Fungal event and palynological record of ecological crisis and recovery across the Permian-Triassic boundary

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ABSTRACT

The end of the Permian Period was marked by the most severe mass extinction in the geologic record. Detailed quantitative study of pollen and spores from shallow-marine deposits spanning the Permian-Triassic (P-Tr) boundary in Israel reveals a sequence of palynological-ecological stages reflecting a major crisis among land plants. The disappearance of the gymnosperm-dominated palynoflora of the Late Permian *Lueckisporites virkkiae* Zone is recorded at a claystone horizon containing almost exclusively abundant fungal remains and carbonized terrestrial plant debris. This "fungal spike" is followed by a zone dominated by marine acritarchs and a succession showing ecological recovery with abundant lycopod spores and eventual reappearance of bisaccate gymnosperm pollen in the Early Triassic. The latest Permian proliferation of fungi is recognizable worldwide and can be correlated with other paleontological and geochemical markers of a global ecological disaster.

INTRODUCTION

Recent studies suggest that the end of the Permian Period (~250 Ma) was marked by a severe crisis event (Wang et al., 1994; Retallack, 1995), culminating in the greatest mass extinction in the geologic record, which affected marine and terrestrial animals and plants (Erwin, 1993). Changes in terrestrial plant communities can serve as sensitive indicators of environmental stress, and thus the nature and timing of the end-Permian crisis should be reflected in palynological assemblages across the P-Tr boundary. The Permian-Triassic succession in Israel consists of an apparently conformable sequence of shallow-marine deposits of the Arqov and overlying Yamin and Zafir Formations (Druckman et al., 1982). These strata are nowhere exposed, but they have been penetrated in several petroleum explo-

ration wells (Druckman et al., 1982; Druckman, 1974; Eshet, 1992) (Fig. 1A). The sequence contains recognized palynological markers for the Late Permian and the Early Triassic; the uppermost Permian *Lueckisporites virkkiae* Zone is defined by the total range of *L. virkkiae* and *Klausipollenites schaubergeri*, and its top is marked by the disappearance of almost all typical Late Permian pollen and spores (Eshet, 1990a, 1990b, 1992) (Fig. 2).

The locally defined P-Tr boundary occurs within a thin, brownish to reddish claystone horizon that cuts across the lithostratigraphic units from the upper Arqov Formation to the lower part of the Yamin Formation (Fig. 1B) (Eshet, 1990a, 1990b, 1992). The base of the Lower Triassic *Endosporites papillatus* Zone, as defined by the first-appearance datum (FAD) of *E. papillatus*, is found immediately above this claystone layer. A sharp palynological break between latest Permian and earliest Triassic palynoflora has in the past been taken as evidence for a possible disconformity between the two systems (Balme, 1979), but recent studies suggest that sections showing the abrupt pollen transition probably do not contain significant hiatuses (e.g., Broglio-Loriga et al.,
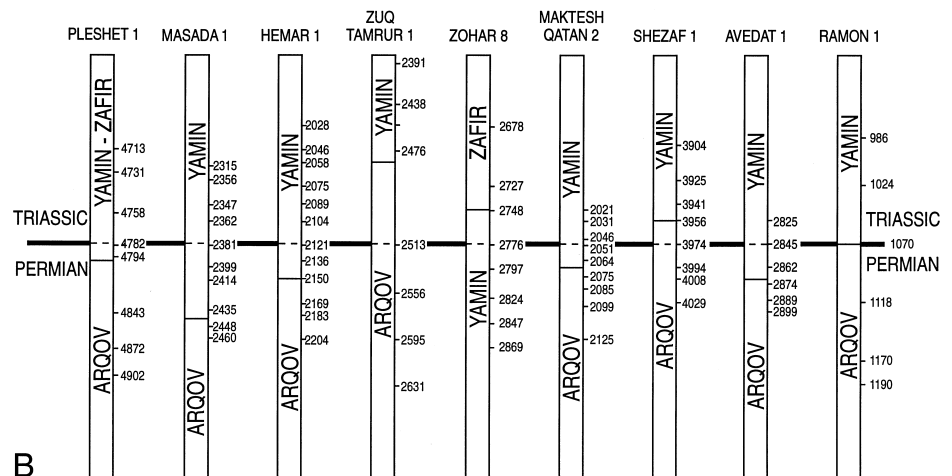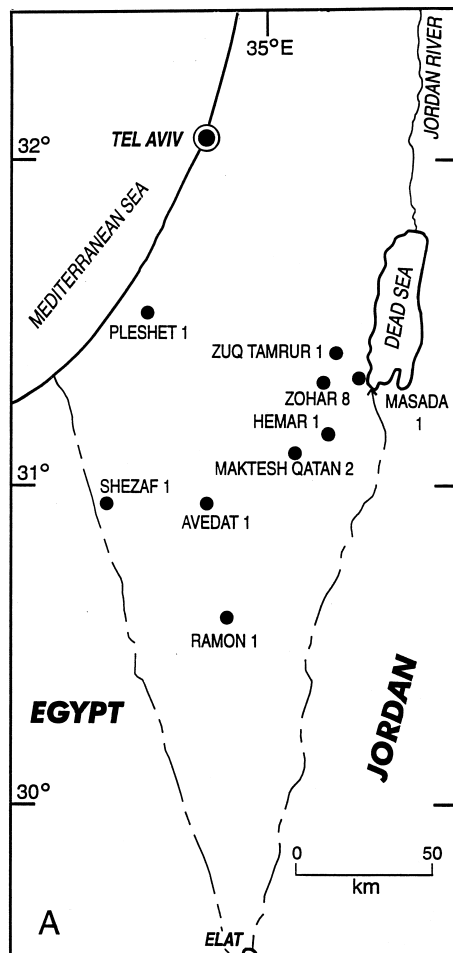

