



Rapid demise and recovery of plant ecosystems across the end-Permian extinction event[☆]

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ABSTRACT

The end-Permian extinction event was the most pronounced biotic and ecological crisis in the history of the Earth. It is assumed that over 80% of marine genera disappeared, and that this event had a major impact on the evolution of marine organisms. The impact of this event on terrestrial biota is poorly known and a matter of controversial discussions. In contrast to the fundamental changes in marine fauna most major groups of plants range from the Late Palaeozoic into the Mesozoic. Consequently the impact of the end-Permian extinction event on the evolution of plants was often regarded as minor. However, major changes in the composition of the plant communities have been documented and a number of catastrophic scenarios have been envisioned – including the almost total destruction of plant ecosystems.

Based on expanded sections from the Southern Barents Sea (Northern Norway) we trace mid-latitude terrestrial ecosystems across the Permo–Triassic transition with a time resolution in the order of 10 kyr, based on a high resolution C_{org} -isotope stratigraphy. Our results show that the floral turnovers are linked with major changes in the C-isotope record and hence with global carbon cycling. The palynological records document the successive steps in the evolution of terrestrial ecosystems. After gradual changes during the latest Permian, plant ecosystems suffered from a major environmental perturbation leading to a rapid turnover from gymnosperm dominated ecosystems to assemblages dominated by lycopods. The dominance of the lycopods, expressed in a spore-spike, represents a relatively short-lived event in the order of 10 kyr. This perturbation of the terrestrial ecosystems preceded the globally recognized negative $\delta^{13}C_{org}$ isotope spike by up to 100 kyr. It coincides with a first end-Permian negative shift of the C-isotope curve and was probably induced by a first major perturbation of the chemistry of the atmosphere, related to the onset of the volcanic activity of the Siberian Traps. Gymnosperms recovered prior to the major isotopic shift. The fast recovery of terrestrial ecosystem explains why all major plant groups survived the end-Permian extinction event while the majority of marine organisms were wiped out.

The concordance of pattern of the $\delta^{13}C_{org}$ in globally distributed marine and terrestrial sequences enables us to link turnovers in the terrestrial environment with marine extinction events. It demonstrates that the demise and the onset of the recovery of the terrestrial ecosystems was a global phenomenon and occurred prior to the major isotopic shift. The successive negative shifts in $\delta^{13}C_{org}$ isotope values are thought to reflect CO_2 input into the atmosphere by multiphase volcanic activity (Siberian Traps) or other consecutive events (e.g. methane release).

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[☆] P.A.H. designed the project together with H.B and wrote the paper. P.A.H. studied the palynology and palynofacies of the cores together with E.H. and J.O.V. The isotopes were measured by E.H who also analysed the data together with H.W. All authors discussed the results and implications and commented on the manuscript at all stages.

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1. Introduction

In contrast to the fundamental changes in marine faunas (Brayard et al., 2009; Erwin, 1993; MacLeod, 2003) the major plant groups range from the Late Palaeozoic into the Mesozoic. Consequently the impact of the end-Permian extinction event (e-PEE) on terrestrial ecosystems was often regarded as minor. However, major changes in the composition of plant communities have been documented and apocalyptic scenarios have been drawn (Retallack, 1999).

Since most previous palynological studies focused on biostratigraphy and the qualitative distribution of taxa detailed quantitative

data from stratigraphically controlled sections are rare. So far for the Northern hemisphere most of our perceptions of floral changes around the e-PEE were based upon condensed sections with an inherent strong preservational bias (Looy et al., 1999; Ouyang and Utting, 1990; Visscher and Brugman, 1986; Zhang et al., 2007). Compared to the relatively high diversity in the expanded sections of higher latitudes the extremely low diversity recorded in central and north-western European assemblages (Kürschner and Hergreen, 2010) is most probably another expression of this bias. Accordingly the e-PEE is supposed to have induced a heavy loss in plant diversity and the replacement of Late Palaeozoic plant assemblages dominated by woody gymnosperms by assemblages with prevailing herbaceous lycopods. Some authors even assumed an almost complete devastation of terrestrial ecosystems and interpreted most palynomorphs occurring in Early Triassic sediments as reworked from older sections, implying an evolutionary renewal as in marine ecosystems (Utting et al., 2004). Many sections covering the e-PEE are characterized by the abundance of the enigmatic palynomorph genus *Reduviasporonites* spp., which is considered by some authors of fungal (Eshet et al., 1995; Visscher et al., 1996) and by others of algal origin (Foster et al., 2002). This feature, termed “fungal event”, was interpreted to reflect the excessive dieback of the gymnosperm dominated ecosystems leading to their devastation and to proliferation of herbaceous lycopods (Eshet et al., 1995; Visscher et al., 1996). The detailed records from the expanded sections from the Barents Sea, the Norwegian Sea and Greenland (Hochuli et al., 2010; Looy et al., 2001; Mangerud, 1994) show sporadic occurrences of *Reduviasporonites* spp. without any obvious link to the observed environmental and ecological changes. The data suggest that high abundances of *Reduviasporonites* spp. and the concomitant abundance of carbonized

terrestrial plant debris (Eshet et al., 1995) are probably due to preferential preservation of this thick-walled palynomorph.

The most plausible evidence for massive environmental stress acting on plants around the e-PEE is the regular presence of unseparated spore tetrads (Visscher et al., 2004). The global occurrence of these tetrads has been explained by genetic damage of the spore-producing plants caused by increased radiation of UV-light possibly induced by the release of halocarbons or other pollutants into the atmosphere (Beerling, 2007; Visscher et al., 2004).

Some authors presume that plant ecosystems suffered from a major diversity loss and did not recover from the e-PEE until the onset of the Middle Triassic implying a recovery phase of about four million years (Looy et al., 1999; McElwain and Punyasena, 2007). Detailed studies of several expanded sections show that the loss of Palaeozoic taxa is counterbalanced by newly appearing species in the Early Triassic and that diversity increases (De Jersey, 1979; Hochuli et al., 2010; Lindström and McLoughlin, 2007; Mangerud, 1994). Here we present the results of an investigation comprising the spore–pollen and stable C-isotopes of organic matter from two extended sections from Northern Norway (Fig. 1) covering the interval around the e-PEE. These high resolution data show the direct link between changes in global carbon cycling and multiple floral turnovers including the impact of the catastrophic end-Permian event affecting the terrestrial ecosystems.

2. Stratigraphic terminology

In order to avoid terminological confusion the chronostratigraphic concept applied in this paper is shown in Fig. 2. Here we use the terms Late Permian and Griesbachian in the sense of Tozer (1994) based on

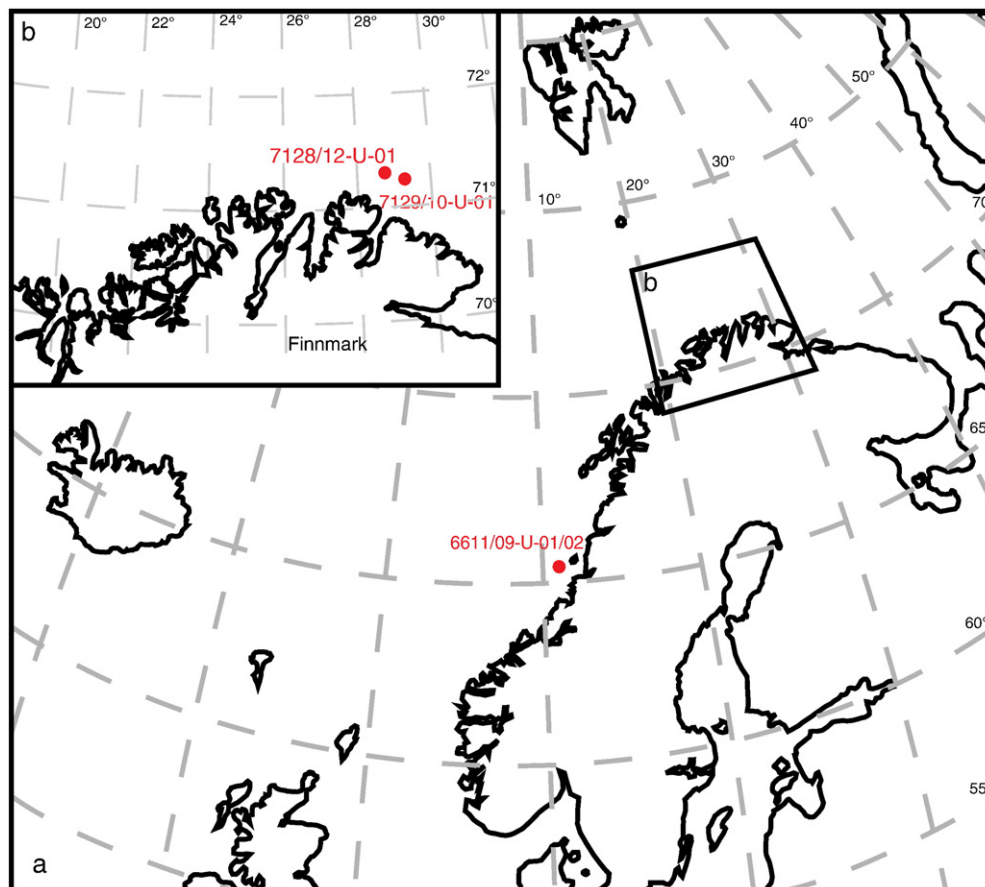


Fig. 1. Location of core holes 7128/12-U-01 and 7129/10-U-01 on the Finnmark Platform, Southern Barents Sea (Norway) and the shallow cores 6611/09-U-01 and 6611/09-U-02 on the Trøndelag Platform offshore mid-Norway.

