Gondwana Research 20 (2011) 630–637

Contents lists available at ScienceDirect

Gondwana Research

journal homepage: www.elsevier.com/locate/gr

Terrestrial ecosystems on North Gondwana following the end-Permian mass extinction

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ARTICLE INFO

Article history:
Received 27 October 2010
Received in revised form 21 January 2011
Accepted 25 January 2011
Available online 2 March 2011

Handling Editor: R.D. Nance

Keywords:
Early Triassic
Terrestrial ecosystems
Palynology
Pakistan

ABSTRACT

The impact of the end-Permian mass extinction on terrestrial ecosystems is still highly controversial. Here, new high-resolution palynological data from biostratigraphically well-dated Upper Permian to Middle Triassic successions of the Salt Range and Surghar Range (Pakistan) are presented. Our results reveal seven successive floral phases between the Late Permian and the Middle Triassic. At the onset of the Mesozoic, the flora is characterised by high abundances of lycopods associated with pteridosperms and conifers. This association prevails up to the middle Smithian and is followed by a prominent spore spike similar to the global spore spike reported from the Permian–Triassic boundary. Like that of the end-Permian, the middle Smithian spore spike is associated with a negative isotope excursion and is succeeded by a major marine faunal extinction event in the late Smithian. The recurrent patterns observed at the Permian–Triassic boundary and in the middle–upper Smithian suggest a common cause such as massive ejections of volcanic gases. The increasing abundance of conifers still associated with common lycopods in the Spathian suggests fading volcanically induced environmental perturbations and stabilisation of terrestrial ecosystems ca. 2.1 My after the end-Permian event.

1. Introduction

The end-Permian mass extinction about 252 My ago was the largest crisis in the Phanerozoic history of marine life. However, the impact of this event on terrestrial plant communities is still debated and views about the magnitude of the deterioration of terrestrial ecosystems are strongly diverging. Interpretations range from virtually no effects on terrestrial plants (e. g. Knoll, 1984; McElwain and Punyasena, 2007; Xiong and Wang, 2011) to an almost complete devastation of terrestrial ecosystems (e. g. Utting et al., 2004; Visscher et al., 1996). The first hypothesis points to a long-term (25 My) gradual floristic transition across the Permian–Triassic boundary reflected in the fossil record by a gradual change from palaeophytic floras to mesophytic floras without evidence for a major plant biomass decay (Knoll, 1984). Long-term floristic turnover has been documented in the macrofossil data from the South African Karoo Basin. There, the diversity of woody vegetation is already decreasing at the transition from the middle to the Late Permian. The succession of the Upper Permian to Middle Triassic assemblages is marked by unchanged diversity and replacement of the glossopterids by other plant groups (cycads, benettitaleans, ginkgos and other seed ferns, Bamford, 2004). This does not preclude significant short-term changes in ecosystems during the Palaeozoic–Mesozoic transition. Opposing scenarios rely on the so-called fungal event (Visscher et al., 1996), advocating instead the total collapse of terrestrial ecosystems after the end-Permian mass extinction. Some authors even attribute most of the Lower Triassic palynofloral records to reworking (Utting et al., 2004). To assess whether or not these short-term changes affected the functionality of the ecosystem, it is essential to incorporate abundance data and dominance structures of plant communities rather than relying solely on total biodiversity data (McElwain and Punyasena, 2007).

The significance of palynofloral records on the reconstruction of terrestrial ecosystem responses to mass extinction has received major attention over the last decade (e. g. Hochuli et al., 2010b; Looy et al., 1999, 2001; McLoughlin et al., 1997). Reviews of floral records have revealed that faunal mass extinctions are commonly associated with instabilities of terrestrial ecosystems (McElwain and Punyasena, 2007). The onsets of these instabilities are often marked by a short interval during which pteridophytes dominate terrestrial plant assemblages. The fern spike at the Cretaceous–Palaeogene boundary is assumed to represent the devastation of vegetation caused by the climatic and atmospheric perturbations of the impact event at this boundary (Vajda et al., 2001). High abundances of fern spores are also reported from the Triassic–Jurassic boundary (van de Schootbrugge et al., 2009). Pioneering studies documenting ecological perturbation

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doi:10.1016/j.gr.2011.01.008

around the Permian–Triassic boundary and in the Early Triassic have been published by Looy et al. (1999, 2001). They documented a spore peak close to the end-Permian extinction event in sections from Jameson Land in East Greenland and suggested a great loss of plant diversity from their data. Furthermore, they inferred that the recovery of plant communities took 4–5 My.

The aforementioned floral changes (spore spike) observed in the palynological records have been interpreted as responses of terrestrial ecosystems to palaeoenvironmental perturbations. For the Triassic–Jurassic spore spike, Bonis et al. (2010) demonstrated that the high abundances of spores are related to climatic changes. Recent publications of Hochuli et al. (2010a,b), and Lindström and McLoughlin (2007) also showed that the palynological turnover near the Permian–Triassic boundary is associated with changes in humidity. The striking recurrent patterns of high spore abundances, large perturbations of the global C-cycle and faunal mass extinctions suggest major and geologically rapid climatic changes affecting both marine and terrestrial biotas. The ultimate causes that triggered these global changes still need to be determined.