Figure 1. A: Location of boreholes in Negev, southern Israel, penetrating locally defined Permian-Triassic boundary. B: Palynostratigraphic correlation of Permian-Triassic boundary interval in subsurface of southern Israel from borehole information (Eshet, 1992). Widespread reddish claystone horizon marks palynologically defined P-Tr boundary. Sample depths given in metres.
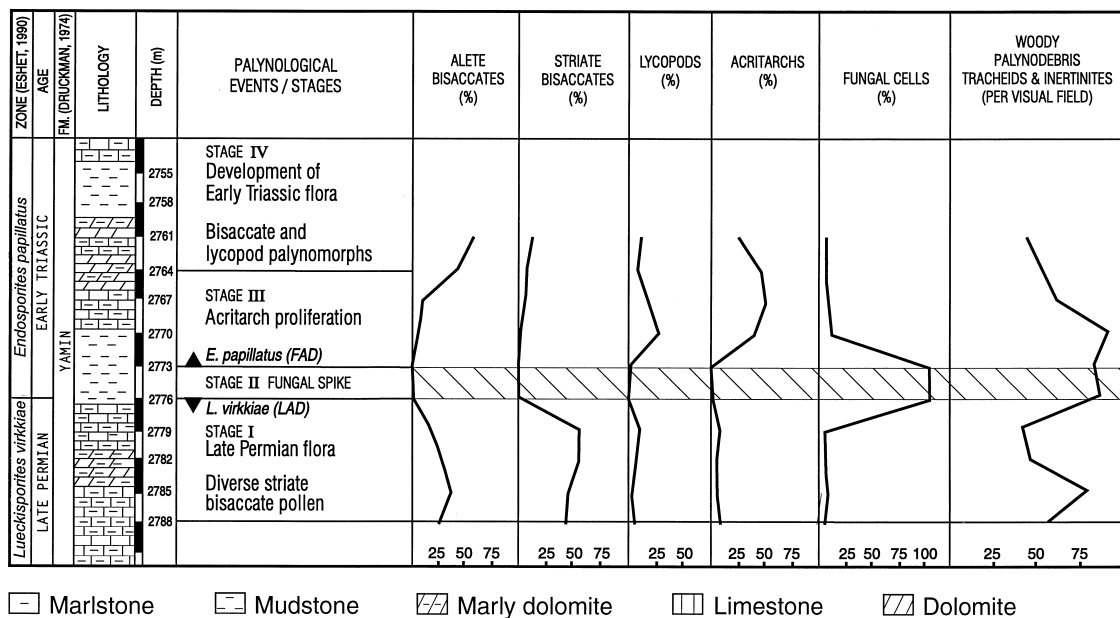
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Figure 2 chart (Zohar-8 borehole)

Column headers: ZONE (ESHET, 1990) | AGE | FM. (DRUCKMAN, 1974) | LITHOLOGY | DEPTH (m) | PALYNOLOGICAL EVENTS / STAGES | ALETE BISACCATES (%) | STRIATE BISACCATES (%) | LYCOPODS (%) | ACRITARCHS (%) | FUNGAL CELLS (%) | WOODY PALYNODEBRIS TRACHEIDS & INERTINITES (PER VISUAL FIELD)

ZONE: *Endosporites papillatus* / *Lueckisporites virkkiae*
AGE: EARLY TRIASSIC / LATE PERMIAN
FM.: YAMIN

