Turner et al., 2009). Ginkgoales returned in moderate abundance to the Gondwanan floras in the Aptian in association with an interval of cooler temperatures (Walkom, 1919; Douglas, 1969; Drinnan and Chambers, 1986; Dettmann et al., 1992). They persisted in low numbers and diversity into the mid-Cretaceous (Douglas, 1970; Daniel et al., 1990; McLoughlin et al., 1995; Mays et al., 2015) but seem to have disappeared from most parts of the southern continents some time after the Turonian. In southern Gondwana, they appear to have survived the end-Cretaceous mass extinction and are preserved in lower Paleogene strata in Tasmania (*Ginkgo* sp. cf. *G. australis*: Carpenter and Hill, 1999). A similar pattern is evident in southwestern Gondwana with the last sparse occurrences of Ginkgoales represented in lower–middle Eocene strata of Patagonia (*Ginkgoites patagonica*: Berry, 1935, see Villar de Seoane et al., 2015). Notably, these last occurrences in South America are from plant assemblages that probably represent humid, possibly montane rainforest vegetation surrounding high-altitude caldera lakes (Wilf, 2012).

## 4.4 Analogies With Low- and Mid-Latitude Montane Refugia

In the icehouse world today, where polar landmasses are covered by thick continental ice sheets, relict gymnosperm taxa—such as *Ginkgo* and *Sciadopitys*—typically occur in montane refugia in low and middle latitudes. Similar to past high-latitude terrestrial ecosystems, these environments are characterized as equable mesic, with overall lower energy-input and low water-stress. Humid forests in modern regions that formerly constituted the southeastern corner of Gondwana (southeastern Australia, Tasmania, New Zealand, and New Caledonia), for instance, host a range of conifers that can be considered to have relictual distributions (Brodrribb and Hill, 1999). Members of several major Mesozoic conifer families (Araucariaceae, Podocarpaceae, Cupressaceae) are represented in this region by genera with narrow geographic ranges and climatic envelopes. Notable among these are *Wollemia*, *Microcachrys*, *Pherosphaera*, *Parasitaxus*, *Halocarpus*, *Manoao*, *Lagarostrobos*, *Diselma*, *Athrotaxis*, *Papuacedrus*, and *Libocedrus*. Several other genera, including *Araucaria*, *Agathis*, *Phyllocladus*, *Prumnopitys*, *Dacrydium*, and *Dacrycarpus*, have their centers of extant diversity in this region but include some species from southern South America or have representatives that appear to have re-radiated recently into tropical regions. Therefore, it would seem reasonable to assume that mesic high-elevation forests at lower and middle latitudes may have acted as biodiversity refugia in the geological past as well; however, such patterns may be difficult to detect since any rare taxon with patchy distribution in montane settings, away from lowland depositional centers, is unlikely to be recorded in fossil assemblages.

## 5. CONCLUSIONS

The imperfection of the fossil record (Darwin, 1859; see Kidwell and Holland, 2002) impedes any attempt at a precise reconstruction of the distribution of extinct plant groups through space and time. Nevertheless, we are confident that the examples outlined above demonstrate that despite these limitations, identifying geographic and/or stratigraphic outlier occurrences of plant taxa will contribute to a better understanding of the dynamics of vegetation turnover through geologic time. There is mounting evidence to confirm that plants in general were less dramatically affected by global environmental crises than animals (Traverse, 1988; see Lucas and Tanner, 2015). Stratigraphic ranges of many plant groups thus turn out to cross system boundaries that mark some of the greatest faunal mass extinctions in Earth history (see Fig. 24.3): *Glossopteris* may have survived the Permian–Triassic extinction; *Dicroidium* even thrived through both the



**FIGURE 24.3** Comparison of the main stratigraphic distributions of selected plant groups discussed in the text with stratigraphic (left) and palaeogeographic (right) settings of youngest outlier occurrences. See main text (Section 4.3) for details on individual plant groups.

