Fungal abundance spike and the Permian–Triassic boundary in the Karoo Supergroup (South Africa)

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Abstract

The most severe mass extinction of marine species and terrestrial vertebrates and plants is associated with the Permian–Triassic boundary ($\sim$251 Ma). The extinction interval is also marked by the disappearance of most Late Permian gymnosperm palynomorphs at a layer containing solely the abundant remains of fungi. This 'fungal spike' apparently represents widespread devastation of arboreous vegetation. Stratigraphic and palynological study of the Carlton Heights section in the southern Karoo Basin of South Africa revealed a 1-m-thick fungal spike zone that occurs simultaneously with the last appearance of typically Late Permian gymnosperm pollen. The plant extinction and fungal spike zone are found above the last occurrence of Late Permian mammal-like reptiles of the *Dicynodont* Zone at other Karoo sections. Using the fungal event as a time line in marine and non-marine sections allows placement of the marine extinctions and the extinction of terrestrial plants and reptiles within a brief crisis interval of less than about 40 000 years at the end of the Permian.
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1. Introduction

The end-Permian mass extinction eliminated more than 90% of marine species (Raup, 1979; Jin et al., 2000). Terrestrial biota also suffered dramatically: an estimated 70% of terrestrial vertebrate families were eradicated (Maxwell, 1992),

insects suffered a major loss of taxa (Labandiera and Sepkoski, 1993), and more than 90% of Late Permian gymnosperm species died out (Retallack, 1995; Visscher et al., 1996; Looy et al., 1999). The plant extinction is evidenced by the disappearance of almost all Late Permian gymnosperm pollen at a horizon containing only fungal remains and woody debris (Visscher et al., 1996). This fungal abundance event was followed by appearance of an Early Triassic palynoflora dominated by lycopod spores and bisaccate gymno-

sperm pollen (Eshet et al., 1995; Visscher et al., 1996). The widespread plant extinction and subsequent flood of fungal remains has been interpreted as indicating destruction of terrestrial vegetation and accumulation of decaying organic debris (Ouyang and Utting, 1990; Eshet et al., 1995; Visscher et al., 1996; Poort et al., 1997).

This fungal proliferation event has been observed both in terrestrial and shallow marine sequences. In marine sections, the brief interval rich in fungal remains is found close to the level marked by the mass extinction of marine organisms (Visscher and Brugman, 1986; Visscher et al., 1996; Twitchett et al., 2001). An abrupt negative shift in carbon isotopes in the oceans also occurs close to the time of the reduction in gymnosperms (Looy et al., 2000), and the zone marked exclusively by abundant fungal spores (Visscher et al., 1996; Wignall et al., 1996). In some Permian–Triassic sections enrichment in fungal remains occur at other levels (commonly the tops of regressive subtidal cycles; Cirilli et al., 1998), but these are not associated with the major disappearance of Late Permian pollen, and the concentration of fungal remains does not reach the ∼ 100% levels seen in the end-Permian abundance spike.

The widespread end-Permian fungal spike could provide a timeline for correlating the marine and non-marine records. A good place to establish this correlation is the Upper Permian and Lower Triassic Beaufort Group of the Karoo Supergroup of South Africa, which is well known for its record of the succession of mammal-like reptiles across the Permian–Triassic (P–T) boundary (Kitching, 1977; Rubidge, 1995). The demise of the herbivorous dicynodonts of the *Dicynodon* assemblage zone, and their replacement by the *Lystrosaurus* assemblage fauna has served in the past as the approximate definition of the P–T boundary in the Karoo, although the first occurrence of *Lystrosaurus* is now known to precede the last occurrence of *Dicynodon* (e.g. Smith, 1990, 1995; Smith and Ward, 2001).

The Beaufort Group consists of an apparently uninterrupted succession of alluvial sedimentation (Catuneanu and Elango, 2001). Sediments shed from the Cape Fold Belt region produced a fluvial network which prograded across the Karoo Basin during Late Permian time. Lacustrine mudstones, fluvial overbank mudstones and channel sandstones make up a sedimentary sequence up to 6 km thick in the Karoo Basin in South Africa. A change from predominantly green mudstone and sandstone deposited by high sinuosity river systems to multistoried channel and sheet sandstones intercalated with maroon mudstones, typical of deposition by braided streams, occurs close to the P–T boundary (as defined by the vertebrate assemblages) (Smith, 1990, 1995; Ward et al., 2000; Smith and Ward, 2001).