Depths (m): 2755, 2758, 2761, 2764, 2767, 2770, 2773, 2776, 2779, 2782, 2785, 2788

Palynological events / stages:
- STAGE IV — Development of Early Triassic flora
- Bisaccate and lycopod palynomorphs
- STAGE III — Acritarch proliferation
- ▲ *E. papillatus* (FAD)
- STAGE II FUNGAL SPIKE
- ▼ *L. virkkiae* (LAD)
- STAGE I — Late Permian flora
- Diverse striate bisaccate pollen

Axis scales: ALETE BISACCATES 25 50 75; STRIATE BISACCATES 25 50 75; LYCOPODS 25 50; ACRITARCHS 25 50 75; FUNGAL CELLS 25 50 75 100; WOODY PALYNODEBRIS 25 50 75

Legend: ⊟ Marlstone   ⊡ Mudstone   ▨ Marly dolomite   ⊞ Limestone   ▨ Dolomite

Figure 2. Palynological stages across P-Tr boundary in Zohar-8 borehole from Negev, southern Israel. Sampling interval was 3 m.

1986; Eshet, 1992; Broglio-Loriga and Cassinis, 1992; Retallack, 1995).

In the present quantitative palynological study, we utilized careful sampling of cores and cuttings to overcome problems of borehole caving that have plagued previous stratigraphic work (Eshet, 1990a, 1990b). Palynologic slides were prepared for microscopic study by using conventional procedures (Eshet, 1992), and 200 palynomorphs per sample were counted and identified in order to construct relative frequency curves.

PALYNOLOGICAL STAGES ACROSS THE PERMIAN-TRIASSIC BOUNDARY

Our analysis of the Permian-Triassic boundary interval from borehole samples in Israel (Fig. 1) reveals a sequence of discrete palynological-ecological stages (Fig. 2).

Stage I, consisting of the typical Late Permian flora (within the *L. virkkiae* Zone), is dominated by a diverse assortment of striate bisaccate pollen grains (mostly of the genus *Protohaploxypinus*) originating from gymnosperms (Fig. 3). Spores of lycopods (club mosses) are present in low abundances. Toward the top of the stage, single cells and multicellular fragments of land-dwelling fungi (*Tympanicysta*) become increasingly abundant. The top of the stage is marked by the disappearance of more than 95% of the Late Permian pollen and spore taxa (Eshet, 1990a, 1990b).

Stage II, with a palynological assemblage composed almost entirely of abundant fungal remains (≥95% of palynomorphs), and here defined as the "fungal spike" (Fig. 2), is found within the widespread claystone horizon that marks the locally defined P-Tr boundary (Fig. 1B). This horizon also con-

tains a large amount of terrestrial organic detritus (Fig. 2), composed of carbonized plant debris (Eshet, 1990a, 1990b, 1992). In this layer, <1% in-situ pollen, spores, or marine acritarchs were observed.

Stage III (Early Triassic), immediately above the fungal spike horizon, is marked by proliferation of acritarchs of the *Veryhachium-Micrhystridium* complex (Fig. 3). These are commonly regarded as marine phytoplankton, although Brinkhuis and Visscher (1994) suggested that some forms identified as acritarchs (e.g., *Scythiana*) may

be small spores of bryophytes (mosses). The acritarchs increase abruptly, making up ~50% of the total assemblage (Fig. 2), and remain abundant throughout the Lower Triassic in the boreholes studied (Eshet, 1990b). Characteristic Early Triassic palynomorphs, mostly lycopod spores (*Endosporites* and *Kraeuselisporites*) and some bisaccate pollen grains, are present in minor amounts and increase upward.

