

# Extinction and recovery patterns of the vegetation across the Cretaceous–Palaeogene boundary — a tool for unravelling the causes of the end-Permian mass-extinction

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## Abstract

High-resolution palynofloral signatures through the Cretaceous–Palaeogene boundary succession show several features in common with the Permian–Triassic transition but there are also important differences. Southern Hemisphere Cretaceous–Palaeogene successions, to date studied at high resolution only in New Zealand, reveal a diverse palynoflora abruptly replaced by fungi-dominated assemblages that are in turn succeeded by low diversity suites dominated by fern spores, then gymnosperm- and angiosperm-dominated palynofloras of equivalent diversity to those of the Late Cretaceous. This palynofloral signature is interpreted to represent instantaneous (days to months) destruction of diverse forest communities associated with the Chicxulub impact event. The pattern of palynofloral change suggests wholesale collapse of vascular plant communities and short-term proliferation of saprotrophs followed by relatively rapid successional recovery of pteridophyte and seed-plant communities. The Permian–Triassic transition records global devastation of gymnosperm-dominated forests in a short zone synchronous with one or more peaks of the fungal/algal palynomorph *Reduviasporonites*. This zone is typically succeeded by assemblages rich in lycophyte spores and/or acritarchs. Higher in the succession, these assemblages give way to diverse palynofloras dominated by new groups of gymnosperms. Although different plant families were involved in the mass-extinctions, the general pattern of extinction and recovery is consistent between both events. The major difference is the longer duration for each phase of the Triassic recovery vegetation compared to that of the Paleocene. The protracted extinction-recovery succession at the Permian–Triassic boundary is incompatible with an instantaneous causal mechanism such as an impact of a celestial body but is consistent with hypotheses invoking extended environmental perturbations through flood-basalt volcanism and release of methane from continental shelf sediments.

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## 1. Introduction

The evolution of life on Earth has been interrupted by mass-extinction events at least five times. Of the major extinction events identified in the geological record, the Cretaceous–Palaeogene (K–Pg) extinction event (65 Ma)

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has been investigated most extensively and the impact of a celestial body is widely recognized as the primary cause for this biological crisis, which extinguished about 75% of species (Alvarez et al., 1980). However, this crisis was dwarfed by the largest of all mass-extinctions, the so-called Permian–Triassic event (251 Ma), which witnessed the loss of up to 95% of species according to reverse rarefaction analysis (Raup, 1979).

Both events record massive devastation of animal and plant communities. We compare the turnover and recovery of the vegetation between the two events by analysis of the dispersed spore–pollen record. There is now general agreement on an impact-related mechanism for mass-extinction at the Cretaceous–Palaeogene boundary (Alvarez et al., 1980). Our approach is to compare the broad composition of palynomorph assemblages at successive intervals through the well-studied Cretaceous–Palaeogene transition to provide clues to decode the causes of the less-studied and more enigmatic Permian–Triassic (P–Tr) mass-extinction and the influences on subsequent phases of vegetation recovery.

## 2. Material and methods

Our study principally utilizes palynological records from high latitude Southern Hemisphere (southeast Gondwana) terrestrial sequences for both the Permian–Triassic and Cretaceous–Palaeogene events. This minimizes the palaeoenvironmental/palaeoclimatic differences between the compared successions as southeastern Gondwana was consistently located in high southern latitudes from Late Carboniferous to Palaeogene times (Veevers, 1984). Additionally, most studies of these extinction events have focused on the Northern Hemisphere and palaeotropical successions and have neglected the biota occupying southern high latitudes that might have been responding to different sets of environmental pressures. We have also endeavoured to compare assemblages from similar depositional settings to eliminate taphonomic biases between data sets.

We provide a general overview of the palynoflora of known Cretaceous–Palaeogene floral assemblages of Antarctica (Seymour Island) and Australia but we particularly utilize recent high resolution palynological records from New Zealand to interpret floristic change through the Cretaceous–Palaeogene transition in southern high latitudes. These data derive from five sections: two bore cores and two outcrop sections from Grey-mouth Coalfield (Nathan, 1978), and one outcrop section from the marine units of mid-Waipara (Vajda et al., 2003; Vajda and Raine, 2003). The Cretaceous–Palaeogene boundary palynological signal in all five

sections is characterized by massive vegetation disruption (Vajda et al., 2001, 2003; Vajda and Raine, 2003; Vajda and McLoughlin, 2004). The most complete records are from the coal-rich (braided fluvial) Paparoa Group, Greymouth Coalfield (Ward, 1997). In Moody Creek Mine, the Cretaceous–Palaeogene boundary falls within a coal seam indicating persistence of mire environments through the mass-extinction event. Data for the Permian–Triassic transition derives from a broad range of more coarsely resolved published palynostratigraphic studies from eastern Australia, Antarctica, South Africa, India and Greenland.

## 3. Patterns of extinction

### 3.1. The pre-extinction floras

#### 3.1.1. Cretaceous–Palaeogene event

Late Cretaceous global palynofloras are divided into three major floristic provinces (Herngreen et al., 1998): (1) The Northern Hemisphere Province incorporating the *Aquillapollenites*, *Normapolles* and *Schizaeoisporites* Subprovinces, (2) The Equatorial Palmae Province, and (3) The Austral *Nothofagidites/Proteacidites* Province. During the latest Cretaceous, New Zealand (together with Australia and Antarctica) was part of the Austral floristic region characterized by *Phyllocladidites mawsonii*, trisaccate gymnosperm pollen, and angiosperm pollen such as *Proteacidites* and *Nothofagidites*.

Southeast Austral palynofloras show a steady increase in absolute diversity through the Cretaceous. Angiosperms diversified significantly in the later stages of the Cretaceous, largely at the expense of free-sporing plants, whereas gymnosperms maintained consistent diversity levels (Nagalingum et al., 2002). Maastrichtian assemblages from New Zealand terrestrial sequences (PM2 Zone of Raine, 1984) incorporate around 100 species of pollen and spores. Gymnosperms and ferns show the greatest relative abundance. Gymnosperm pollen constitute an average relative abundance of 46% of the palynoflora and are represented by Podocarpaceae (40%) and Araucariaceae (6%). Ferns comprise 34% of the miospore assemblage. Based on comparisons with modern taxa and evidence from *in situ* fossil spores (Balme, 1995), the miospores can be divided into groups derived from tree ferns and ground ferns. Tree ferns are represented by Cyatheaceae (*Cyathidites*, 17% relative abundance), and Dicksoniaceae (*Cibotidiites*, 2%). Ground-fern spores are dominated by Gleicheniaceae (*Gleicheniidites*, 8%), Lygodiaceae and related families (*Ischyosporites*, 3%), and the form-genus *Laevigatosporites* (representing several ground-fern families, 4%). Angiosperms were the most

diverse group but accounted for only 10–20% of pollen relative abundance (Vajda et al., 2001; Vajda and Raine, 2003). Lycophytes and bryophytes, collectively constituted < 5% relative abundance.