| Age / Chronostratigraphy (GSSP) | | Original subdivision (Tozer, 1994) | | Event stratigraphy |
|---------------------------------|-----------|------------------------------------|--------------|--|
| Early Triassic | Olenekian | | Smithian | ← 251.2 ± 0.2 ^{c)} |
| | Induan | | Dienerian | |
| Late Permian | Lopingian | Changhsingian | Griesbachian | ↑ FAD <i>H. parvus</i> ~252.5 ± 0.3 ^{a,b)} |
| | | Wuchiapingian | | ← PT-boundary event 252.6 ± 0.2 ^{a)} |
| | | | | |

Fig. 2. Stratigraphic terminology: chronostratigraphic subdivision of the Late Permian and the Early Triassic with radiometric ages (not to scale), expressing the different views on the position of the Permian/Triassic boundary including the concept of the Griesbachian substage and the biostratigraphy events applied in this study. The U/Pb ages are taken from the following sources: a) Mundil et al. (2001), b) Mundil et al. (2004) and c) Galfetti et al. (2007b). The inferred age range of the studied cores is marked with a vertical line. Correlation between the boreal sections and the Tethyan GSSP section has been discussed by Twichett et al. (2001) and Bjerager et al. (2006).

ammonoid biostratigraphy. Presently the Permian–Triassic boundary (PTB) is defined by the first appearance datum (FAD) of the conodont species *Hindeodus parvus* in the condensed global stratotype section and point (GSSP) of Meishan, South China (Yin et al., 2001). This biostratigraphic event considerably postdates the negative C-isotope spike and a series of marine extinction events traditionally associated with the PTB. According to the present definition of the boundary (GSSP) all the extinction events, which can be differentiated based on the high resolution chemostratigraphic $\delta^{13}\text{C}$ isotopic records, fall into the Late Permian (Changhsingian) (Hermann et al., 2010-this volume and references therein). Confusions with the occurrence and the range of *H. parvus* have been shirked by the introduction of new species such as *H. praeparvus* and *H. postparvus* (Korte et al., 2010) whereas other authors showed the diachronicity of this event (Hermann et al., 2010-this volume; Shevyrev, 2006).

3. Material and methods

Two cores, 7129/10-U-01 and 7128/12-U-01, have been drilled on the Finnmark Platform, offshore Northern Norway (Fig. 1) for the mapping program of IKU (today SINTEF Petroleum Research, Trondheim, Norway). For this study we sampled in detail the Late Permian and the Griesbachian part of the two cores and focused on lithologies suited for palynological studies (e.g. marls, clay- and siltstones).

38 samples have been collected from core 7128/12-U-01, and 7 from core 7129/10-U-01. All of them have been processed with standard palynological method (e.g. Traverse, 2007). Most of the samples yielded well preserved palynomorph assemblages. For the palynofacies analysis we counted a minimum of 350 (350–1550) organic particles. The quantitative palynological analysis has been carried out on the slightly oxidized residue. For the palynological study a minimum of 300 (304–490) palynomorphs has been counted for each sample. The critical interval showing the floral turnover between the Late Permian and the lowermost Griesbachian is represented in both cores.

For the $\delta^{13}\text{C}$ analysis the core samples have been ground and treated with 3 N HCl for at least 24 h to remove all carbonates. The residue was homogenised and analysed with a ThermoFisher Flash-EA1112 elemental analyser coupled with a ConFlo IV interface to a

ThermoFisher Delta V isotope ratio mass spectrometer (IRMS). The system was calibrated with NBS22 ($\delta^{13}\text{C} = -30.03$) and IAEA CH-6 ($\delta^{13}\text{C} = -10.46$). Reproducibility of the measurements is better than $\pm 0.15\%$. The carbon-isotope ratios are expressed in the standard δ notation in per mil (‰) relative to the international VPDB isotope standard.

4. Palaeogeography and geological setting

For the Late Permian and the Early Triassic interval the two drill sites represented a mid-latitude (~45°N) palaeogeographic position (Larssen et al., 2005). They were located north of an extended landmass that shed siliciclastic material into the subsiding basin (Larssen et al., 2005). The sections are marked by a prominent change in lithology from the Late Permian limestone and chert dominated Isbjørn Formation to the Griesbachian siliciclastic sequence of the Røye Formation. The cores are biostratigraphically and chemostratigraphically dated (Mangerud, 1994; Hermann et al., 2010-this volume.); they cover the Late Permian (Changhsingian) interval immediately below the Permian–Triassic boundary (PTB), in the sense of the GSSP definition (Yin et al., 2001; see Fig. 2). The $\delta^{13}\text{C}_{\text{org}}$ isotope record shows a stepwise decrease of values to the characteristic minimum (negative spike) prior to the PTB (sensu GSSP). The essentially gradual changes in the isotope records suggest nearly continuous sedimentation.

The geological setting and the lithological succession of these sections have been described in several papers (Bugge et al., 1995; Larssen et al., 2005; Mangerud, 1994). The core holes have been drilled at a distance of about 1.5 km. According to seismic data and the lithological succession (Figs. 2 and 5 in Mangerud, 1994) core 7128/12-U-01 represents a more distal position and compared to core 7129/10-U-01 comprises a more complete section.

The Permian part of the section is marked by a predominance of carbonate deposition in a shallow to outer shelf depositional environments. In the present study only the upper part of the Permian section is considered. Based on palynology a Late Permian (Kazanian–?Tatarian–Wuchiapingian–Changhsingian (in updated terminology)) age has been assigned to it (Mangerud, 1994). In core 7129/10-U-01 the top of the carbonates is marked by a phosphoritic

layer, which coincides with a gamma ray peak that can be correlated with a corresponding peak in the unrecovered interval of core 7128/12-U-01. The phosphoritic layer is overlain by a brownish coloured conglomeratic bed characterizing the base of the Griesbachian section (Bugge et al., 1995). Palynological assemblages from this layer show peak abundances of acritarchs, which probably reflects the base Griesbachian transgression. The lithological interpretation of Larsen et al. (2005) implies that the uppermost Permian (Ørret Formation) is missing from the two cores. However, the consistently decreasing $\delta^{13}\text{C}$ curves suggest that only a minor hiatus exists at this level (Figs. 3 and 4).

The Griesbachian represents a siliciclastic unit consisting of bioturbated sandstones and siltstones, deposited in several fining upwards cycles. Coarse wood and other plant debris are common in the sandstones. The depositional environment has been interpreted as shallow storm influenced shelf (Bugge et al., 1995). The palynological data from this unit (Mangerud, 1994) indicate an early Griesbachian age, thus confirming ammonoid data from coeval sections from Svalbard and Greenland (Bjerager et al., 2006; Tozer and Parker, 1968; Korchinskaya, 1986). Mangerud (1994) differentiated three palynological zones assigning the Late Permian assemblages to the