During Late Permian and Triassic times, Gondwana provided a stable plate configuration of southern hemisphere continents that had been established in the late Proterozoic and continued to exist until the Early Cretaceous (Comin-Chiaramonti et al., 2010; Meert and Lieberman, 2008; Renne et al., 1992). Despite the stable configuration of landmasses, physical environmental conditions fluctuated through time (Veevers, 2006) and environmental changes determined the Triassic vegetation history on Gondwana (Spalletti et al., 2003).

Here we present the composite palynological record from Nammal, Chhidru, Chitta-Landu, and Narmia in the Salt Range and Surghar Range in Pakistan (Fig. 1), spanning the latest Permian to early Middle Triassic time interval. The palynological assemblages record floral turnovers, which reflect profound changes in the composition of the terrestrial plant community on the northern margin of Gondwana bordering tropical Tethys. The detailed ammonoid age control of the studied sections allows precise dating of the floral events (Brühwiler et al., in press, 2010). Our data provide detailed insights into terrestrial ecosystem turnovers associated with the environmental changes during the Palaeozoic–Mesozoic transition.

2. Methods

Samples were preferentially taken from the fine-grained siliciclastic intervals of the sections at Nammal, Chhidru, Chitta-Landu and Narmia. Siltstones and, in a few cases, limestone and fine-grained sandstone were sampled. The samples were crushed and weighed (5–25 g) and subsequently treated with hydrochloric and hydrofluoric acid according to standard palynological preparation techniques. A short oxidation with nitric acid was performed before the residues were sieved over an 11 µm mesh screen. From strew mounts a minimum of 300 spores and pollen per sample were counted. In a few samples with high amorphous organic matter contents, low sporomorph concentration or poor preservation, the intended 300 sporomorph counts could not be reached.

3. The palynological record and its significance

The excellently preserved organic walled microfossils from the Nammal, Chhidru, Chitta-Landu and Narmia gorges in the Salt Range and Surghar Range allowed a detailed succession of palynological assemblages to be established for the first time. The assemblages

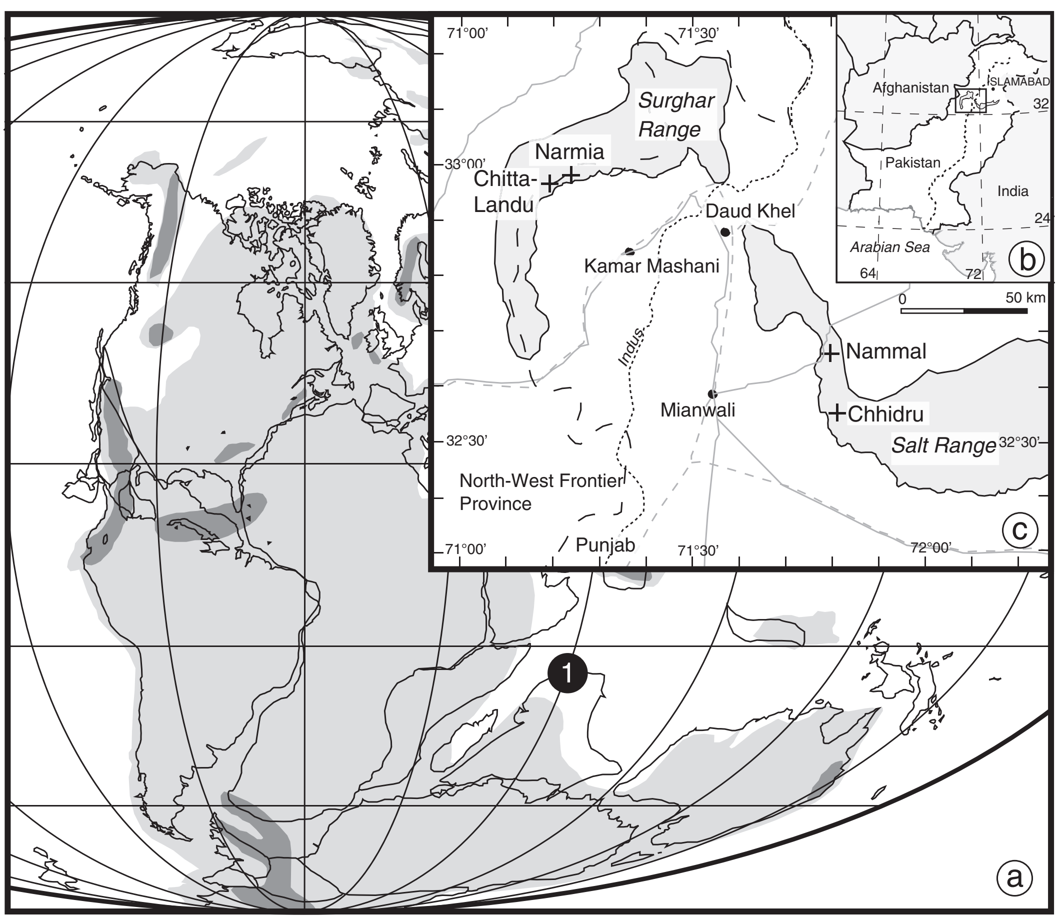

Fig. 1. Location of the studied sites. a) Early Triassic palaeogeographic position of the Salt Range and the Surghar Range in Pakistan after Smith et al. (1994) and Golonka and Ford (2000), b) location of the Salt Range and Surghar Range in Pakistan, and c) location of Nammal, Chhidru, Chitta-Landu, and Narmia gorges.