The New Zealand Maastrichtian terrestrial palynoflora reflects a mixed podocarp-angiosperm forest vegetation with an understorey and ground stratum dominated by tree-ferns, ground-ferns, lycophytes and bryophytes. The presence of taxa with nearest modern relatives having humid temperate distributions, such as *Nothofagus* (*Nothofagidites*) and *Gunnera* (*Tricolpites reticulatus*), indicate cool moist climates prevailed in the Maastrichtian of New Zealand. The high proportion of ferns suggests consistently moist conditions and lack of severe winter freezing.

Cretaceous palynofloras from Seymour Island, Antarctic Peninsula (Askin, 1990; Askin and Jacobsen, 1996) reveal that during the Maastrichtian, this area was characterized by conifer-dominated temperate rainforest vegetation, a common element being *Lagarostrobos franklinii*, which is represented by pollen assigned to *Phyllocladidites mawsonii*. These gymnospermous elements co-habited with *Nothofagus*, other angiosperms and hydrophilic cryptogams (Askin, 1990).

Investigations of southern Australian late Maastrichtian miospore assemblages indicate that the vegetation consisted of cool-temperate rainforests with a canopy dominated by conifers (mainly podocarps). *Proteaceae*, *Nothofagus* and other angiosperms made up the sub-canopy whereas the ground stratum was dominated mainly by ferns and other cryptogams (Table 1; Dettmann, 1994).

### 3.1.2. Permian–Triassic event

Late Permian floras show pronounced provincialism (Meyen, 1987; Utting and Piasecki, 1995). The southern high latitude Gondwanan flora was matched by the northern high latitude (moist, cool temperate) Angaran flora, which was dominated by cordaitaleans and peltasperms. Palaeoequatorial floras were generally represented by conifer- and peltasperm-dominated assemblages typical of warm, dry climates (Euramerican

Province), or gigantopterid- and lycophyte-dominated assemblages characteristic of warm humid settings (south Cathaysian Province).

Latest Permian floras of Gondwana were overwhelmingly dominated by glossopterid gymnosperms — an enigmatic group with no close modern relatives. Glossopterid pollen, represented particularly by taeniate bisaccate taxa such as *Protohaploxyipinus* and *Striatopodocarpidites*, commonly constitute > 40% relative abundance of latest Permian palynomorph assemblages across Gondwana (Foster, 1979; Retallack, 1995). Non-glossopterid gymnosperm pollen is less abundant (typically < 20%) but represents a moderately diverse array of conifers, cordaitaleans, ginkgoaleans, gnetaleans, cycadaleans, and possibly peltasperms. Ferns and sphenophytes are moderately diverse and represent a significant component of the palynofloras (commonly 30% relative abundance). Lycophyte spores represent a minor but consistent component of Gondwanan Late Permian assemblages (Foster, 1979). Western Gondwanan and Tethyan-margin assemblages of this age have a higher diversity compared to Australian (southeastern Gondwanan) assemblages, which are characterized by abundant large fern spores (e.g., *Dulhuntyispora* and *Didecitriletes*; Kemp et al., 1977).

Gondwanan Late Permian macrofloras are generally consistent with the palynofloral record in terms of glossopterid dominance, but they are notably deficient in fern taxa. Glossopterids have been interpreted to represent tree-sized plants predominantly occupying mire and moist floodplain settings as their roots (*Vertebraria*) contain schizogenous cavities that were adaptations for aeration of tissues in dysaerobic waterlogged settings analogous to the roots of extant *Taxodium distichum*. Late Permian climates of southeast Gondwana have generally been interpreted as cool and moist (Table 1; Ziegler, 1990; Rees et al., 2002). This is supported by the dominance of glossopterids with broad, amphistomatic leaves, thin cuticle and relatively unsophisticated stomatal protection (Fig. 1). However, at least some parts of Gondwana show reduced leaf size among glossopterids near the end of the

Table 1  
Summary of vegetation characteristics preceding the end-Permian and end-Cretaceous mass-extinctions at southern high latitudes

Southeast Gondwanan floristic signatures	Dominant plant groups	Floristic diversity	Climate	Successional state of vegetation
Latest Cretaceous: Maastrichtian (pre-extinction)	High abundance of podocarp conifers and ferns; moderate diversity of angiosperms.	High.	Cool temperate, moist.	Complex, stratified, temperate, closed forests.
Latest Permian: Changxingian (pre-extinction)	Overwhelming dominance of glossopterids; moderate range of pteridophytes.	Moderate.	Cool temperate, moist.	Open, stratified, temperate, deciduous forests.

Permian and this may have been a response to warming and drying of the climate (Anderson and Anderson, 1985; McLoughlin et al., 1997).

### 3.2. The disaster zone

#### 3.2.1. Cretaceous–Palaeogene event

Biostratigraphy is the most reliable tool for identifying the New Zealand K–Pg boundary as the sequences do not show a macroscopic lithological change at this level. New Zealand latest Cretaceous–Palaeogene palynostratigraphic zones are based primarily on first and last appearances of taxa (Raine, 1984; Fig. 2). Maastrichtian palynofloras belong to zone PM2 defined by the first appearance of *Tricolpites lilliei*. Earliest Paleocene assemblages are assigned to the PM3 Zone, the base of which correlates to the Cretaceous–Palaeogene boundary marked by the extinction of taxa such as *Tricolpites lilliei*, *Nothofagidites kaitangata*, *Proteacidites palisadus*, *Quadruplanus brossus*, and *Granelispora evansii*, and higher up in the sequences, first occurrences of other “Cenozoic” taxa including *Tricolpites phillipsii*, *Myrtacoidites* spp., *Myricipites harrisii* (Couper), and *Nothofagidites waipawaensis* (Fig. 2).