Stage IV represents the establishment of typical Early Triassic flora of the *E. papillatus* palynozone (although the assemblage is
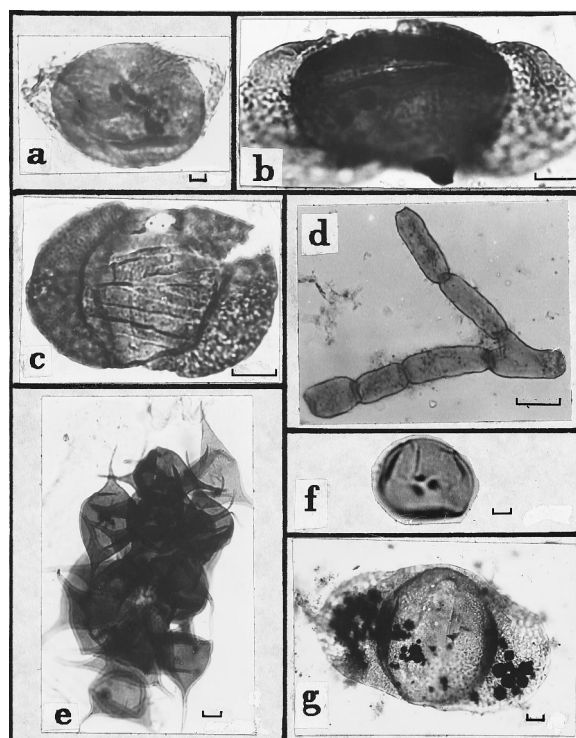
Figure 3. Palynomorphs from Permian-Triassic boundary interval in Israel (Eshet, 1990a, 1990b). A–C are typical Late Permian palynomorphs (stage I). A: *Klausipollenites schaubergeri*. B: *Lueckisporites virkkiae*. C: *Protohaploxypinus* sp. D: Chain of fungal cells (*Tympanicysta*) from fungal spike (stage II). E: Cluster of acritarchs *Veryhachium* from stage III. F and G are typical Early Triassic palynomorphs (stage IV). F: *Endosporites papillatus*. G: *Falcisporites stabilis*. (All scale bars represent 10 μm.)

much reduced in diversity compared with the Late Permian), dominated by alete bisaccate gymnospermous pollen (mostly *Alisporites-Falcisporites* spp.), with some striate bisaccate forms (mostly *Lunatisporites* spp.) and lycopod spores (including *Densoisporites*, *Endosporites*, and *Kraeuselisporites*) (Fig. 3). Recovery of a more diverse Early Triassic gymnosperm flora, however, was delayed until near the end of the Scythian Stage (Eshet, 1990a), about 4 m.y. after the P-Tr boundary.

LATEST PERMIAN "FUNGAL EVENT"

A widespread event (Visscher and Brugman, 1986), marked by increases in fungal remains (*Tympanicysta* and its taxonomic equivalents *Chordecystia* and *Reduviasporonites*), in some cases culminating in a distinct fungal spike, in the uppermost Permian or lowermost Triassic rocks, has been documented at many localities, including North America (Utting, 1989, 1994), Greenland (Balme, 1979), Europe (Ecke, 1986; Haas et al., 1986; Mangerud and Konieczny, 1993; Wood and Mangerud, 1994), Asia (Ouyang and Utting, 1990), East Africa (Hankel, 1992), Madagascar (Wright and Askin, 1987), and Australia (Foster, 1982; Retallack, 1995). The wide geographic distribution of this increase in fungal abundance makes it unlikely that the increase is everywhere an artifact resulting from sedimentary processes or local conditions, and the apparent thinness of the abundance spike suggests that a similar peak of >95% fungal remains could have been missed at many P-Tr localities. The observed increase in acritarchs in the lowermost Triassic has also been reported widely from North America (Fisher, 1979), Greenland (Balme, 1979), Europe (Visscher and Brugman, 1986; Wood and Mangerud, 1994; Goczan et al., 1987), Pakistan (Balme, 1970), and Australia (Retallack, 1995), although in some areas, Upper Permian marine strata have also yielded abundant acritarchs (Visscher and Brugman, 1986; Utting, 1994; Ouyang and Utting, 1990).

In the southern Alps (Italy), the increase in fungal remains has been recognized in the uppermost Bellerophon Formation limestones and within the thin, oolitic Tesero horizon at the base of the overlying Werfen Formation (Visscher and Brugman, 1986; Broglio-Loriga et al., 1990). The P-Tr boundary is placed by many workers at the base or within the lower part of the Tesero horizon (Broglio-Loriga et al., 1986; Sweet et al., 1992; Broglio-Loriga and Cassinis, 1992), where >95% of Late Permian foraminifera disappear (Broglio-Loriga et al., 1986; Broglio-Loriga and Cassinis, 1992). In

these sections, the fungal remains increase from values of ~20% of nonmarine palynomorphs to a peak of >95% over a few metres of sedimentary strata. This effect is in contrast to the apparently more abrupt onset of the fungal increase seen in the Israeli sections, although the differences might be attributed to different sedimentation rates, reworking, and/or possible hiatuses. In the Italian sections, the fungal increase is followed by proliferation of acritarchs of the *Veryhachium-Micrhystridium* complex ~1 to 2 m above the Tesero horizon (Visscher and Brugman, 1986).