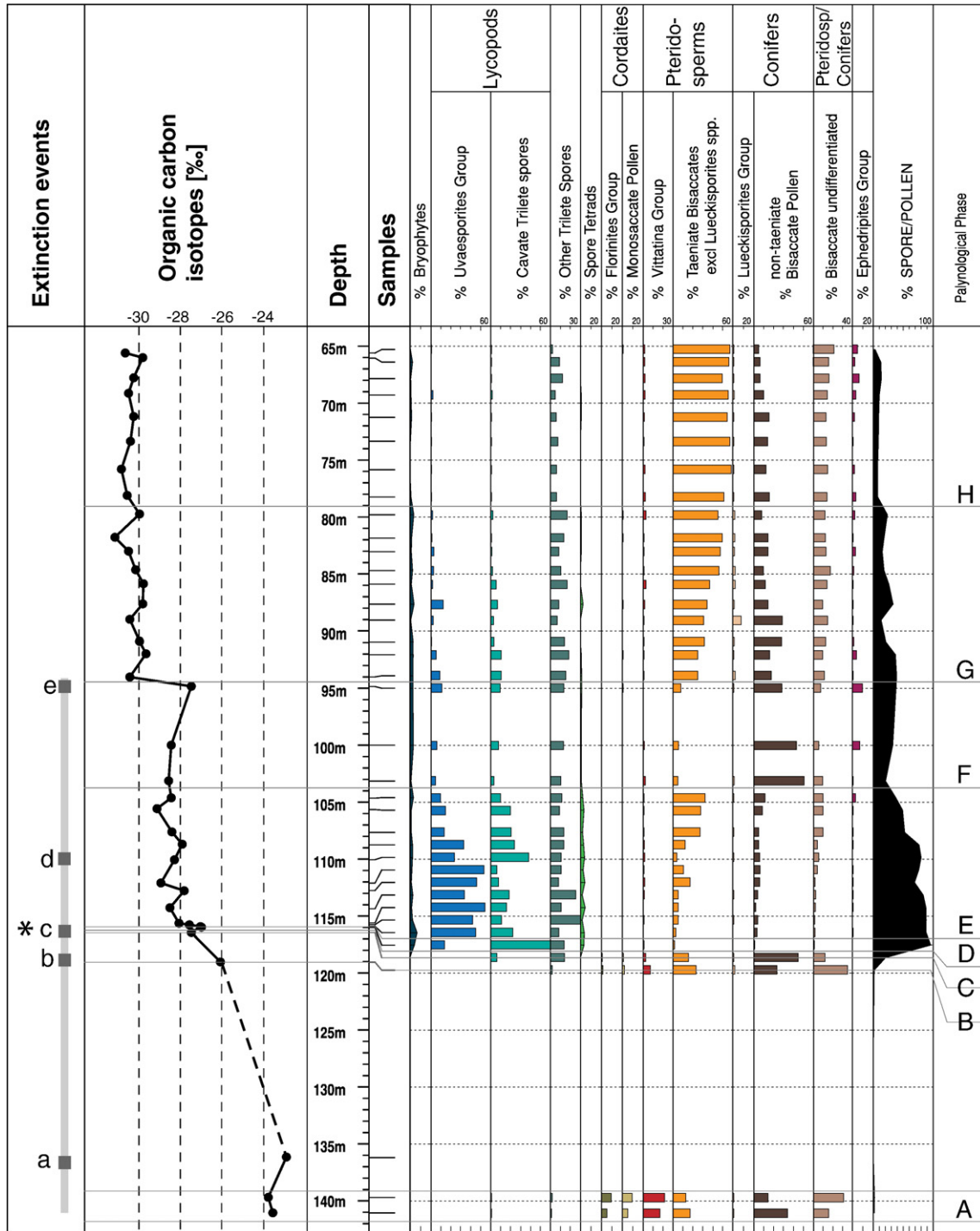


Fig. 3. $\delta^{13}\text{C}_{\text{org}}$ isotope and palynological records of core 7128/12-U-01 with published extinction events of the marine realm: a) E-Greenland (Twitchett et al., 2001); b) Iran (Heydari et al., 2008); c/d) E-Greenland (Stemmerik et al., 2001); e) Meishan, China (Jin et al., 2000), Gartnerkofel, Austria (Holser et al., 1989); Canada, Buchanan Lake, (Grasby and Beauchamp, 2008); and * extinction of glossopterids on Gondwana (Morante, 1996).

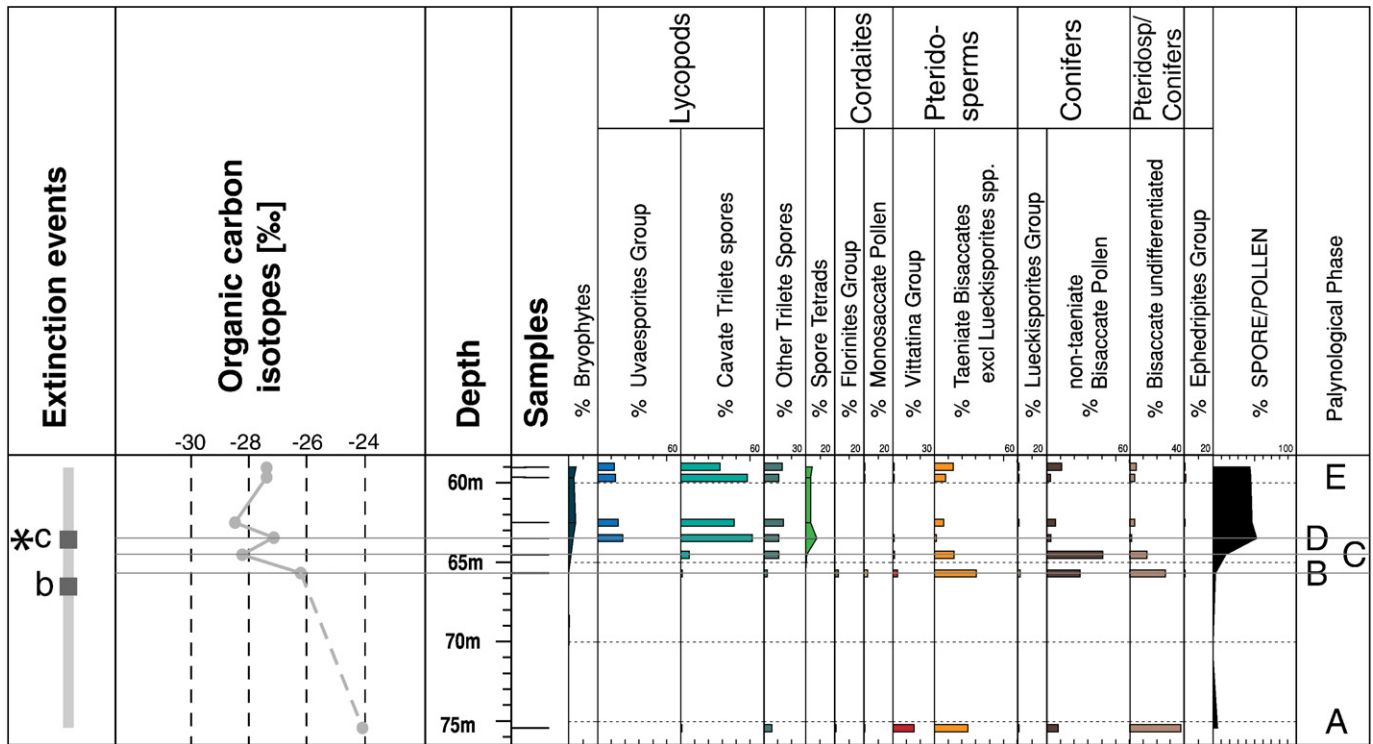


Fig. 4. $\delta^{13}\text{C}_{\text{org}}$ isotope and palynological records of core 7129/10-U-01 with published extinction events of the marine realm: b) Iran (Heydari et al., 2008); c) E-Greenland (Stemmerik et al., 2001); and * extinction of glossopterids (Morante, 1996).

Dyupetalum sp.-*Hamiapollenites bullaeformis* assemblage zone and to the *Scutasporites* sp. cf. *S. unicus*-*Lunatisporites* sp. concurrent range zone and those of the Griesbachian part of the section to the *Lundbladispora obsoleta*-*Tympanicysta stoschiana* assemblage zone.

Additional information including core photos can be found under:

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doi:10.1594/GFZ.SDDB.7129-10u01-01

5. Results

5.1. Palynofacies and C-isotope chemostratigraphy

In most samples the particulate organic matter is strongly dominated by terrestrial OM. Kerogen of marine origin is represented by the rare but continuous presence of acritarchs and a few prasinophycean algae (Figs. 5 and 6). An exception is found in the assemblage with abundant occurrence of acritarchs in lowermost part of the Griesbachian. In core 7128/12-U-01 this feature is restricted to a single sample; in 7129/10-U-01 the initial abundance is fading out in two subsequent samples. No amorphous organic matter (AOM) has been observed. The kerogen assemblages reflect well oxygenated depositional environments throughout the sections without any sign of oxygen deficient conditions. The consistent dominance of terrestrial organic matter precludes major impact on the isotopic composition of the organic matter ($\delta^{13}\text{C}_{\text{org}}$), therefore the $\delta^{13}\text{C}_{\text{org}}$ record reflects real changes and therefore major perturbations in the global carbon cycle.

