

The terminal Paleozoic fungal event: Evidence of terrestrial ecosystem destabilization and collapse

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ABSTRACT Because of its prominent role in global biomass storage, land vegetation is the most obvious biota to be investigated for records of dramatic ecologic crisis in Earth history. There is accumulating evidence that, throughout the world, sedimentary organic matter preserved in latest Permian deposits is characterized by unparalleled abundances of fungal remains, irrespective of depositional environment (marine, lacustrine, fluvial), floral provinciality, and climatic zonation. This fungal event can be considered to reflect excessive dieback of arboreal vegetation, effecting destabilization and subsequent collapse of terrestrial ecosystems with concomitant loss of standing biomass. Such a scenario is in harmony with predictions that the Permian–Triassic ecologic crisis was triggered by the effects of severe changes in atmospheric chemistry arising from the rapid eruption of the Siberian Traps flood basalts.

Terminal Paleozoic extinctions reflect the most profound crisis in the marine biosphere of all time (1, 2). Analysis of biodiversity levels now suggests that $\approx 80\%$ of Late Permian invertebrate species had become extinct by the end of the Permian (3). Elimination of species may have occurred stepwise over a prolonged period, but toward the Permian–Triassic (P–Tr) junction sustained diversity decline was punctuated by a final extinction pulse, affecting benthos, nekton, and zooplankton without obvious selectivity (4, 5). This final pulse is also reflected in a conspicuous negative shift in $^{13}\text{C}/^{12}\text{C}$ isotope ratios of organic carbon, suggesting marine ecosystem collapse as a result of significant reduction of marine primary productivity (6, 7). A concomitant long-term extinction pattern in the Late Permian terrestrial biosphere can be inferred from biodiversity levels of vertebrates (8) and insects (9). In remarkable contrast, it has long been assumed that land plants show a high persistence capacity at the time of the marine P–Tr crisis. However, because of its prominent role in global biomass storage and its sensitivity to environmental perturbation, land vegetation remains the most obvious biota to be investigated for records of past terrestrial ecosystem collapse. Recently, it was emphasized that disappearance of the high-diversity *Glossopteris* flora of Permian Gondwanaland can be regarded as a significant P–Tr event in the southern hemisphere (10). Here we illustrate that the sedimentary record of land-derived organic matter in P–Tr transition sequences testifies to world-wide destruction of standing woody biomass resulting from excessive dieback of dominant gymnosperm vegetation.

The “conquest of the atmosphere” by plant life was successfully completed at the beginning of the Carboniferous. Since that time, standing biomass has been stored principally

in the wood of land plants rather than in aquatic organisms. Sustained stability of this single largest biotic carbon reservoir is basically determined by a functional equilibrium between primary productivity and decomposition in arboreal ecosystems. Apart from bacteria, saprophytic fungi represent a prominent category of decomposers; they are particularly efficient in the rapid degradation of woody tissue under aerobic conditions. Fungi are known to adapt and respond quickly to environmental stress and disturbance (11). Fossil records indicating excessive fungal activity may therefore provide confirming evidence of past ecosystem destabilization.

Extreme abundances of fungal remains have been recorded in sedimentary organic matter associations from fine-clastic intercalations in the shallow-marine P–Tr transition sequences of the Southern Alps (Italy) (12, 13) and the Negev (Israel) (14–17). The remains include single cells as well as multicellular chains (Fig. 1), representing both hyphae and asexual reproductive spores (conidia) of ascomycetous fungi. A comprehensive morphological and taxonomic evaluation of this fungal material is in progress. Most of the remains may correspond to *Reduviasporonites*, a broad-form genus for fungal palynomorphs, first-described from the Middle Permian (Wordian) Flowerpot Formation in Oklahoma (22). This name has priority over *Tympanicysta* and *Chordecystia* (*incertae sedis* genera) to which fungal material from the P–Tr transition has been most frequently referred.