The palynological data from the Zohar-8 borehole (Fig. 2) can be used to estimate the duration of the fungal abundance spike in Israel. The earliest Triassic Scythian Stage (duration of ~4 m.y.) is represented by ~223 m of sedimentary rocks in that borehole (Eshet, 1990a), giving average sedimentation rates of ≥56 m/m.y., a reasonable rate for shallow-marine environments (Wang et al., 1994). This result yields ≤54 ka for the ≤3-m-thick fungal-spike horizon. This duration could be an underestimate if the horizon represents a hiatus or a time of very slow sedimentation. On the other hand, the presence of unrecognized hiatuses in Triassic section of the borehole would lead to a higher estimated average sedimentation rate and, hence, to a shorter estimated duration of the fungal spike. For comparison, Sweet's (1992) graphic correlation analyses suggest that the duration of sedimentation of the Tesero horizon in the southern Alps (where it averages ~6 m thick) was ~74.5 ka (Sweet et al., 1992), which would give an estimated duration of ≤25 ka for the ~2-m-thick zone of maximum fungal abundance (>95%) at that locality. In the Meishan section in China, however, fungal remains and acritarchs seem to have dominated the palynomorph assemblage over an estimated period of ~200 ka in the latest Permian (Ouyang and Utting, 1990), suggesting a more extended interval of environmental deterioration.

ECOLOGICAL TRAUMA IN THE LATEST PERMIAN

The sequence of palynological changes can be used to propose a scenario for the ecological changes that occurred during the transition from the Permian Period to the Triassic Period. Fungi are known to adapt and respond quickly to environmental stress and disturbance (Harris and Birch, 1992). During high-stress intervals, fungi may proliferate in the resulting severely disturbed ecosystems, where dead biomass supplies abundant organic resources for saprotrophs (e.g., Pugh and Boddy, 1988; Harris and

Birch, 1992). The decimation of autotrophic plant life, as indicated both by the palynological record and the abrupt and profound changes in plant macrofossils (e.g., >95% extinction of fossil leaf species in China [Yang et al., 1992] and Australia [Retallack, 1995]), could have created a large pool of decaying organic matter, as evidenced by the abundant plant debris seen in the fungal-spike horizon. The sequence of changes in land plants that followed the period of fungal proliferation (spread of nonarborescent lycopods, and possibly bryophytes, followed by reintroduction of gymnosperms) reflects stages in the gradual recovery of the devastated terrestrial ecosystems (Visscher and Brugman, 1986).

A concurrent loss of primary productivity in the oceans and the collapse of the marine food chain is suggested by the worldwide decrease in planktonic and nektonic groups and in organisms with planktonic growth stages (Valentine, 1986). Greatly reduced oceanic productivity in the wake of a mass extinction of phytoplankton at the end of the Permian could have led to the marked negative $\delta^{13}C$ shift reported from both carbonate and organic carbon fractions in marine sections (e.g., Magaritz et al., 1992; Wang et al., 1994). Such an event, termed the "Strangelove" ocean, is recorded at the Cretaceous-Tertiary (K-T) boundary (65 Ma) and possibly at other mass-extinction boundaries (Hsü and McKenzie, 1990; McLaren and Goodfellow, 1990; Rampino and Haggerty, 1994), and it could occur on time scales as short as 10^3 yr.

The proliferation of acritarchs seen in many P-Tr sections suggests a population explosion of opportunistic survivor species in the surface oceans (Visscher and Brugman, 1986), as also evidenced by the low diversity of shallow-marine faunas in the earliest Triassic, marked by dominance of the primitive brachiopod *Lingula* (Xu and Grant, 1992; Erwin, 1993) and widespread stromatolitic algal mats (Schubert and Bottjer, 1992). Similar spikes in the abundance of opportunistic and stress-tolerant groups are seen at other times of mass extinction, such as the K-T boundary, where marine sections commonly show spikes in abundance of stress-tolerant taxa such as the calcareous algae *Thoracosphaera* (e.g., Eshet et al., 1992). Stages in floral recovery analogous to those seen at the P-Tr boundary have been observed in many terrestrial K-T boundary sections in western North America, which are marked by floral extinctions, a thin, barren horizon containing carbonized plant debris, and a spike in fern spores, representing recolonization by pioneer flora (Spicer, 1989).

Evidence from the Permian-Triassic boundary interval in Israel and elsewhere suggests a relatively brief episode of severe ecological stress and associated terrestrial floral extinctions, an episode that seems to have been part of a global ecological crisis on land and in the oceans. The worldwide environmental disaster, marked by a massive die-off of terrestrial plants and spread of fungi, was followed by a gradual recovery involving floral succession and eventual establishment of a new, Triassic floral suite.

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