The high resolution $\delta^{13}\text{C}_{\text{org}}$ record in the studied extended sections of the Finnmark platform reveals a stepwise decrease of C-isotope values between the Late Permian and the lowermost part of the Griesbachian. In most published sections the extinction event(s) affecting the marine realm are linked with a sharp negative $\delta^{13}\text{C}$ isotope shift (Grasby and Beauchamp, 2008; Jin et al., 2000; Krull et al., 2004). In the Finnmark

cores as in other expanded sections the negative C-isotope shift is spread to a stepwise decrease with more stable phases separating the individual steps. In the Meishan (GSSP) section (Jin et al., 2000) the corresponding isotopic shifts take place within an interval of about 30.0 cm, while it comprises a 75 m thick sequence in core 7128/12-U-01. This distinct pattern (Fig. 7, and Hermann et al., 2010-this volume) allows for precise correlations between globally distributed records (e.g. Canada (Grasby, and Beauchamp, 2008), E-Greenland (Looy et al., 2001; Stemmerik et al., 2001; Twitchett et al., 2001), Austria (Holser et al., 1989), Iran (Heydari et al., 2008), Australia (Morante, 1996), and China (Krull et al., 2004)); some of them include well calibrated faunal extinction events.

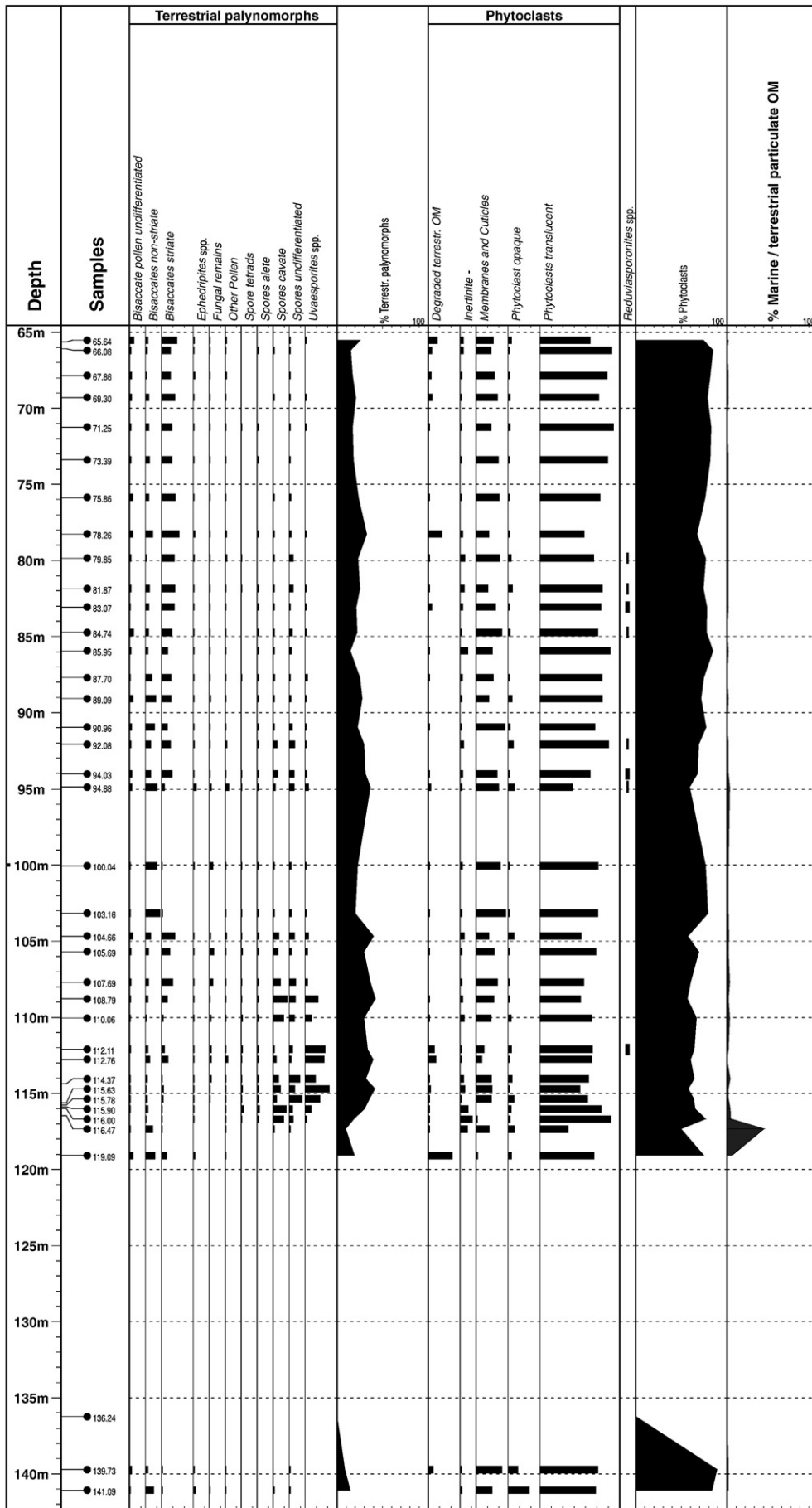
5.2. Floral succession

In the palynological record (Figs. 3 and 4 and Table 1: list of floral elements) we differentiate eight spore-pollen assemblages. In core 7129/10-U-01 only the lower five are preserved. The match of our palynological results with records from E-Greenland (see later discussion) proves that the observed breaks in the assemblages reflect real floral turnovers which occur independently from changes in the depositional environment. This is also confirmed by the homogeneous composition of palynofacies throughout the sections (Figs. 5 and 6).

5.2.1. Floral succession of the Late Permian

The Late Permian assemblages (phase A) reveal an overwhelming dominance of gymnosperm pollen. They are composed of pteridosperms (*Vittatina* group and taeniate bisaccate pollen) and conifer pollen (non-taeniate pollen and *Lueckisporites* spp.). Subordinate elements are Cordaites (*Florinites* spp. and monosaccate pollen) and rare pteridophytes, essentially ferns. *Vittatina*, *Lueckisporites* spp. and the representatives of the Cordaites are generally considered typical Permian

Fig. 5. Palynofacies of core 7128/12-U-01: quantitative distribution of particulate organic matter (terrestrial palynomorphs, and phytoclasts) and *Reduviasporonites* spp. (semi-quantitative) together with the ratio of marine (black) to terrestrial (white) organic particles.