In this report, the proxy record of fungal proliferation in Italy and Israel is presented by calculating the proportion of fungal remains in the land-derived component of palynomorph associations (Fig. 2). In outcrops in the Southern Alps, the transitional sequence across the P–Tr boundary includes parts of the Bellerophon and Werfen Formations. The proportion of fungal remains shows an increase toward the top of the Bellerophon Formation. In the basal part of the Tesero Horizon, they may become overwhelmingly dominant, but above an interval with last-occurrences of characteristic Late Permian brachiopods, foraminifera, and calcareous algae (18–21) the fungal component abruptly declines. In the Negev, extreme fungal dominance is confined to a 3-m interval of brownish clay within the Yamin Formation that is considered to mark the P–Tr junction in boreholes (14–17). In general, fungal abundances are accompanied by increased amounts of woody plant debris.

There is accumulating evidence that the fungal proliferation documented from Italy and Israel can be traced throughout the world, irrespective of depositional environment (marine, lacustrine, fluvial), floral provinciality, and climatic zonation. Identical or similar organic microfossils are known to occur, often in relatively high frequencies, in other P–Tr transition sequences in Europe, North America, Asia, Africa, and Australia (24–45, 72–75) (Fig. 3). Regular records from

Abbreviation: P–Tr, Permian–Triassic.



FIG. 1. Sedimentary organic matter assemblage with extreme dominance of fungal remains from the Tesero Horizon, Southern Alps, at the level of last occurrences of typical Late Permian faunal elements (18–21). (× 215.)

nonmarine deposits contradict concepts that the remains would represent marine rather than terrestrial fungi (46, 47). In some of the investigated basins, a fungal acme already serves as a practical bioevent for recognizing the P–Tr transition in subsurface exploration. It should be noted that the abundance

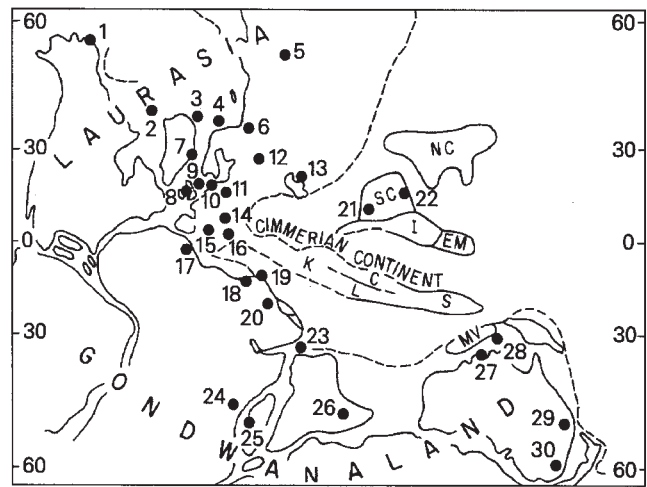


FIG. 3. Known occurrences of fungal remains in P–Tr transition sequences (LPP refers to unpublished information at the Laboratory of Palaeobotany and Palynology, Utrecht University). 1, North Alaska (24); 2, Sverdrup Basin, Canada (25–27); 3, Svalbard (28, 29); 4, Barents Sea (29, 30); 5, Tunguska Basin, Siberia (31); 6, Pechora Basin, Russia (32); 7, East Greenland (24); 8, British Isles (ref. 24; LPP); 9, North Sea (LPP); 10, Zechstein Basin, Germany (ref. 33; LPP); 11, Zechstein Basin, Poland (34, 35); 12, Moscow Basin, Russia (36, 37); 13, Mangyshlak, Kazakhstan (LPP); 14, Transdanubian Mountains, Hungary (72–75); 15, Southern Alps, Italy (12, 13); 16, Dinarides, Bosnia (LPP); 17, Tunisia (38); 18, Negev, Israel (14–17); 19, South Anatolia, Turkey (LPP); 20, Saudi Arabia (LPP); 21, Sishuan, South China (LPP); 22, Meishan, South China (39); 23, Salt Range, Pakistan (24); 24, Mombasa Basin, Kenya (40); 25, Morondava Basin, Malagasy (41); 26, Raniganj Basin, India (LPP); 27, Bonaparte Gulf Basin, Western Australia (24); 28, Banda Sea (LPP); 29, Bowen Basin, Queensland (42, 43); 30, Sydney Basin, New South Wales (10, 44). Paleogeography for Asian terranes is from ref. 45. NC, North China; SC, South China; I, Indochina; EM, East Malaya; K, Kreios; C, Changtang; L, Lhasa; S, Sibumasu; MV, Mount Victoria Land.