The Cretaceous–Palaeogene boundary in New Zealand (base of Zone PM3) is coincident with a pronounced geochemical anomaly in both marine and continental sections (Brooks et al., 1986; Vajda and McLoughlin, 2004). In Moody Creek Mine, Greymouth Coalfield, the

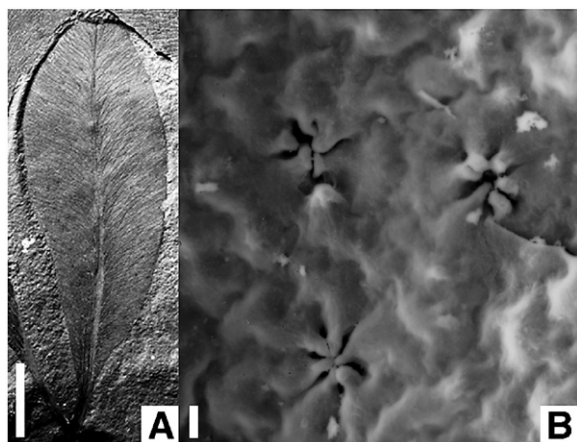


Fig. 1. *Glossopteris* from the Upper Permian of southeast Gondwana. A: *Glossopteris duocordata* Holmes (Illawarra Coal Measures equivalents, western Sydney Basin); broad, relatively unspecialized leaf with broadly spaced venation; scale bar = 10 mm. B: Charcoalified Late Permian *Glossopteris* leaf from (Bainmedart Coal Measures, Amery Group, Prince Charles Mountains, Antarctica) showing details of unspecialized or weakly raised epidermal cells and a simple ring of narrow papillae surrounding each stomata; scale bar = 10  $\mu$ m.

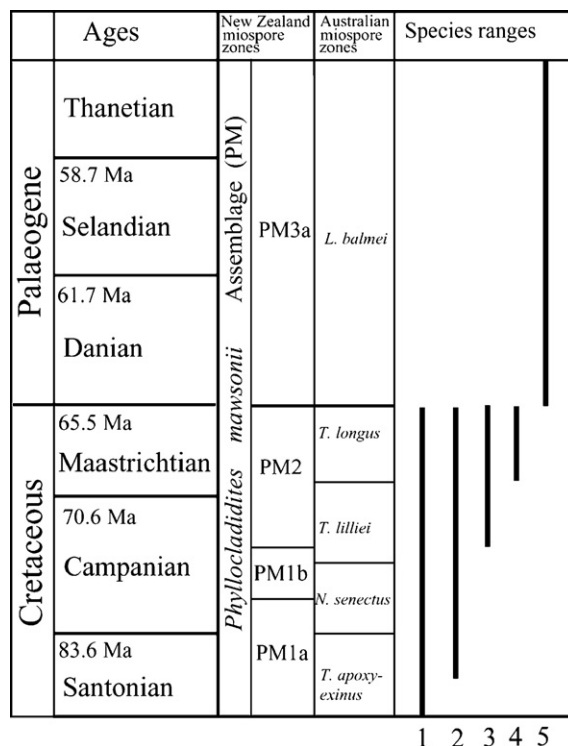


Fig. 2. Generalized range chart for key taxa through the Cretaceous–Palaeogene transition in New Zealand, Australia and Antarctica based on ranges indicated by Raine (1984, 1990), Vajda and Raine (2003), Helby et al. (1987), Askin (1990), and Askin and Jacobsen (1996). Precise ranges of individual taxa vary slightly across this region (see specific references). 1. *Ornamentifera sentosa*; 2. *Tricolpites confessus*; 3. *Proteacidites retiformis*, *Nothofagidites kaitangata*, *Tricolpites lilliei*; 4. *Granelispora evansii*, *Quadruplanus brossus*, *Tricolpites longus*; 5. *Tricolpites phillipsii*, *Nothofagidites waipawaensis*.

diverse latest Maastrichtian palynoflora is suddenly replaced, following the geochemical anomaly (iridium levels of 4.1 ppb), by a thin (4 mm) lamina yielding fungal spores and hyphae, woody debris and sparse cuticle fragments (Vajda and McLoughlin, 2004; Table 2). Although petrological studies have not yet been undertaken, the “barren” interval shows no significant macroscopic differences to the coal below or above suggesting continuous organic accumulation across the K–Pg boundary.

High resolution palynological studies of non-marine mid-continental North American sections have consistently shown that plant communities on that continent experienced severe simultaneous disruption at the Cretaceous–Palaeogene boundary (see Sweet and Brannan, 2001; Nichols and Johnson, 2003 and references therein). The extinction rate of plants based on the palynoflora ranges from 15% in the Raton Basin (Fleming, 1985) to 34% in the western Powder River

Table 2  
Summary of vegetation characteristics during the end-Permian and end-Cretaceous mass-extinction crises at southern high latitudes

Southeast Gondwanan floristic signatures	Dominant plant groups	Floristic diversity	Climate	Successional state of vegetation
Cretaceous–Palaeogene transition	Fungi	Very low.	Cool temperate, moist, low insolation.	Post-impact disaster community dominated by saprotrophs.
Permian–Triassic transition	Locally high abundance of <i>Reduviasporonites</i> ; inconsistent signatures of other plant groups. Demise of glossopterids.	High due to short overlap in the ranges of typical Permian and Triassic taxa.	Temperate; transitional from moist to dry.	Oscillating conditions between complex and depauperate vegetation.

Basin, eastern Wyoming (Nichols et al., 1992). However, the high extinction rate is not consistent throughout North America as a detailed study of a Cretaceous–Palaeogene boundary section in Saskatchewan, Canada, demonstrated a mass-kill of standing vegetation but lacked evidence of mass-extinction (McIver, 1999). Regan et al. (2001) extensively discussed the problems associated with calculation of background extinction rates in relation to various groups of animals and plants. Background extinction rates are generally quoted to vary from <1% to 25% per million years. For the short intervals targeted in this study (<1 Ma), we consider any turnover values higher than 25% as indicative of a mass-extinction.

No fungal anomaly has yet been reported from Cretaceous–Palaeogene boundary sections outside New Zealand. However, considering the very thin lamina in which fungal dominance was recorded it is possible that fungal spikes have either been missed in other sections by less close sampling or diluted by selection of coarse samples. Alternatively, the extensive ejecta blanket in North and Central America may have rapidly buried plant detritus and inhibited fungal proliferation.

According to Askin (1990), several of the angiosperm key taxa that disappear at the K–Pg boundary in southeastern Australia (Helby et al., 1987) and in New Zealand (Raine, 1984; Vajda and Raine, 2003) also disappear in the miospore assemblages at Seymour Island (Fig. 2). Those extinctions are suggested to be related to a “global environmental upheaval at the end of the Cretaceous” (Askin, 1990).