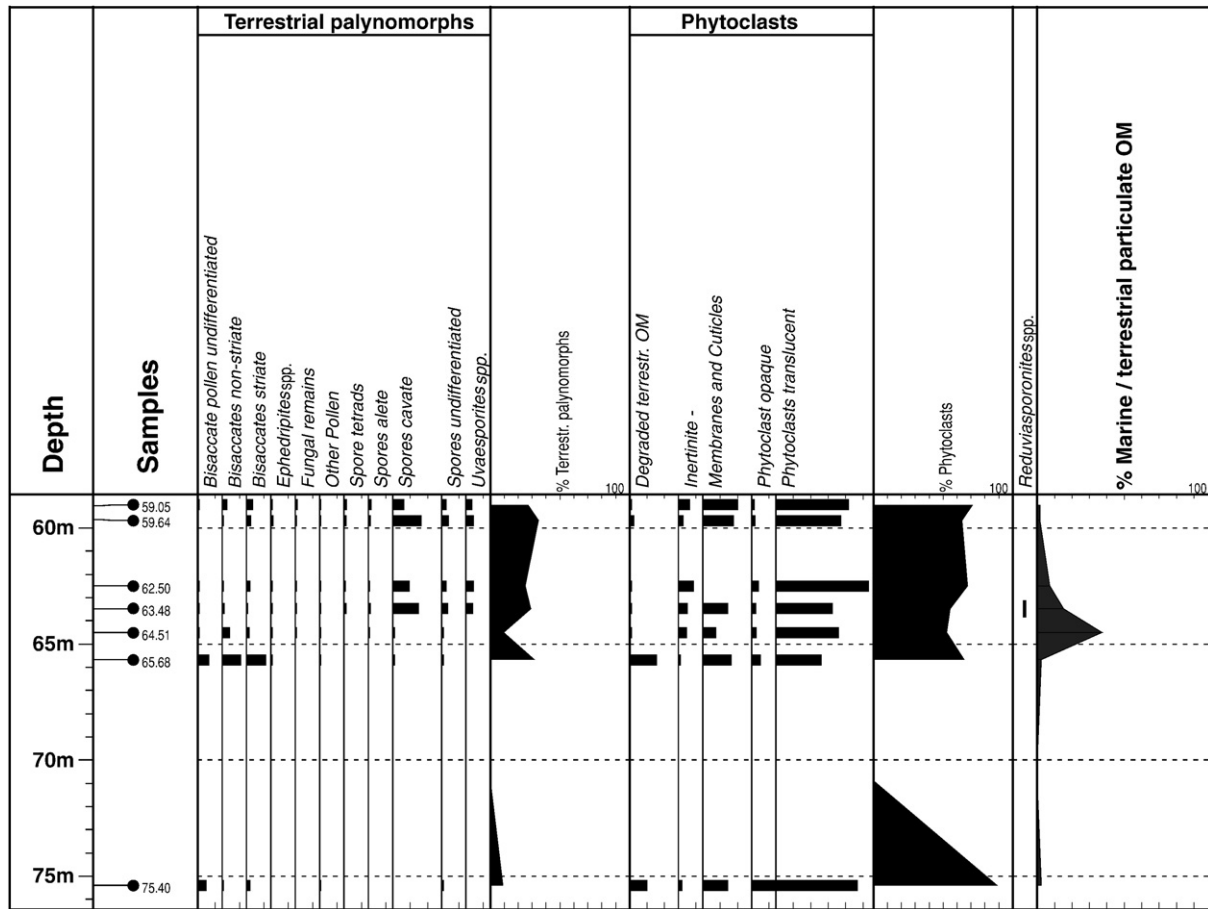


Fig. 6. Palynofacies of core 7129/10-U-01: quantitative distribution of particulate organic matter (terrestrial palynomorphs, and phytoclasts) and *Reduviasporonites* spp. (semi-quantitative) together with the ratio of marine (black) to terrestrial (white) organic particles.

elements. The interval covered by phase A is characterized by stable $\delta^{13}\text{C}_{\text{org}}$ values around -22% . Due to a recovery gap in core 7128/12-U-01 and the lack of sediments sufficiently rich in organic matter in core 7129/10-U-01 our record is intermittent in phase A. According to Mangerud (1994) it corresponds to the *Dyupetalum* sp.-*Hamiapollenites bullaeformis* assemblage zone. The assemblage from the uppermost samples of the Late Permian (phase B), represented by one sample in both cores, reflects the demise of *Vittatina* spp. and of *Florinites* spp. Pteridosperms, other than *Vittatina*, and conifers are more common. Non-cavate trilete spores (ferns) are still rare; cavate forms (lycopsids) are absent. Together with the two overlying phases (C/D) this interval falls within the first negative $\delta^{13}\text{C}_{\text{org}}$ shift towards values around -28% . Phase B falls within the *Scutasporites* sp. cf. *S. unicus-Lunatisporites* sp. concurrent range zone (Mangerud, 1994).

5.2.2. Floral succession of the basal Griesbachian

Separated from the underlying interval by a lithological break the samples of the basal Griesbachian are characterized by overabundant marine acritarchs (Figs. 5 and 6) reflecting the basal Triassic transgression. The terrestrial assemblages (phase C) are distinguished by abundant conifers and in contrast to the underlying intervals by the appearance of rare lycopod and fern spores, as well as by a further decrease of *Vittatina* spp. and the disappearance of *Florinites* spp. The following phase (D) marks the most pronounced turnaround of the sequence. The representation of gymnosperms drops to the lowest level; they are replaced by the proliferating lycopod spores with *Uvaesporites* spp. as a new and common element. With the onset of this phase appear spore tetrads and bryophyte spores. The following phase E is characterized by a peak abundance of lycopod spores including the acme of the *Uvaesporites* group. The abundance of

gymnosperm pollen (pteridosperms, conifers and *Ephedripites* spp.) being strongly reduced in the lower part of this interval gradually increases, marking a gradual change of the flora and the first step of the recovery of these plants. Within this interval and the following phase F $\delta^{13}\text{C}_{\text{org}}$ values stabilize around -28% . A further decrease of the lycopod spores and a strong increase of conifer pollen characterizes phase F. Here pteridosperms are relatively uncommon; whereas the frequency of fern and bryophyte spores remains essentially unchanged. The significant $\delta^{13}\text{C}_{\text{org}}$ drop to values around -30% coincides with the limit between phases F and G; subsequently the values stabilize. With increasing percentages of pteridosperms, and a general decrease of conifers and lycopods phase G represents a transitional assemblage between phases F and H. Phase H is marked by a pronounced dominance of pteridosperms. During this phase bryophytes and pteridophytes become rare.

An extended floral record of Griesbachian age is known from the Trøndelag Platform offshore mid-Norway from the shallow cores 6611/09-U-01 and 6611/09-U-02 (Hochuli et al., 2010). According to the chemostratigraphic correlation (Hermann et al., 2010-this volume) the lower part of core 6611/09-U-01 overlaps with the upper part of core 7128/12-U-01. The interval between the upper part of Phase E up to the top of Phase H of the latter core corresponds to phase II in core 6611/09-U-01. In this core the distribution of floral elements shows little variation and the assemblages are characterized by a dominance of pollen, however with a considerable percentage of spores (average 40%). Probably due to the semi-quantitative approach used in this record the floral changes are less pronounced. However, the cavate spores (lycopsids) show a distinct decrease during this interval, while gymnosperms (pteridosperms, conifers and *Ephedripites* spp.) dominate the assemblages. Diversity remains quite stable

Table 1

List of floral elements: spore–pollen groups applied in this paper with corresponding botanical affinity essentially based on the compilation of Balme (1995).

| Floral elements | Taxa included | Affinity | Remarks |
|---|---|---|---|
| Bryophytes | <i>Maculatasporites</i> spp. <i>Propriisporites</i> spp. "Apiculatisporis" <i>lanjouwii</i> Alete spores | Bryophytes | |
| <i>Uvaesporites</i> group | <i>Uvaesporites</i> spp., <i>U. imperialis</i> <i>U. cf. imperialis</i> | Lycopsids | Group with variable morphology |
| Cavate spores | <i>Densoisporites</i> spp., <i>Kraeuselisporites</i> spp., <i>Endosporites</i> spp., <i>Lundbladispota</i> spp. | Lycopsids | |
| Other trilete spores | <i>Leiotriletes</i> spp., <i>Apiculatisporites</i> spp., <i>Converrucosisporites</i> spp., <i>Verrucosisporites</i> spp., <i>Calamospora</i> spp. | Mostly Filicales (ferns), but probably also including some additional Lycopsids | |
| Spore tetrads | This group includes unseparated tetrads of several of the above mentioned genera (mostly lycopsids) | Equisetopsids Lycopsids and Filicales | |
| <i>Florinites</i> group | <i>Florinites</i> spp. | Cordaites | |
| Monosaccate pollen | Undifferentiated monosaccate pollen <i>Cordaitina</i> spp. <i>Grebespora</i> spp. | Cordaites and some forms of uncertain botanical affinity | |
| <i>Vittatina</i> group | <i>Vittatina</i> spp. <i>Weylandites</i> spp. | Pteridosperms (Peltaspermales) | Diverse group in the Late Permian; regarded here as in place also in the Griesbachian. |
| Taeniate bisaccate pollen (exc. <i>Lueckisporites</i>) | <i>Lunatisporites</i> spp., <i>Protohaploxylinus</i> spp., <i>Striatoabieites</i> spp., <i>Striatopodocarpites</i> spp. | Pteridosperms | |
| <i>Lueckisporites</i> group | <i>Lueckisporites</i> spp. <i>L. virkkia</i> | Conifers | Generally considered as restricted to the Late Permian; regarded here as in place also in the Griesbachian. |
| Non-taeniate bisaccate pollen | <i>Alisporites</i> spp., <i>Klausipollenites</i> spp., <i>Scutasporites</i> spp., <i>Limitisporites</i> spp., <i>Platysaccus</i> spp. | Mostly conifers, <i>Alisporites</i> have also been produced by pteridosperms (Peltaspermales) | |
| Undifferentiated bisaccate pollen | | Pteridosperms or conifers | Undeterminable bisaccate pollen, due to their preservation or orientation in the slide. |
| <i>Ephedripites</i> group | <i>Ephedripites</i> spp. | Gnetales | |

over this interval (Fig. 2 in Hochuli et al., 2010). The subsequent floral record, extending over another 300 m shows distinct variations in the hygrophyte/xerophyte ratio or the spore/pollen ratio, respectively. The phases D–H correspond to the *Lundbladispota obsoleta*–*Tympanicysta stoschiana* assemblage zone.