We studied the stratigraphy and palynology of the well-exposed Carlton Heights section, located along the Graaff-Reinet–Colesburg highway between Middleburg and Neupoort, South Africa (Fig. 1). Samples were collected in gullies to the southeast and below the main highway (on the B.P. Erasmus farm, 'Beskuitfontein'), and along the main highway itself (the road is at the 57 m level in our section) about 500 m north of the Carlton Heights railway stop (GPS: 31°13.03′S, 24°56.96′E).

2. Stratigraphy of the Carlton Heights section

At the Carlton Heights locality (Fig. 2), flat lying, predominantly greenish mudstone, siltstone and thin tabular sandstones dominate the lower part of the section. These were previously mapped as Upper Permian (Balfour Formation) (Keyser, 1977) based on lithology and stratigraphic position relative to the subsequent widespread change from mudstone to dominantly sandstone facies. A Late Permian age for these deposits is also suggested by our discovery of a large hip bone and other skeletal elements possibly belonging to *Dicynodon* sp. in the lower part of the section (between 2.8 and 10.5 m above the base of the section) (Fig. 2).

At about 33.5 m above the base of the Carlton Heights section, the green mudstone/sandstone sequence is overlain by ∼ 15 m of laminated to massive maroon mudstone with occasional thin sands (Fig. 3; well-exposed in the railroad cut
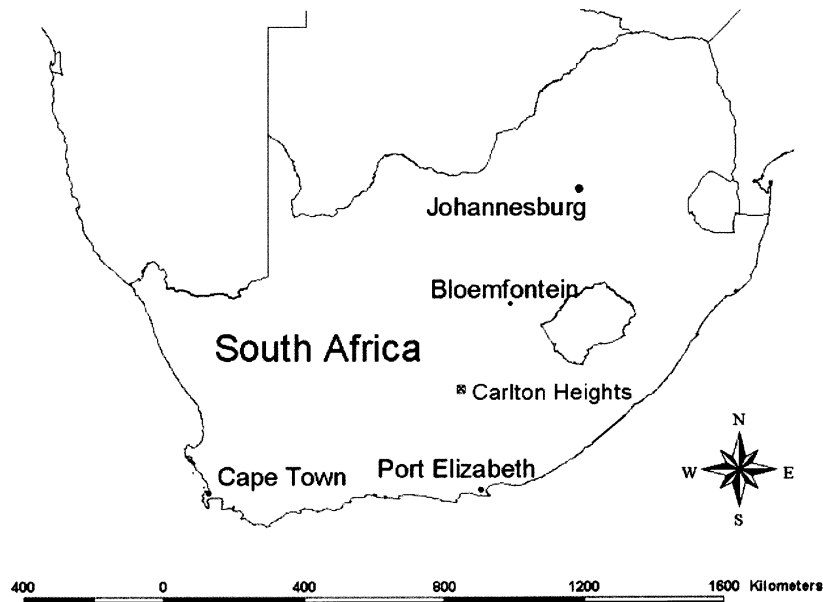
Fig. 1. Location map showing the Carlton Heights locality, Karoo Basin, South Africa.

just to the south of our section), capped by a 4–5 m-thick grayish–green sand unit. *Lystrosaurus* first occurs in our section at 38 m above the base. Based on lithology and stratigraphic position, we correlate this laminated maroon mudstone with a similar unit recently identified by Smith and Ward (2001) at the Bethulie and Lootsberg Pass sections in the Karoo. An increased number of *Lystrosaurus* fossils were noted near the top of this unit at Carlton Heights (∼51 m above the base of the section).