Broad-scale palynostratigraphic investigations across the Cretaceous–Palaeogene transition in Australia indicate that the boundary lies between the pollen zones *Tricolpites longus* and *Lygistepollenites balmei* (Partridge, 1976; Helby et al., 1987; Fig. 2). Macphail (1994) and Macphail et al. (1994) recorded an extinction of 16% of the miospore taxa, based on published and unpublished data. These numbers agree well with the extinction rates

calculated for miospore assemblages in the marine sediments of mid-Waipara, New Zealand (Vajda and Raine, 2003) and, as in the New Zealand and Antarctic assemblages, extinction was most severe among angiosperm taxa. Macphail (1994) interpreted these extinctions as evidence for a catastrophic event but the low sample resolution (typically over 10 m) does not reveal the detailed signal of vegetation disruption and recovery.

### 3.2.2. Permian–Triassic event

The position of the Permian–Triassic boundary in southeastern Gondwana based on palynological data has been long debated (Balme and Helby, 1973; Foster et al., 1998). Problems pinpointing the boundary relate especially to strong provincialism of the latest Palaeozoic floras and difficulties correlating continental and marine sequences. Despite these problems, the Permian–Triassic boundary in Australia is commonly placed at the base of the *Lunatisporites pellucidus* Zone, marked by the first abundant occurrence of *L. pellucidus* and a dramatic decrease in glossopterid *Protohaploxipinus* and *Striatopodocarpidites* pollen (Helby et al., 1987; Fig. 3). Coeval Angaran and Cathaysian floras saw the collapse of cordaitalean pollen and gigantopterids respectively. Where palynozone boundaries are uncertain, and marine index fossils absent, a globally reported, marked negative excursion in  $\delta^{13}\text{C}$  is commonly used as a proxy for the Permian–Triassic boundary.

Disparate studies have reported abundant fungal remains at the Permian–Triassic boundary in both marine and terrestrial successions (Eshet et al., 1995; Retallack, 1995; Utting and Piasecki, 1995; Visscher et al., 1996; Looy et al., 2001; Steiner et al., 2003; Table 2). However, some workers regard these fossils (*Reduviasporonites* and its synonyms) as algal affiliates based on morphological and biochemical characteristics (Afonin et al., 2001; Foster et al., 2002). In several places, including Israel and the Karoo Basin, South Africa, the floristic extinction and *Reduviasporonites* spike are coincident with the top of the

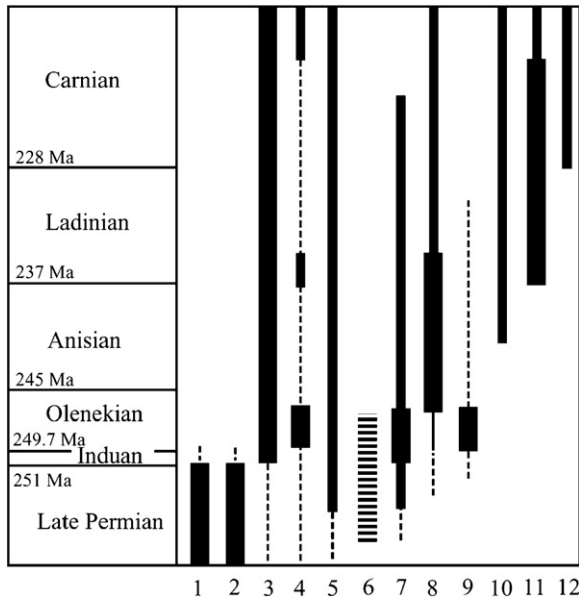


Fig. 3. Generalized range chart for key taxa through the Permian–Triassic transition in southeast Gondwana based on ranges indicated by Balme (1963, 1970), Balme and Helby (1973), Helby (1973), Foster (1979), Helby et al. (1987), and McLoughlin et al. (1997). Precise ranges of individual taxa vary slightly across this region (see specific references). Taxa grouped according to the following scheme: 1. Glossopterid pollen (mostly *Protohaploxypinus* and *Striatopodocarpidites* spp.); 2. *Dulhuntyispora*–*Acanthotriletes trisinus*–*Didecitriletes* complex; 3. *Falcisporites* spp.; 4. Acritarchs; 5. *Triploxisporites playfordii*, *Playfordiaspora velata*, *Dictyophyllidites mortoni*; 6. *Reduviasporonites* spp.; 7. *Lunatisporites* spp.; 8. *Ara-trisporites* spp. 9. *Krauselisporites* spp.; 10. *Apiculatisporis carnavonensis*, *Duplexisporites problematicus*, *Cardagasporites senectus*; 11. *Staurosaccites quadrifidus*, *Aulisporites astigosus*, *Infernopol-lenites claustratus*, *Samaropollenites speciosus*, *Enzonalsporites vigens*; 12. *Ephedripites macistriatus*, *Craterisporites rotundus*, *Ca-dargasporites reticulatus*, *Nevesisporites vallatus*, *Minutosaccus crenulatus*, *Ashmoripollis reducta*, *Cycadopites stonei*. Thick line: very abundant and consistent. Intermediate line: moderately abundant and generally consistent. Thick dashed line: abundant but inconsistent. Thin dashed line: rare and inconsistent.

*Dicynodon* Zone, which is marked by the last occurrence of a range of therapsid reptiles (Eshet et al., 1995; Kitching, 1995; Steiner et al., 2003).

### 3.3. Stage 1 recovery flora (herbaceous pioneer communities)

#### 3.3.1. Cretaceous–Palaeogene event

Apart from the sudden disappearance of diverse Maastrichtian pollen assemblages, the most striking palynological feature of the Cretaceous–Palaeogene transition globally is the low-diversity fern-dominated assemblages that characterize the earliest Palaeogene. This so-called fern-spike, succeeding sediments enriched

in iridium, is well-documented in North American Cretaceous–Palaeogene boundary sequences (Tschudy et al., 1984; Nichols et al., 1992; Nichols and Johnson, 2003). A fern spike has also been reported from marine Cretaceous–Palaeogene boundary sediments in Japan (Saito et al., 1986). Europe lacks terrestrial, Cretaceous–Palaeogene sections but a bryophyte (moss spore) spike has been reported from marine boundary sections at Curf Quarry (Hengreen et al., 1998) and the Geulhemmerberg caves (Brinkhuis and Schiöler, 1996) in The Netherlands. Proliferation of bryophytes immediately after the Cretaceous–Palaeogene boundary is consistent with the North American signal of a major change in post-Cretaceous terrestrial ecosystems in which woody plants were apparently replaced by herbaceous cryptogams.