The duration of the Griesbachian and the Dienerian substages is estimated at 1.4 ± 0.4 myr (see Fig. 2). Within the Griesbachian the FAD of *H. parvus* is estimated to occur at about -252.5 ± 0.3 . Hence the Griesbachian part of the studied section has an estimated duration in the order of 100 kyr. Hence, we estimate that the main floral turnover – between the floral phases C and E – which is documented to occur in an interval of less than 2 m in both cores took place within a time span in the order of 10 kyr.

6. Discussion

6.1. Coeval floral records

Based on the correlation of the $\delta^{13}\text{C}_{\text{org}}$ isotope high resolution records we are able to compare coeval floral patterns on a global scale. Our data concur with the data from Late Permian/basal Griesbachian outcrop sections in E-Greenland (Stemmerik et al., 2001). The succession from the Schuchert Dal Formation of Jameson Land (Stemmerik et al., 2001) shows the same stepwise decrease of the $\delta^{13}\text{C}_{\text{org}}$ isotopes (Fig. 7) and the palynomorph assemblages are also

characterized by a strong reduction of the *Vittatina* group leading to a bisaccate dominated assemblage with increased diversity of pteridophytes. The following sudden increase in pteridophyte abundance (spore peak) marking the "palynological P/T boundary" of Stemmerik et al. (2001) occurs near the top of this formation. At this level $\delta^{13}\text{C}_{\text{org}}$ isotope values stabilize after a first initial drop (Fig. 7). The sequence of events is identical to our phases A to D. The marine record of the uppermost Schuchert Dal Formation reflects two extinction events. The first one, affecting bivalves, brachiopods and bryozoans occurs prior to the spore peak during the phase of decreasing $\delta^{13}\text{C}_{\text{org}}$ values. The second one striking agglutinated foraminifera is located within the spore peak and coincides with the formation change (Stemmerik et al., 2001). A second record from Jameson Land (Looy et al., 2001; Twitchett et al., 2001) shows a more discontinuous C-isotope record, e.g. with an abrupt drop of $\delta^{13}\text{C}_{\text{org}}$ values at the boundary between the Schuchert Dal and the overlying Wordie Creek Formation and also more abrupt changes in the palynological record. A collapse of the marine ecosystems has been reported to occur below the onset of the spore dominance in the interval with $\delta^{13}\text{C}_{\text{org}}$ values around -24‰ (Twitchett et al., 2001) corresponding to our phase A or B (Figs. 3 and 4).

Most European Tethyan sections are condensed and being deposited in carbonate dominated systems contain poorly preserved spore–pollen assemblages with an apparent preservational bias (Looy et al., 1999; Ouyang and Utting, 1990; Visscher and Brugman, 1986; Zhang et al., 2007). Numerous Tethyan records are known from China.

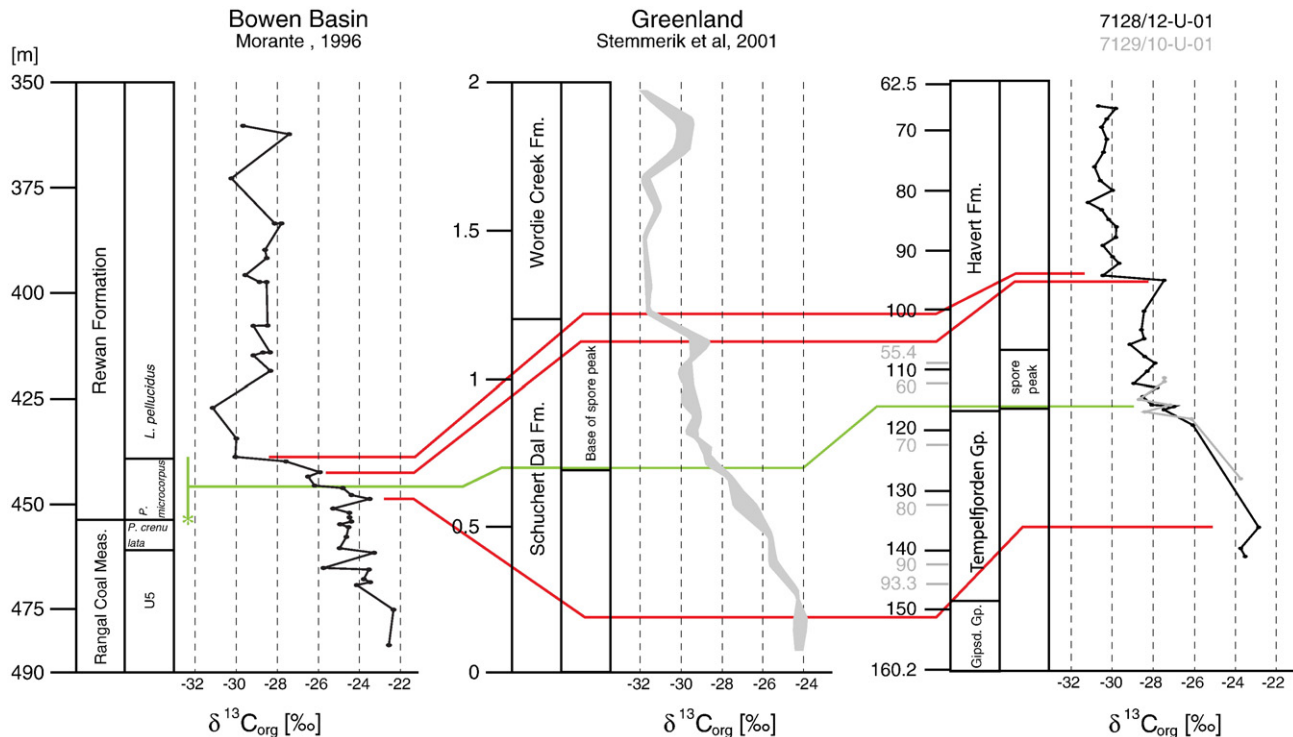


Fig. 7. Chemostratigraphic correlation ($\delta^{13}\text{C}_{\text{org}}$ isotope records) of the Bowen Basin (Queensland, Australia; Morante, 1996), E-Greenland (Stemmerik et al., 2001) and S-Barents Sea, shallow cores 7128/12-U-01 and 7129/10-U-01 (this study).

However, no detailed quantitative data are available and palynological data, averaged over entire formations are unsuitable to reflect short term floral changes. Several authors describe the transitional character of the palynomorph assemblages around the e-PEE of Northern China (Metcalf et al., 2009; Ouyang and Utting, 1990; Peng et al., 2005).

Contrasting floral patterns have been described from the Cathaysian floral province in South China (Peng et al., 2006; Peng and Shi, 2009). Here the spore dominated assemblages of the Late Permian (sensu GSSP, Yin et al., 2001) were successively replaced by gymnosperm dominated assemblages. These changes, accompanied by a major loss of abundance and diversity, started in the early Late Permian (Wuchiapingian) and continued up to the earliest Triassic (sensu GSSP, Yin et al., 2001). According to the chemostratigraphic ($\delta^{13}\text{C}_{\text{org}}$) correlation the transitional zone corresponds to the interval covered by our phases E and F and is characterized by a continuous dominance of spores (Peng et al., 2006). A more pronounced change associated with an increase of gymnosperms coincides with the onset of the $\delta^{13}\text{C}_{\text{org}}$ minimum.

The detailed $\delta^{13}\text{C}_{\text{org}}$ record from the Bowen Basin (Queensland, Australia; Morante, 1996) combined with the palynological zonation (Foster, 1982; Helby et al., 1987) provide an overview of the mid-latitude floral succession of Southern Gondwana and allow for a correlation with Northern hemisphere records. The Late Permian *Playfordiaspora crenulata* zone covers the uppermost part of the pre-shift $\delta^{13}\text{C}_{\text{org}}$ interval ($-24/-26\%$). It is characterized by predominance of gymnosperm pollen. This interval contains the ultimate remains of the *Glossopteris* group and the youngest coal seams (Foster, 1982; Morante, 1996). Bounded by a lithological break, the overlying *Protohaploxipinus microcorpis* zone corresponds to the first major shift of the $\delta^{13}\text{C}_{\text{org}}$ interval ($-26/-28\%$). This zone is characterized by the abundance of lycopod spores. A spore peak occurring immediately above the coal measures has also been documented from core samples from the Sydney Basin (N.S.W.) (Grebe, 1970; Retallack, 1995). As documented in several palynological records there is a minor change in diversity since the decreased

diversity of gymnosperm pollen in the *P. microcorpis* zone is counterbalanced by numerous first appearances in the following zone (Foster, 1982; Grebe, 1970). In contrast to that the megafossil record from the Sydney Basin suggests a dramatic loss in plant diversity with the disappearance of 97% of fossil leaf species (Retallack, 1995). This contrasting evidence might be due to the different preservation potential of leaves compared to spore-pollen. The lower part of the overlying *Lunatisporites pellucidus* zone comprises the interval with minimal $\delta^{13}\text{C}_{\text{org}}$ values ($-30/-32\%$). Except for the presence of marker species, the assemblages of this zone are not well constrained. Originally characterized by the dominance of the eponymous gymnosperm pollen taxa (Helby et al., 1987) other authors report continuous high abundance of spores (De Jersey, 1979; Foster, 1982).