of fungal remains is sometimes considered to characterize the earliest Triassic rather than the latest Permian. This discrepancy can be related to different conventions applied in defining the P–Tr boundary. Time equivalence of presumed latest Permian and earliest Triassic abundances is in accordance with concepts of a temporal coextension of the conodont *Neogondolella changxingensis* and the ammonoid *Otoceras woodwardi*,

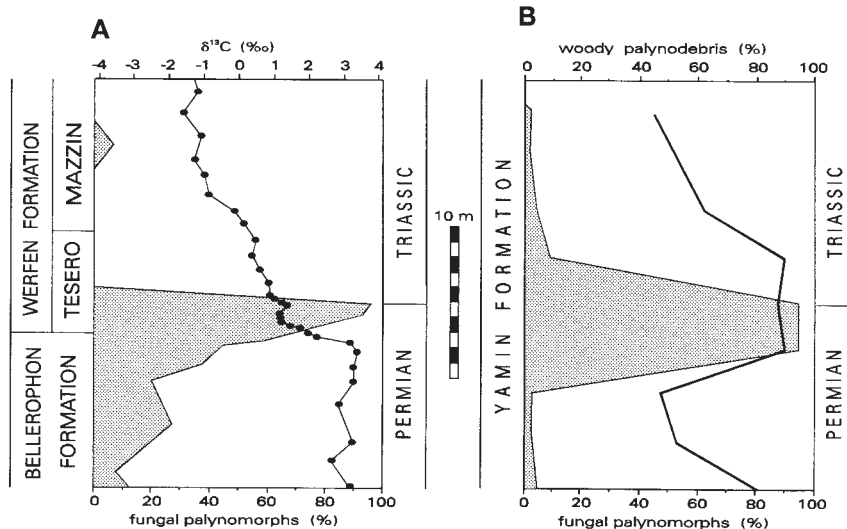


FIG. 2. Relative proportion of fungal remains in the land-derived component of palynomorph assemblages from P–Tr transition sequences. (A) Southern Alps (composite Butterloch and Tesero sections in the western Dolomites); fungal proliferation compared with carbon isotope profile for carbonates (23). (B) Negev, southern Israel (Zohar-8 exploration borehole); fungal proliferation compared with woody organic debris estimates.

conventional age-diagnostic faunal elements for the latest Permian and earliest Triassic, respectively (48).

The P–Tr fungal event is unique in the Phanerozoic sedimentary organic matter record. The Paleozoic and Mesozoic history of all major groups of fungi is becoming well-documented on the basis of early Devonian to Triassic permineralizations (49). In palynomorph assemblages, on the other hand, dispersed robust-walled fungal remains are not regularly encountered until the late Jurassic. The onset of a continuous record of diverse associations of fungal palynomorphs occurs by late Cretaceous and Paleogene time (50–53). Their relative abundance, however, generally remains significantly lower than that of pollen and spores of vascular plants. Recent distribution of land-derived fungal palynomorphs corresponds to a wide variety of continental and marine depositional settings, ranging from peat deposits to deep-sea sediments.

World-wide fungal proliferation at the P–Tr junction implies an excessive heterotrophic presence. The necessary organic resource can have originated only from dieback of arboreal vegetation. In the Southern Alps and Israel, the resulting ecosystem destabilization and collapse is reflected in pollen and spore records that testify to a marked floral turnover at the P–Tr junction. Abundance and diversity patterns among gymnospermous pollen types rapidly decline. Their last-occurrences suggest that notably arborescent conifers were affected by a significant extinction (12). Accurate taxonomic analysis on the basis of leaf remains and reproductive organs (54–56) confirms that, at least in Europe, Late Permian conifers became extinct at the family level. Since there is no evidence of rapid replacement, this extinction event will have caused large-scale loss of standing biomass. Concomitantly, microspores of herbaceous and subarborescent lycopodiophytes frequently become characteristic elements of palynological assemblages. There is some evidence that in Europe bryophytes also played a prominent role in early Triassic vegetation recovery; the palynomorph *Scythiana*, originally described as phytoplankton (acritarchs) and abundantly present in Italy and Hungary (12, 72–75), could well represent moss spores (57). Renewed diversification and proliferation of arborescent gymnosperms took place after ≈ 4 million years ago, at the junction between Early and Middle Triassic (12, 58).