In New Zealand, the pioneer recovery flora consists predominantly of ground ferns (represented by *Laevigatosporites ovatus*, *Baculatisporites comaumensis* and *Gleicheniidites* spp.). Significantly, iridium values are still at their peak 5 mm above the boundary when ground-ferns recover, suggesting rapid re-establishment of ferns in the aftermath of the Chicxulub impact event (Table 3). Ground-fern spores dominate until about 80 mm above the boundary in the continental succession at Moody Creek Mine, but they are also locally abundant higher in the succession (Vajda et al., 2001).

The fern spike identified from lowermost Paleocene terrestrial sediments world wide has not been identified in the Australian and Antarctic assemblages, possibly due to extensive reworking of the near-shore marine host sediments (Askin, 1990) in combination with a relatively low sampling resolution (Macphail, 1994; Macphail et al., 1994). High-resolution palynological studies are lacking for the Cretaceous–Palaeogene transition in other regions of Gondwana, in some cases due to a desional hiatus.

#### 3.3.2. Permian–Triassic event

In some Gondwanan, Lower Triassic successions (Balme, 1963, 1970; Retallack, 1995) the *Reduviasporonites* spike is followed by an interval rich in spinose acritarchs and/or abundant lycophyte ( $\pm$ fern) spores. The acme of acritarchs characterizes an Early Triassic marine transgression in several marginal basins in which there was an apparent dearth of heterotrophs. Trilete, cavate lycophyte spores (e.g., *Lundbladispora*, *Krauselisporites*, *Rewanispora*, *Uvaesporites*, *Limitisporites*, and *Densoisporites*) are abundant in both Gondwanan marine and non-marine strata of this age (Fig. 3, Table 3). They have affinities to herbaceous isoetean and possibly selaginellalean lycophytes (Balme, 1995) and are locally associated with diverse megaspore assemblages (Maheshwari and

Table 3

Summary of vegetation characteristics in the immediate aftermath of the end-Permian and end-Cretaceous mass-extinction events at southern high latitudes (stage 1 recovery phase)

Southeast Gondwanan floristic signatures	Dominant plant groups	Floristic diversity	Climate	Successional state of vegetation
Very early Paleocene	Ferns, especially Blechnaceae and Gleicheniaceae.	Very low	Cool temperate, moist.	Herbaceous pioneer communities dominated by ground-ferns.
Very early Triassic (early Induan)	Isoetalean and selaginellalean lycophytes; local abundance of ferns and spinose acritarchs.	Low	Temperate; relatively dry but many basins influenced by marine transgressions.	Herbaceous pioneer communities dominated by lycophytes.

Tewari, 1987; McLoughlin et al., 1997) and macrofossils (Helby and Martin, 1965; Retallack, 1997; Cantrill and Webb, 1998). Some assemblages from this interval are also rich in fern spores, most notably *Tripлексisporites*, *Nevesisporites*, *Retusotriletes*, *Apiculatisporis*, and *Dicthyophyllidites* species (Helby, 1973; Helby et al., 1987).

### 3.4. Stage 2 recovery flora (Lazarus taxa and re-establishment of stratified vegetation)

#### 3.4.1. Cretaceous–Palaeogene event

Above the initial ground-fern spike in the New Zealand Cretaceous–Palaeogene sections, a gradual transition to tree-fern dominance is witnessed in the form of assemblages rich in *Cyathidites* and *Cibotidites*. This interval extends from about 8 to 40 cm above the Cretaceous–Palaeogene boundary in the continental section sampled at Moody Creek Mine. The distinction between ground-fern dominance and tree-fern dominance is less clear in the mid-Waipara marine section and the collective fern-rich assemblages dominate the 20–25 cm interval above the boundary. Small quantities of podocarp and araucarian conifer pollen also occur within these fern-rich assemblages. Most of these pollen represent ‘Cretaceous’ taxa that return following an absence from several consecutive samples of the lowermost Paleocene beds. In this sense they represent Lazarus taxa (Jablonski, 1986). This group is especially represented by *Phyllocladites mawsonii* and *Podocarpidites ellipticus*, which appear 25–40 cm above the boundary (Vajda et al., 2001; Vajda and Raine, 2003). Angiosperm pollen remain consistently sparse through this interval. Following the initial flourish of opportunistic herbaceous species, this interval is interpreted to represent the recovery phase of shrub- to tree-sized plants over a period of a few thousand years (Vajda and Raine, 2003; Table 4).

#### 3.4.2. Permian–Triassic event

A similar, though more complex and protracted recovery succession is evident following the initial pulse

of acritarchs and herbaceous lycophytes in the lowermost Triassic. There is a notable diversification and increased abundance of shrub-sized pleuromeian lycophytes in southeastern Gondwana from the late Induan to Anisian (Retallack, 1980; Helby et al., 1987; Cantrill and Webb, 1998; Table 4). This group is represented mainly by *Ara-trisporites* microspores, and is associated with a broad array of mostly undescribed megaspores (McLoughlin et al., 1997). Peltasperm (*Lepidopteris*) and voltzialean conifer (*Voltziopsis*) palynomorphs and macrofossils are also locally abundant in this interval (Retallack, 1980; McLoughlin et al., 1997; Retallack, 2002). Foliage of these groups show striking xeromorphic adaptations: very small laminae, thick cuticle, abundant papillae, and sunken stomates that are heavily protected by over-arching subsidiary cell papillae (Fig. 4). This contrasts with the less-protected stomates and thin cuticle of the Permian broad-leaved glossopterids (Fig. 1). The presence of gnetalean pollen during this interval (Helby, 1973) may

Table 4

Summary of vegetation characteristics during the stage 2 recovery phase following end-Permian and end-Cretaceous mass-extinction events at southern high latitudes

Southeast Gondwanan floristic signatures	Dominant plant groups	Floristic diversity	Climate	Successional state of vegetation
Very early Paleocene	Cyatheaceae and Dicksoniaceae tree-ferns; re-establishment of some conifers.	Low–moderate.	Cool temperate; moist.	Shrub to open forest communities dominated by tree-ferns.
Early Triassic (Induan–Olenekian)	Pleuromeian lycophytes; local abundance of peltasperms and voltzialean conifers.	Low–moderate.	Temperate; seasonally dry; warming phase	Shrub- to tree-sized communities dominated by xerophytic plants.