6.2. Inferred environmental impacts

The results from the Barents Sea (Figs. 3, 4 and 8) reflect the climatic evolution and environmental upheavals across the interval during which marine biota suffered the most extreme extinction of the Earth's history. Changes start during the Late Permian (Changhsingian) with the onset of the negative $\delta^{13}\text{C}$ shift and the gradual change in the floral assemblages (phases A and B). A more pronounced change of the flora, coinciding with the basal transgression of the Griesbachian Røye Formation and a further negative $\delta^{13}\text{C}$ shift, is indicated by a higher representation of conifers and ferns (phase C). These changes might be explained with an increase in pCO_2 inducing a first temperature and humidity increase. The most pronounced floral turnover leading to a dominance of the lycopods is documented in the overlying interval (phase D). Chemostratigraphic correlations indicate that similarly expressed changes occur simultaneously in distant areas (e.g. Greenland (Stemmerik et al., 2001), China (Krull et al., 2004), and Australia (Metcalf et al., 2009)) proving the global extent of this event. This interval falls within a phase of almost stable $\delta^{13}\text{C}_{\text{org}}$ values indicating stabilization of the C-cycle. Consequently the global turnover in terrestrial ecosystems

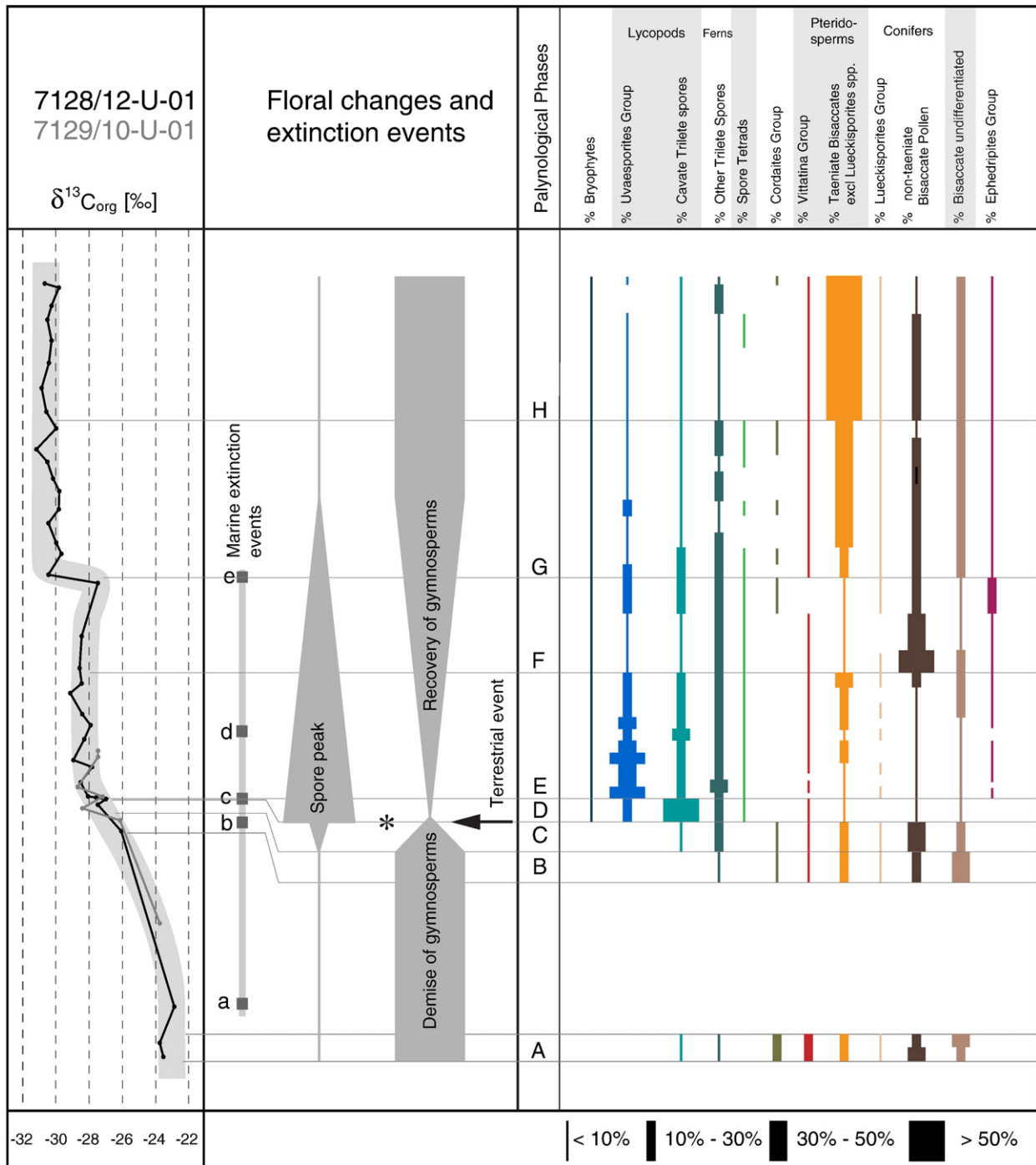


Fig. 8. Environmental changes across the end-Permian extinction event. $\delta^{13}\text{C}_{\text{org}}$ isotope record in cores 7128/12-U-01 and 7129/10-U-01 and quantitative distribution of spore-pollen with published extinction events of the marine realm: a) E-Greenland, Jameson Land (Twitchett et al., 2001); b) Iran (Heydari et al., 2008); c/d) E-Greenland, Jameson Land (Stemmerik et al., 2001); e) Meishan, China (Jin, et al., 2000); Gartnerkofel, Austria (Holser et al., 1989); Canada, Buchanan Lake (Grasby and Beauchamp, 2008); and * extinction of glossopterids (Morante, 1996).

was probably unrelated to a significant perturbation in the C-cycle; therefore other triggers must be considered. One plausible cause is the postulated pollution by halocarbons and other toxic aerosols produced by volcanic intrusions heating organic rich sediments and evaporites (Svensen et al., 2009). Unseparated spore tetrads of pteridophytes, first appearing at this level, possibly reflect genetic damage of the pteridophytes caused by increased UV-radiation as an effect of pollution (Beerling, 2007; Visscher et al., 2004). The dominance of pteridophytes per se indicates stressful conditions. Pteridophytes are known to rapidly colonize disturbed and polluted areas and to resist harmful conditions, potentially fatal to other plants

(McElwain and Punyasena, 2007; Page, 2002). The abundance of lycopods is reminiscent of the “fern spike” observed at the Cretaceous/Tertiary boundary, which has been interpreted to reflect a post bolide impact winter (Vajda et al., 2001). A similar fern spike related to the extinction event at the Triassic/Jurassic boundary has been associated with atmospheric pollution (e.g. halocarbon and SO_2) caused by volcanic activity of the Central Atlantic Magmatic Province (Van de Schootbrugge et al., 2009).

Following the deterioration of the terrestrial ecosystem during the e-PEE our data suggest a rapid recovery of the gymnosperms following this event, since within the same interval of relatively stable $\delta^{13}\text{C}_{\text{org}}$

values (around –28‰) and within a second lycopod dominated assemblage (phase E) gradually increasing abundance of pteridosperms heralds their recovery. During the following phase (F) lycopods are gradually replaced by pteridosperms and conifers. The latter dominate the associations up to the most extreme negative $\delta^{13}\text{C}_{\text{org}}$ shift. In the interval with the most negative but relatively stable $\delta^{13}\text{C}_{\text{org}}$ values (phase G/H) pteridosperms become the dominant group and the low representation of pteridophytes may be associated with decreased humidity. In our record as in other expanded sections (Norwegian Sea and Greenland) there is no trace of the putative “fungal event”; the rare occurrence of *Reduviasporonites* shows no obvious link to the observed environmental and ecological changes (compare Hochuli et al., 2010; Looy et al., 2001; Mangerud, 1994., and present study Figs. 5 and 6).