Among the varied environmental factors that are known to disturb autotrophic productivity on land, only severe changes in atmospheric chemistry may have world-wide dramatic effects. Such changes may include excessive CO₂ increase, ozone depletion and acidification. Research at the ecosystem level for the terrestrial effects of CO₂ increase (59) and ozone depletion (60) is barely beginning. Destabilizing effects of severe CO₂ increase can be anticipated but patterns are not yet easily predicted. This also applies to effects of enhanced UVB radiation resulting from stratospheric ozone depletion. On the other hand, despite the scale difference, acidification scenarios developed in relation to present-day forest dieback may well be applied in understanding the pattern of terrestrial ecosystem destabilization at the end of the Paleozoic. Forest ecosystems respond to increasing pollution stress in a predictable pattern (61). Under severe pollution conditions, the direct phytotoxic effects of gaseous pollutants as well as long-term effects of acid fallout disturb plant growth and community structure. The size of plants becomes important to survival; trees and tall shrubs die off, followed by short shrubs and herbs. Productivity will become progressively minimized as the capacity of the ecosystem to substitute tolerant for intolerant species is surpassed. Accelerated by autogenous processes, this pattern of destabilization becomes irreversible, ultimately resulting in ecosystem collapse.

Since there is no compelling evidence for an extraterrestrial forcing of the P–Tr biosphere crisis (1, 2), a conceptual model of dramatic change in atmospheric chemistry would call upon

an episode of massive volcanic activity that could have been responsible for excessive emission of CO₂ and/or acidifying gases and their derivative liquid aerosols. There is a growing realization that the Late Permian represents a time interval with exceptionally widespread volcanism that can be related to the fundamental reorganization of plate boundaries and intraplate stress regimes succeeding the assembly of the Pangaea supercontinent. All along the margins of Pangaea, there was accelerated orogenic activity with associated volcanism (62). In addition, there was widespread intracratonic volcanism. It has been hypothesized that notably the paroxysmal eruption of flood basalts in Siberia could have caused the biotic crisis in the marine biosphere (63–65). Radiometric age assessments of the Siberian Traps and tuffs at the P–Tr junction in South China have now confirmed the temporal association of the terminal Paleozoic crisis with this most prominent subaerial volcanic event in Phanerozoic geologic history, responsible for the production of up to 3×10^6 km³ of ejecta in 1 million years or less (65). Due to magma ascent through massive evaporates and the relatively explosive nature of the eruptions, yield of sulfur and chlorine to the atmosphere may have been significantly higher than during other periods of flood volcanism. A concept of excessive CO₂ release is more difficult to conceive.

In South China, fungal abundances (30–80% of the land-derived palynomorph component) occur throughout the Changxing Formation (39), which typifies the latest Permian Changxingian Stage. The presence of fungal remains in interflow sediments associated with the Siberian Traps (31) still awaits a quantitative evaluation. However, biostratigraphic analysis of plant remains, conchostracs, and ostracodes supports a Changxingian age for the main eruption phase of the Siberian Traps (66–68). It may be assumed, therefore, that fungal proliferation is essentially a Changxingian event that took place in <1 million years.

In the Southern Alps, the proxy pattern of fungal proliferation mirrors the carbon isotope profile for carbonates from the Bellerophon–Tesero transition (Fig. 2), suggesting synchronicity of terrestrial and marine ecologic change. Superimposed on a long-term declining trend, the marked negative $\delta^{13}\text{C}$ shift close to the P–Tr boundary (23) represents a conspicuous isotope event that has been recorded in marine P–Tr sections throughout the world (69–71). When compared with the coeval decline in $\delta^{13}\text{C}$ values for organic carbon (6, 7), this event is likely to reflect marine ecosystem collapse.

Any understanding of biosphere crises requires temporal information on primary producers and decomposers, the two essential components of both terrestrial and marine ecosystems. Such information is notably preserved in the sedimentary organic matter record. The reported link between fungal proliferation and gymnosperm extinction exemplifies that detailed organic matter analysis can contribute to a coherent picture of P–Tr ecosystem destabilization, collapse, and subsequent recovery. To understand marine biotic change, further organic matter studies should also concentrate on the identification and environmental interpretation of palynological, molecular, and compound-specific $\delta^{13}\text{C}$ signals, characteristic of marine algae and bacteria.

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