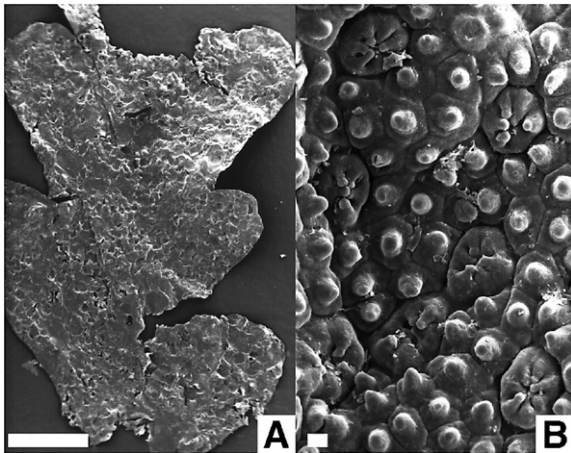


Fig. 4. *Lepidopteris* sp. (Peltaspermales) from the lowermost Triassic of Antarctica (basal Flagstone Bench Formation, Amery Group, Prince Charles Mountains). A: Macerated pinna fragment showing diminutive pinnules with thick cuticle; scale bar=1 mm. B: Details of cuticle surface showing pronounced lappets (solid papillae) and sunken stomates covered by a prominent ring of papillae on up to seven raised subsidiary cells; scale bar=10  $\mu$ m.

also reflect climatic drying and/or warming. Looy et al. (2001) also noted incursions of palaeotropical taxa, including gnetaleans, into the northern high latitudes in the Early Triassic recovery succession in Greenland implying global warming.

### 3.5. Rediversified and stratified “equilibrium” vegetation

#### 3.5.1. Cretaceous–Palaeogene event

New Zealand palynoassemblages suggest that the evolution of new plant species following the Cretaceous–Palaeogene extinction event was rather slow as few new pollen taxa appear within the first few metres of Paleocene sediment (eg. *Tricolpites philipsii* and *Nothofagidites waipawensis*: both angiosperms). Angiosperms appear to have been most severely affected by the Cretaceous–Palaeogene event in New Zealand. In the continental successions at Moody Creek Mine and Compressor Creek, angiosperms recover significant diversity and relative abundance only around 1.4–2.0 m above the boundary (Vajda et al., 2001, 2003). Angiosperm recovery occurs slightly lower in the marine mid-Waipara sequence (Vajda and Raine, 2003), which reflects a lower sedimentation rate (condensed section). Succeeding early Paleocene assemblages (PM3 palynozone of Raine, 1984) are co-dominated by podocarp conifers and proteaceous and nothofagaceous angiosperms with absolute diversities equivalent to, or slightly higher than, those of the latest Cretaceous

(Ward, 1997; Vajda and Raine, 2003). Equivalent southeast Australian palynofloras of the *Lygistepollenites balmei* Zone are dominated by araucariacean and podocarp conifer pollen and pteridophyte spores (Macphail et al., 1994). Angiosperm representation is variable in these assemblages but Proteaceae, Casuarinaceae and Callitrichaceae pollen are locally abundant. Equivalent Antarctic assemblages are characterized by the FAD of a few angiosperm species and a high relative abundance of the gymnosperm pollen *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*: Askin, 1990; Askin and Jacobsen, 1996). These assemblages are interpreted to reflect vegetation of cool temperate, relatively humid climates akin to those of the latest Cretaceous (Table 5). Theoretical modeling of biomass changes following the Chicxulub impact has suggested recovery of woody plants to pre-extinction levels occurred some 40–50 years after the end of the Cretaceous (Lomax et al., 2001). This model further suggests attainment of a steady state of biomass at levels higher than those of the Maastrichtian some 100 years or more after the extinction event.

#### 3.5.2. Permian–Triassic event

Re-establishment of diverse seed–plant floras in the Triassic was apparently a more protracted affair than the corresponding Paleocene recovery. The “coal gap”, an interval lacking coal accumulation spanning the entire Early Triassic, represented a phase in which physical conditions were unfavourable for mire development globally, and/or where plant communities adapted to mire-forming conditions had not re-developed (Retallack, 1995). Complex gymnosperm-dominated mire communities began to re-develop in southeast Gondwana by the Middle Triassic (Holmes, 1982), several

Table 5

Summary of the recovered (equilibrium) vegetation characteristics after the end-Permian and end-Cretaceous mass-extinction events at southern high latitudes

Southeast Gondwanan floristic signatures	Dominant plant groups	Floristic diversity	Climate	Successional state of vegetation
Paleocene	Podocarp conifers and diverse angiosperms.	High	Cool temperate, moist.	Complex, stratified, closed-forest communities.
Middle to Late Triassic	Corytosperms, conifers and a diverse array of subsidiary gymnosperms.	High	Temperate; dry to moist.	Complex, open, stratified, deciduous forest communities.

million years after the mass-extinction event. The acme of Triassic plant diversity in Gondwana was probably not reached until Carnian–Norian times when a broad range of new pteridosperm, ginkgoalean, conifer and cycadalean families appear in the fossil record (Anderson et al., 1999; Anderson and Anderson, 2003; Table 5). This climax phase of Triassic plant diversity is characterized in southeast Gondwana by consistently high relative abundances of *Falcisporites* (Corystospermales) and by the presence of a suite of pollen species that apparently expanded their ranges southward from the Tethyan margin (notably species of *Enzonalaspores*, *Ashmoriipollis*, and *Ovalipollis*).

#### 4. Summary of floristic trends across the mass-extinction events

Vegetation was disrupted globally at the Cretaceous–Palaeogene boundary but there were significant regional differences in floristic turnover. Whereas southern high latitude floras reveal a mass-kill of vegetation evidenced by dramatic but short-term changes in the relative abundance of plant groups (Vajda et al., 2001; Vajda and Raine, 2003; Vajda and McLoughlin, 2004) most North American sections indicate both massive devastation and mass-extinction of plants at the Cretaceous–Palaeogene boundary (McIver, 1999; Hotton, 2002; Nichols and Johnson, 2003). These observations are consistent with simulations of plant productivity related to changes in greenhouse gases and solar irradiance following the Chicxulub impact that suggest the greatest effect on photosynthesis and biomass was experienced in warm, low palaeolatitudes (Lomax et al., 2001).

Despite differences in the scale of species turnover, the general pattern of floristic recovery after the Cretaceous–Palaeogene extinction is similar between New Zealand and North America. Diverse latest Maastrichtian palynofloras are abruptly replaced by very low-diversity assemblages at a level corresponding to a geochemical anomaly.

A fungal spike is locally represented at the level of the peak of the geochemical anomaly succeeded by fern-rich assemblages, which are in turn replaced after a short interval (perhaps corresponding to a few decades to a few centuries) by gymnosperms and angiosperms represented by Lazarus taxa and a few newly evolved species.