At ∼56 m above the base of the Carlton Heights section, the maroon mudstone and sandstone unit grades upward into thin-bedded alternating green and red siltstones and fine sandstones showing abundant sub-horizontal cylindrical burrows (Fig. 4). The thin-bedded burrowed unit is overlain (at 58.5 m above the base of the section) by a thin (∼5-cm-thick), very fine-grained clay-rich layer. This laterally continuous (on outcrop scale) layer is heavily burrowed, and is marked by red and yellow–brown alteration products (Fig. 4). Clay-mineral analysis by standard semi-quantitative X-ray diffraction methods (Brindley and Brown, 1980) shows that the layer is composed predominantly of illite and illite–smectite. The layer also contains quartz, low al-bite, gypsum, chlorite, mica, and jarosite, and thus has a heavily weathered detrital signature. About 0.5 m above this marker layer (at 59 m above the base of the section), the first laterally widespread multistoried sandstone with an erosional base containing lenses of mud-pebble and carbonate-nodule conglomerates (identified with the base of the Katberg Formation) is encountered (Figs. 2 and 4).

The Katberg Formation at Carlton Heights (>270 m in total thickness) is represented by a facies dominated by gray and white fine- to coarse-grained sandstone that is typically multistoried and laterally extensive (Fig. 4). The sands commonly show scoured bases with lenses of intra-formational mud-pebble and pedogenic carbonate-nodule conglomerates, horizontal stratification, and large-scale trough cross stratification (Smith, 1995). The thick multistoried sands are interbedded with thin red mudstone units showing desiccation features, such as sand-filled mudcracks.

3. Palynology

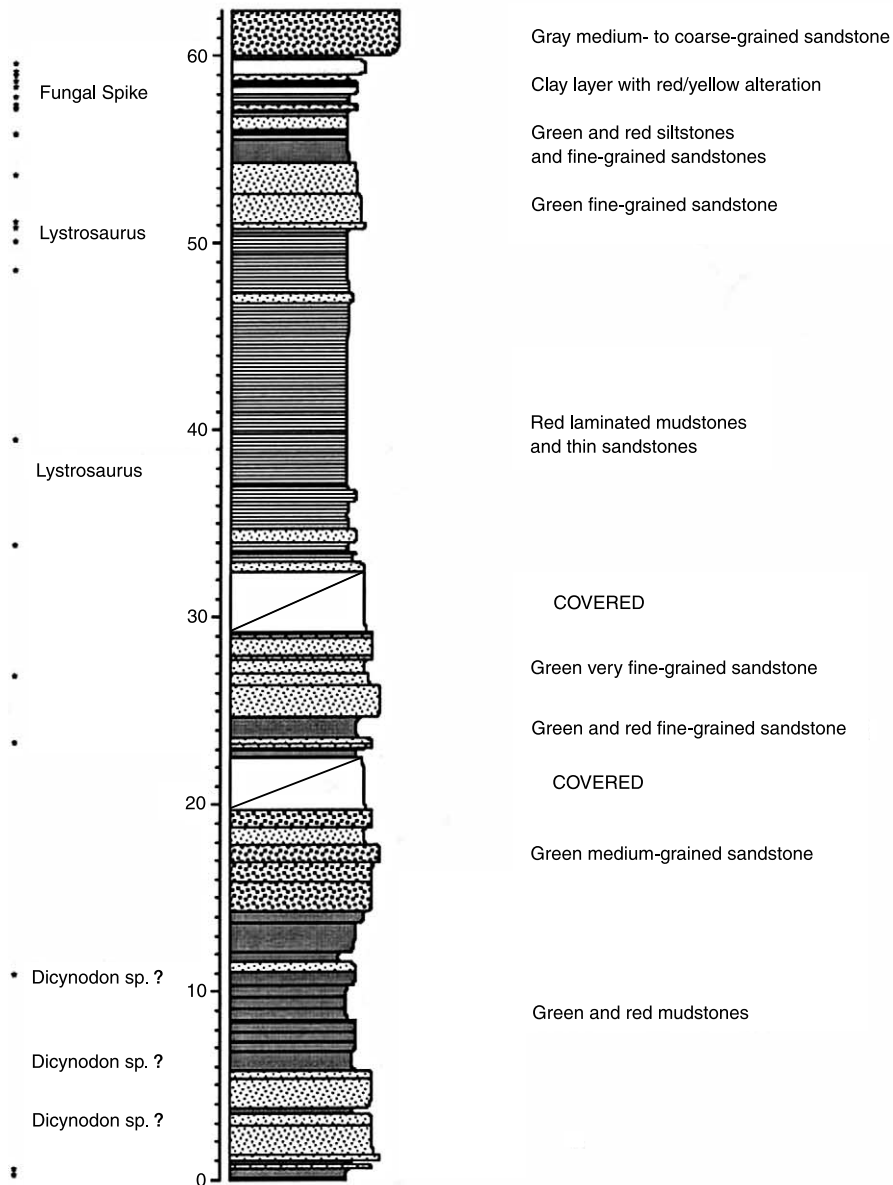We sampled a total of 73 m at 0.5–3-m intervals