Permian–Triassic and the end-Triassic extinctions; and some of the most iconic plant groups of the Mesozoic, including Bennettitales, Cheirolepidiaceae conifers, and “Mesozoic seed ferns”, are now known to have persisted well into the Cenozoic era. In many cases, these plant groups did not vanish in the course of a single catastrophic event, but rather were in gradual decline, eventually eluding documentation in the fossil record—perhaps even long before their actual extinction. Key factors for the decline of plant groups certainly involved the dramatic environmental changes associated with some of the sudden devastating events that punctuated Earth history at major system boundaries, such as asteroid strikes or flood-basalt volcanism (McElwain and Punyasena, 2007). However, instead of representing direct kill mechanisms like in faunal extinctions, these changes may more likely have had indirect effects, remodeling the framework of abiotic factors that govern biotic interaction and competitive success (see Wing and Boucher, 1998). A remarkable example of the power of biotic factors as driving forces in plant evolution is the mid-Cretaceous, a time interval without any catastrophic geological (or extraterrestrial) events but with dramatic turnover in plant communities (Fig. 24.3) caused presumably by the increasing coevolutionary success of angiosperms and insects (Friis et al., 2011). In many cases, these gradual turnovers in vegetation composition follow an intriguing latitudinal pattern in that they sweep from equatorial regions toward the poles (e.g., Crane and

Lidgard, 1989; Wing and Boucher, 1998). High-latitude regions of the Mesozoic–Paleogene greenhouse world thus acted as “evolutionary museums” (Stebbins, 1974) that provided refugia for relictual lineages that had already disappeared from lower-latitude lowlands. Most likely, such last surviving polar populations eventually disappeared as they became outcompeted by newly emerging plant groups in the face of environmental change.

A promising avenue for future investigation will be to elucidate to what degree there are recurring patterns in ecological characteristics between high-latitude relictual lineages and those that take over dominance. By analogy to the rise of angiosperms (see Wing and Boucher, 1998), we assume that warm, humid, high-latitude forests would provide equable mesic environments with low total energy input, favoring competitive (K-strategist) groups that—once established—could maintain dominance throughout periods of stable climatic conditions. In the present case at least, this hypothesis agrees well with the reconstructed habit and ecology of the Antarctic *Dicroidium* plants as typical competitors, i.e., long-lived, deciduous canopy trees with copious litter production and seasonal dispersal of large seeds (see Grime, 1977; Wing and Boucher, 1998). During contrasting icehouse intervals, high-latitude settings become inhospitable for most woody plants. At these times, mesic montane forests and humid middle latitude forests may provide equivalent favorable conditions for the persistence of relict gymnosperms.

In order to reveal such patterns and processes in plant evolution more precisely in the future, an important additional source of information to be tapped should be the palynological record. However, many of the plant groups in question produced universal pollen types whose systematic affinities are difficult to resolve even at high taxonomic ranks. The non-taeniate bisaccate *Alisporites/Falcisporites* pollen types—ubiquitous in late Palaeozoic and earlier Mesozoic deposits worldwide—may have been produced by peltasperms, corystosperms, or various groups of conifers (e.g., Balme, 1995); and the general *Cycadopites* pollen type may be affiliated with a particularly broad range of parent plants, including Bennettitales, Cycadales, Ginkgoales, Peltaspermales, Pentoxylales, and Gnetales (Balme, 1995). To this end, we argue that an important step forward will be a systematic, detailed analysis of *in situ* pollen for selected groups using combined light and scanning-electron microscopy (see e.g., Bouchal et al., 2016) and possibly chemotaxonomy (see e.g., Julier et al., 2016) in order to resolve the taxonomy of these pollen types more precisely, such that the distribution of the parent plants can be more fully documented in the absence of macrofossils.

Finally, we concur with Mittelbach et al. (2007, p. 324) that, “[...] the full potential of palaeontological data for understanding the evolutionary dynamics underlying the latitudinal diversity gradient has yet to be realized.”

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