The geochemical anomaly, which can be traced globally at the Cretaceous–Palaeogene transition, strengthens the hypothesis that the turnover seen in the palynological record is indeed instantaneous and not an artefact of an unrecognized hiatus in the sedimentolog-

ical record as outlined by MacLeod et al. (1997). However, plants have the advantage compared to animals that many have a dormant phase in their life cycle (spores and seeds), which potentially allowed them to survive long-term environmental upheaval and make a “come back”, evident in the geological record. This probably explains their lower extinction rates compared to some animal groups.

The Permian–Triassic transition is also marked by radically altered terrestrial plant communities (Retallack, 1995; Jin et al., 2000). Although, the Permian–Triassic boundary transition has not been examined at the same level of resolution as the Cretaceous–Palaeogene succession, some broadly consistent global trends are evident and some of these are comparable to the Cretaceous–Palaeogene patterns (Tables 1–5). All floristic provinces show dramatic demise of the dominant gymnosperm groups but in contrast to the Cretaceous–Palaeogene, the effects seem to have been most dramatic in cool higher latitudes [extinction of glossopterids in Gondwana (Fig. 5) and of cordaitaleans in Angara], and in the wet tropics (extinction of gigantopterids in Cathaysia). Dry-climate, low-latitude floras (Euramerican Province) appear to have been less affected — the major floristic turnover in that region having occurred earlier in the Permian (Knoll, 1984; DiMichele et al., 2004).

Although there is a clear signal of major disruption to the flora at the Permian–Triassic transition in Gondwana, small numbers of typically Late Permian palynomorph and macroplant taxa persist in lowermost Triassic beds of several regions (Pant and Pant, 1987; Looy et al., 2001; McManus et al., 2002). Diversity signatures across the boundary are variable, some indicating reduced plant diversity (Helby et al., 1987), others indicating initially increased diversity (McLoughlin et al., 1997). The latter is attributable to time-delayed extinction of Permian taxa during the transition zone when environmental conditions strongly fluctuated and competing plant communities coexisted before the vegetation fully adjusted to new environmental equilibria in the Triassic (Looy et al., 2001).

The Permian–Triassic mass-extinction is coincident with one or more peaks in *Reduviasporonites* (either fungal or algal) abundance, then an increase in opportunistic herbaceous lycophytes, ferns and acritarchs (Fig. 5). Succeeding floras show a transition to abundant pleuromeiid lycophytes, peltasperms and voltzialean conifers, then a gradual return to diverse gymnosperm-rich floras (dominated by Corystospermales in Gondwana).

The principal palynological contrast following the mass-extinctions is the more protracted recovery following the Permian–Triassic event (Fig. 5). Whereas the

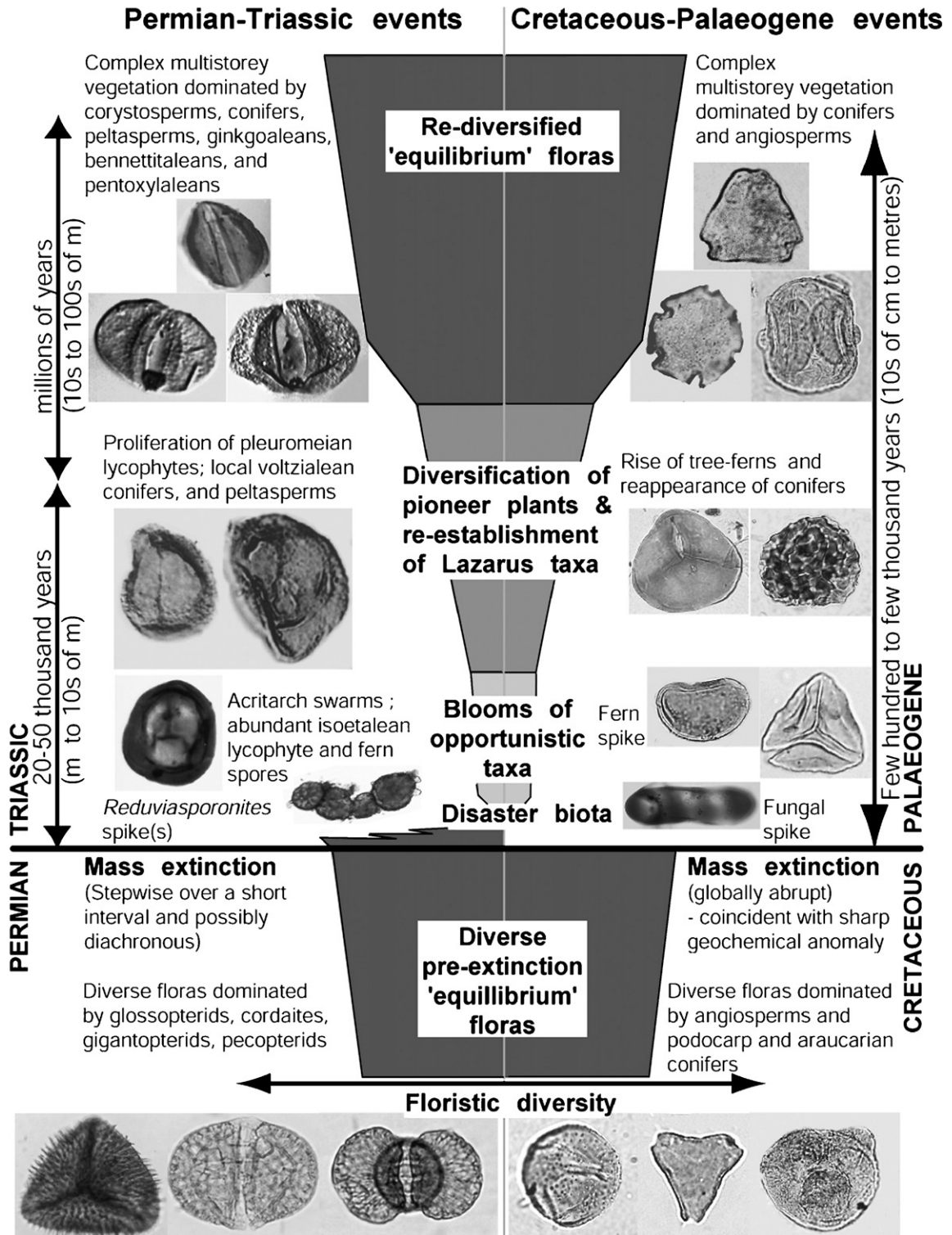


Fig. 5. Diagram summarizing the major changes in floristic diversity across the Permian–Triassic and Cretaceous–Palaeogene boundaries in southeast Gondwana with illustrations of representative palynomorphs found in successive pre-extinction and post-extinction recovery stages. Major palynomorph groups are mentioned in the text.