Carlton Heights Section

Fig. 2. Stratigraphic section across the P–T boundary in Karoo Supergroup strata at Carlton Heights, South Africa. The upper-most 11 m in the Katberg Formation sandstones studied are not shown, as they were barren of palynofossils. Asterisks indicate samples analyzed for pollen and spores. *Dicynodon* sp.? indicates skeletal material possibly belong to *Dicynodon* sp.

(Fig. 2). Palynological slides were prepared for microscopic study using standard procedures (Doher, 1980). Out of the 29 samples that were analyzed for palynomorphs, only seven were bar-ren. The palynomorph species distribution within the sampled section is shown in Fig. 5. Three palynological assemblage zones were identified in the Carlton Heights section:

Fig. 3. Laminated to massive maroon mudstone with thin siltstone interbeds along the railway cut northeast of the Carlton Heights railway stop (person for scale) (see Fig. 2). This lithologic unit is believed to be correlative with the P–T event beds of Smith and Ward (2001) described from the Bethulie and Lootsberg Pass sections in the Karoo.

(1) The Late Permian *Klausipollenites schaubergeri* Zone, dominated by taxa of the form genera *Protohaploxypinus* and *Falcisporites*.

(2) An interval composed almost entirely of fungal cell remains (*Reduviasporonites* or its junior synonyms *Chordecystia* or *Tympanicysta*) (Visscher et al., 1996) and abundant recycled woody material – the fungal spike zone (Fig. 5). The fungal spike interval is only ∼1 m thick (57.6–58.6 m above the base of the section) (Fig. 2). (We note that some researchers have interpreted *Tympanicysta* as a green alga (Afronin et al., 2001), but most workers agree on the fungal interpretation (Visscher et al., 1996.)

(3) The fungal spike is followed by the Early Triassic *Kraeuselisporites–Lunatisporites* Zone, dominated by species of the lycopod *Kraeuselisporites* and the bisaccate pollen *Lunatisporites* and *Platysaccus*.

The interval from ∼49 m to 51.2 m in the section was found to be barren of palynomorphs, and eight of the 17 Late Permian palynomorph taxa that we identified last occur at or below this barren zone. The other nine Late Permian taxa have last occurrences at or just below the base of the fungal spike zone (Fig. 5). The last occurrences just prior to the lower barren zone could represent an initial decrease in plant diversity as part of a crisis period extending over some tens of thousands of years. On the other hand, the

Fig. 4. The fungal spike zone just below the base of the Katberg Formation on the Graaff-Reinet–Colesburg highway at Carlton Heights. The fungal spike zone, showing thin-bedded stratification and sub-horizontal burrowing, is ∼1 m thick (from 57.5 to 58.5 m in the section). The fungal spike zone is capped by a clay-rich layer with red to yellow–brown alteration. The one meter white bar is for scale.

reduction in palynomorphs could be the result of poor preservation of pollen and spores in sandy deposits.

4. The fungal spike and the end-Permian mass extinction

The characterization of the P–T boundary interval by a severe land-plant extinction and an abrupt, short-lived flood of fungal remains is now apparent from numerous studies around the world (Visscher and Brugman, 1986; Eshet et al., 1995; Visscher et al., 1996). Previous studies of Karoo Supergroup rocks produced a palynozonation scheme for this time span that showed evidence of a major turnover or extinction of palynomorphs at or near the P–T boundary (as defined by the vertebrate assemblages) (Anderson, 1977; Stapleton, 1978; Utting, 1979; Nyambe and Utting, 1997). In sub-Equatorial Africa, a fungal abundance spike has been reported in sections spanning the P–T boundary from Kenya (Hankel, 1992) and Madagascar (Wright and Askin, 1987).