Cretaceous–Palaeogene fungal spike is expressed in only ~ 5 mm of sediment, the equivalent *Reduviasporonites* peak typically spans 1–3 m at the P–Tr boundary (Looy et al., 2001; Steiner et al., 2003). The geochemical signal also indicates rapid vegetation recovery in the earliest Palaeogene as *Laevigatosporites* spores (Blechnaceae) reappear only 5–10 mm above the boundary at which point iridium values had not yet returned to background levels via settling of atmospheric dust. Herbaceous vegetation probably recovered within a few months to years of the Chicxulub impact. In contrast, the Permian–Triassic fungal spike may have spanned 25–54 ka (Eshet et al., 1995). Similar durations (10–30 ka) have been calculated for intervals representing marine ecosystem collapse at the Permian–Triassic boundary (Twitchett et al., 2001). Whether *Reduviasporonites* represents a fungus or alga, its great abundance coincident with global decline of dominant woody plants, suggests that it favoured aberrant environmental conditions (reduced herbivory/competition or conditions favourable to saprotrophism). If *Reduviasporonites* is a fungus (saprotroph), then its global success and the decline of woody plants may have been favoured by a dramatic spike in atmospheric CO<sub>2</sub>, acidification, reduced insolation, or ozone depletion (Visscher et al., 1996). None of these environmental scenarios is yet strongly supported by independent evidence although high CO<sub>2</sub> emissions might be expected from the eruption of the Siberian flood basalts and from the oxidation of methane hydrates released from continental shelf areas (Benton and Twitchett, 2003).

Whereas fern-dominance persists for <2 m above the base of the Paleocene, lycophyte/fern-rich palynofloras persist for tens of metres above the base of the Triassic (Helby, 1973; Looy et al., 2001). Re-establishment of diverse, gymnosperm/angiosperm forest vegetation may have taken as little as a few hundreds to thousands of years in the Paleocene when extinction rates were relatively low (Fig. 5). Corresponding recovery of complex gymnosperm-dominated communities in the Triassic appears to have taken millions to tens of millions of years.

## 5. Discussion and conclusions

The similar signals in the palynological record point to a congruous pattern of vegetation turnover and recovery for the Cretaceous–Palaeogene and Permian–Triassic extinctions. Although this might be used to argue that both turnovers represent impact-related events, the palynofloras appear to reflect a general pattern of successional vegetation recovery manifest after any major environmental disruption as described by Mueller-

Dombois (2000) from recovery successions on Hawaii. Causal models for mass extinctions must take into account important differences in other geological signatures of these events. Evidence for a consistent global anomaly of iridium or other rare elements has not been forthcoming for the Permian–Triassic boundary. Nor have abundant and widespread examples of shocked quartz or spherules been found comparable to those at the Cretaceous–Palaeogene boundary, although strong excursions in carbon, oxygen, strontium and sulphur stable isotopes indicating dramatic environmental perturbation have been recorded (Odin et al., 1982; Oberhänsli et al., 1989; Magaritz et al., 1992; Korte et al., 2003; Krull et al., 2004). Despite the scarcity of shocked quartz or platinoid element anomalies, local abundances of meteoritic fragments (Basu et al., 2003) and even a possible impact site, the so called Bedout structure on the Australian northwest continental shelf (Becker et al., 2004), have been used to argue for impact-related extinction at the Permian–Triassic boundary.

For both extinctions the scenario suggested is that of a devastated landscape depleted in robust seed–plant communities. The acme of fungal spores immediately following the Cretaceous–Palaeogene boundary is envisaged to reflect short-term proliferation of saprotrophs on abundant organic substrates in the wake of forest destruction in the immediate aftermath of the impact event. Impact of a large asteroid in sulphate- and carbonate-rich strata in Yucatan is suggested to have dramatically reduced insolation via injection of sulphur aerosols and dust into the atmosphere, causing extensive precipitation of acid rain in the following months to few years (Pope, 2002). Light levels at the Earth's surface are interpreted to have been sufficiently reduced to kill most photosynthetic plants over a few months but clearing of the atmosphere permitted recovery of many plants from rhizomes, lignotubers, spores and seed banks over a few years.

A fungal spike at the Permian–Triassic boundary might reflect an analogous extinction mechanism. However, the greater time span represented by the *Reduviasporonites* acme (25–54 ka) suggests that fungal proliferation was not reliant on a single, brief episode of vegetation collapse. Indeed, Looy et al. (2001) recorded several intervals containing *Reduviasporonites* in both the latest Permian and earliest Triassic in Greenland. The stepwise extinctions and extended fungal spike and recovery succession at the P–Tr boundary appear to be incompatible with an instantaneous destructive event such as an impact. The more prolonged alteration of environmental conditions at the Permian–Triassic boundary inhibiting re-establishment of complex gymnosperm-dominated communities may be the cause for the much higher extinction rates than those evident at the later (K–Pg) boundary.

Sharp eustatic and climatic changes may account for some features unique to the P–Tr palynofloristic transition. Increasingly continental climate regimes towards the close of the Permian (Parrish, 1995) may have exacerbated the decline of cool-temperate, lowland mire-adapted gymnosperms in southern high latitudes. Pronounced Early Triassic marine transgression (Krystyn et al., 2003) may, furthermore, account for the widespread occurrence of assemblages dominated by marine/brackish-water acritarchs and coastal pleuromeian lycophyte spores following the P–Tr boundary versus fully terrestrial fern-rich assemblages following the K–Pg boundary.

The intensive volcanic activity resulting in the emplacement of the Siberian traps may have produced environmental conditions (lower light levels, altered temperature regimes, shifts in atmospheric chemistry) comparable to, but on a longer temporal scale, than those produced by impact of a celestial body at the K–Pg boundary. Some hypotheses suggest that mild greenhouse conditions generated by volcanism contributed to thermal release of methane from gas hydrates on continental shelves (Benton and Twitchett, 2003), which in turn led to enhanced greenhouse warming. This scenario is supported by multiple negative  $\delta^{13}\text{C}$  excursions reported from many global marine and terrestrial Permian–Triassic boundary successions (de Wit et al., 2002), and appears to be consistent with the transitional or stepwise floristic extinctions and recovery described above.

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