The widespread fungal proliferation near the P–T boundary has been interpreted by a number of workers as reflecting loss of arboreous vegetation on a large scale, a major decrease in standing biomass, and the build-up of decaying vegetation on land (Visscher and Brugman, 1986; Visscher et al., 1996). In the same interval, the plant macrofossil record shows the extinction of the *Glossopteris* flora across Gondwana, and the disappearance of related *Vertebraria* root traces (Retallack, 1995). Recovery from the extinction and renewed diversification in land-plants were relatively slow, taking about 4 Myr (Eshet et al., 1995; Looy et al., 1999).

The flood of fungal remains was apparently a short-lived event. In the Carlton Heights sequence, the zone marked exclusively by fungal remains spans only ∼1 m of the sedimentary rec-
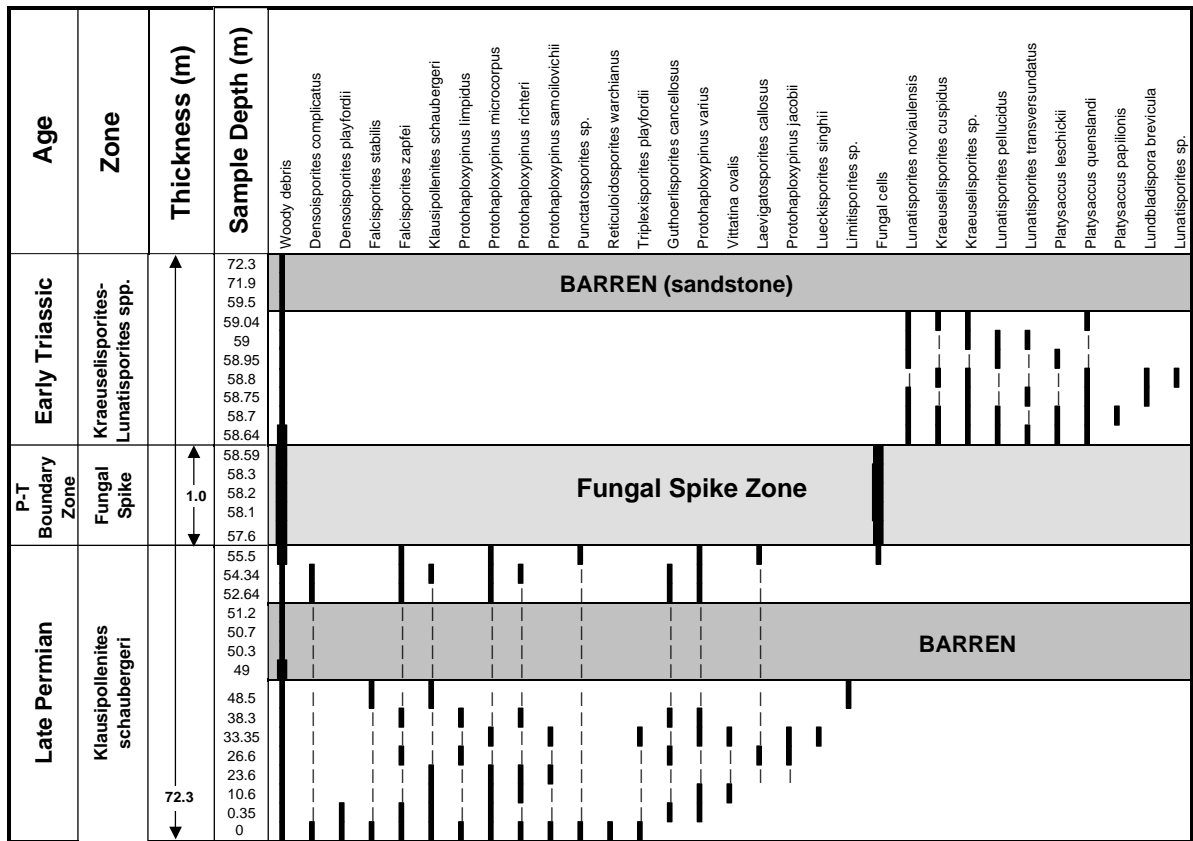
Fig. 5. Distribution chart (not to scale) of palynomorphs identified in the Carlton Heights stratigraphic section. The fungal spike interval, marked exclusively by fungal remains and woody debris, is ∼1 m in thickness.

ord (Figs. 2 and 5). At minimum estimated accumulation rates for the sediments of the Balfour Formation, this would mean ≤2000 years duration for the episode, with burrowing and the mixed depositional regimes probably making this an upper limit. Sedimentologic evidence of the dramatic loss of terrestrial vegetation – the marked lithologic change to the first thick, multistoried channel and sheet sandstones typical of braided streams (Katberg Formation) (Ward et al., 2000) – occurs about 50 cm (estimated as ≤1000 years) above the fungal spike zone at Carlton Heights (Fig. 4).

The results of several recent studies allow us to compare the timing of the extinction of terrestrial plants and reptiles with the marine extinctions. Twitchett et al. (2001) studied a marine section in Greenland that contained abundant and well-preserved marine fauna as well as terrestrial palynomorphs. The sediments also recorded the negative excursion in $\delta^{13}C$ in marine carbonate and organic carbon. Based on estimated sedimentation rates, Twitchett et al. (2001) concluded that the marine and terrestrial ecosystem collapse occurred over the same stratigraphic interval and took just a few tens of thousands of years. The faunal and floral extinctions were apparently coeval with the initial negative shift in $\delta^{13}C$. The rapid $\delta^{13}C$ shift could be a result of the rapid loss of primary productivity in the oceans and on land (Caldeira and Rampino, 1993), and the enhanced delivery of light carbon (including terrestrial plant debris) to the ocean floor (Broecker and Peacock, 1999; Sephton et al., 2002).

A similarly negative δ^{13}C isotope shift has been reported from some terrestrial sections (Morante, 1996; Krull and Retallack, 2000), and from molecular fossils in land-plant leaf cuticles deposited in marine sediments (Sephton et al., 2002), most likely reflecting a synchronous atmospheric carbon isotope shift. Recently, a negative excursion in carbon isotope ratios has been reported from carbonate soil nodules and bone material from the Bethulie section in the Karoo Basin (MacLeod et al., 2000). Thus, based on the results of Twitchett et al. (2001), the negative excursion in δ^{13}C in the Karoo section should be very close to the time of the marine extinction and the devastation of terrestrial ecosystems.

At Bethulie, the initiation of the δ^{13}C excursion at about 45 m in the section coincides with the local first appearance of *Lystrosaurus*; the δ^{13}C values begin to return to their former levels after the last appearance of *Dicynodon* at 57 m (MacLeod et al., 2000). The carbon isotope anomaly corresponds to the base of the laminated maroon mudstone event beds in which Smith and Ward (2001) place the P–T boundary. At average sedimentation rates for Karoo deposits (50 cm/1000 years) the interval of the laminated event beds and the overlap of *Dicynodont* sp. and *Lystrosaurus* would be about 25 000 years.

At the Carlton Heights locality, the base of the fungal spike zone is about 20 m above the base of the maroon mudstone event beds (Fig. 2). At average sedimentation rates for Karoo deposits, the base of the P–T event beds could be about 40 000 years prior to the fungal spike but these calculations are somewhat uncertain.

5. Conclusions

Palynological study at Carlton Heights identified a 1-m-thick zone containing only abundant fungal remains and woody debris coincident with the last appearance of typically Late Permian gymnosperm palynomorphs. The zone apparently represents proliferation of fungi upon large volumes of decaying plant matter. This fungal spike occurs just below the first Katberg Sandstone, which signifies a basin-wide change to braided

stream patterns, probably related to the widespread loss of vegetation (Ward et al., 2000).

The latest Permian flood of fungal remains might serve as a widespread marker bed of brief duration in marine and non-marine deposits. In marine sections, the fungal spike has been estimated to be coeval with the marine extinction and the negative shift in carbon isotopes that occurred at the end of the Permian (Twitchett et al., 2001). The discovery of the fungal spike in the classic fossiliferous Karoo sequence, within the interval of dramatic faunal turnover in terrestrial vertebrates and land-plants, allows correlation of the terrestrial and marine mass extinctions at the P–T boundary.

The stratigraphy at Carlton Heights, when combined with the recent work of Smith and Ward (2001) on other Karoo sections, suggests that the disappearance of typically Late Permian vertebrates in the Karoo Basin and the final gymnosperm plant extinction and fungal spike zone took place over an interval of less than 40 000 years.

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