7. Conclusions

The simultaneous global floral turnover of plant assemblages suggests that the terrestrial ecosystems were affected by a major perturbation of the chemistry of the atmosphere and by successive climatic changes. The effects of these changes varied depending on the palaeogeographic position and the particular boundary conditions of the terrestrial ecosystems. On Southern Gondwana it led to the most dramatic plant extinction event causing the disappearance of the cool-temperate adapted *Glossopteris* flora (Retallack, 1995). The climatic conditions following this event are described as more equable, warmer and less seasonal (Kidder and Worsley, 2004; Lindström and McLoughlin, 2007; Retallack, 1999; Retallack et al., 2003).

The duration of the described ecological changes is difficult to assess. However, based on the radiometric ages from the GSSP section (Meishan) the interval between the End-Permian extinction event and the FAD of *H. parvus* (PTB sensu GSSP) is in the order of 100 kyr (Mundil et al., 2001, 2004). However, according to the latter record the time span between the two events is at the limit of the resolution of radiometric measurements. In the studied cores the turnover of the flora documented in phase C up to the onset of phase E, representing a few meters of sediments, probably happened within a time span in the order of 10 kyr. The short-lived heavily disturbed conditions, reflected in the spore peak, were followed by a recovery phase of the gymnosperms within a comparable time span (Phase F and lower part of phase G). In contrast to the marine realm the impact of the e-PEE on the terrestrial ecosystem was apparently too short to cause a major impact on the evolution of plants. The documented rapid revival of gymnosperm dominated plant communities apparently contradicts the postulated delayed recovery of the demised ecosystems with the continuous lycopods dominance during the Early Triassic (Looy et al., 1999). However, new paleontological and chemostratigraphic data from Early Triassic reveal reiterated crises throughout this epoch, including major disturbances in the C-cycle, which affected not only marine but also terrestrial ecosystems (Brühwiler, 2010; Galfetti et al., 2007a; Hermann et al., 2010; Hochuli et al., 2010; Payne et al., 2004) and caused the apparently delayed recovery of the plant assemblages.

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References

Balme, B.E., 1995. Fossil in situ spores and pollen grain: an annotated catalogue. *Rev. Palaeobot. Palyno.* 87, 81–323.
 Beerling, D., 2007. *The Emerald Planet – How Plants Changed Earth's History*. Oxford University Press, Oxford.

Bjerager, M., Seidler, L., Stemmerik, L., Surlyk, F., 2006. Ammonoid stratigraphy and sedimentary evolution across the Permian–Triassic boundary in East Greenland. *Geol. Mag.* 143 (5), 635–656.
 Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., et al., 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* 325, 1118–1121.
 Brühwiler, T., 2010. Smithian (Early Triassic) ammonoids faunas of the Tethys: Taxonomy, biochronology, diversity dynamics and paleoenvironments. PhD thesis Univ. Zürich (unpublished).
 Bugge, T., Mangerud, G., Elvebakk, G., Mørk, A., Nilsson, I., Fanavoll, S., et al., 1995. The Upper Palaeozoic succession on the Finnmark Platform, Barents Sea. *Nor. Geol. Tidsskr.* 75, 3–30.
 De Jersey, N.J., 1979. Palynology of the Permian–Triassic transition in the Western Bowen Basin. *Geol. Surv. Queensl. Publ.* 374, 1–67.
 Erwin, D.H., 1993. *The Great Paleozoic Crisis; Life and Death in the Permian*. Columbia University Press, New York.
 Eshet, Y., Rampino, M.R., Visscher, H., 1995. Fungal event and palynological record of ecological crisis and recovery across the Permian–Triassic boundary. *Geology* 23 (11), 967–970.
 Foster, C.B., 1982. Spore–pollen assemblages of the Bowen Basin, Queensland (Australia). *Rev. Palaeobot. Palyno.* 36, 165–183.
 Foster, C.B., Stephenson, M.H., Marshall, C., Logan, G.A., Greenwood, P.F., et al., 2002. A revision of *Reduviasporonites* Wilson 1962: description, illustration, comparison and biological affinities. *Palynology* 26, 165–183.
 Galfetti, T., Hochuli, P.A., Brayard, A., Bucher, H., Weissert, H., Vigran, J.O., 2007a. The Smithian/Spathian boundary event: evidence for global climatic change in the wake of the end-Permian biotic crisis. *Geology* 35 (4), 291–294.
 Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Brühwiler, T., et al., 2007b. Timing of the Early Triassic carbon cycle perturbations inferred from new U–Pb ages and ammonoid biochronozones. *Earth Planet. Sci. Lett.* 258, 593–604.
 Grasby, S.E., Beauchamp, B., 2008. Intrabasin variability of the carbon-isotope record across the Permian–Triassic transition, Sverdrup Basin, Arctic Canada. *Chem. Geol.* 253, 141–150.
 Grebe, H., 1970. Permian plant microfossils from the Newcastle coal measures/Narrabeen group boundary, Lake Munmorah, New South Wales. *Rec. Geol. Surv. NSW* 12 (2), 125–136.
 Helby, R., Morgan, R., Partridge, A.D., 1987. A palynological zonation of the Australian Mesozoic. In: *Jell, P.A. (Ed.), Studies in Australian Mesozoic Palynology: Assoc. Austral. Palaeont. Mem.*, 4, pp. 1–94.
 Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Ware, D., Hautmann, M., Weissert, H., Bernasconi, S., Roohi, G., Reman, K., Yaseen, A., 2010. Climatic changes in the aftermath of the end-Permian mass extinction – evidence from palynological records of Pakistan. *Geophysical Research Abstracts* Vol. 12, EGU2010-2394-5.
 Hermann, E., Hochuli, P.A., Bucher, H., Vigran, J.O., Weissert, H., 2010. A close-up view of the Permian Triassic boundary based on expanded organic carbon isotope records from Norway (Trøndelag and Finnmark Platform). *Global and Planetary Change* 74, 156–167 (this volume).
 Heydari, E., Arzani, N., Hassanzadeh, J., 2008. Mantle plume: the invisible serial killer – application to the Permian–Triassic boundary mass extinction. *Palaeogeogr. Palaeoclim.* 264, 147–162.
 Hochuli, P.A., Vigran, J.O., Hermann, E., Bucher, H., 2010. Multiple climatic changes around the Permian Triassic boundary event revealed by an expanded palynological record from Mid Norway. *Geol. Soc. Am. B.* 122 (5/6), 884–896.
 Holser, W.T., Schönlaub, H.-P., Attrep, M., Boekelmann, K., Klein, P., Magaritz, M., et al., 1989. A unique geochemical record at the Permian/Triassic boundary. *Nature* 337, 39–44.
 Jin, Y.G., Wang, Y., Wang, W., Shang, Q.H., Cao, C.Q., Erwin, D.H., 2000. Pattern of marine mass extinction near the Permian–Triassic boundary in South China. *Science* 289, 432–436.
 Kidder, D.L., Worsley, T.R., 2004. Causes and consequences of extreme Permian–Triassic warming to globally equable climate and relation to the Permian–Triassic extinction and recovery. *Palaeogeogr. Palaeoclim.* 203, 207–237.
 Korchinskaya, M.V., 1986. In: *Krasil'shchikov, A.A., Miraev, M.N. (Eds.), Geology of the Sedimentary Blanket of the Archipelago of Svalbard*, pp. 77–93 (Coll. Sci. Pap., Leningrad, 1986).
 Korte, C., Pande, P., Kalia, P., Kozur, H.W., Joachimski, M.M., Oberhänsli, H., 2010. Massive volcanism at the Permian–Triassic boundary and its impact on the isotopic composition of the ocean and atmosphere. *J. Asian Earth Sci.* 37, 293–311.
 Krull, E.S., Lehrmann, D.J., Druke, D., Kessel, B., Yu, Y., Li, R., 2004. Stable carbon isotope stratigraphy across the Permian–Triassic boundary in shallow marine carbonate platforms, Nanpanjiang Basin, South China. *Palaeogeogr. Palaeoclim.* 204, 297–315.
 Kürschner, W.M., Henggreen, G.F.W., 2010. Triassic palynology of central and northwestern Europe: a review of palynofloral diversity patterns and biostratigraphic subdivisions. *Geol. Soc. Lond. Spec. Publ.* 334, 263–283.
 Larssen, G.B., Elvebakk, G., Henriksen, L.B., Kristensen, S.-E., Nilsson, I., Samuelsen, 2005. Upper Palaeozoic lithostratigraphy of the southern part of the Norwegian Barents Sea. *Norg. Geol. Unders.* B. 444, 3–43.
 Lindström, S., McLoughlin, S., 2007. Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains, Antarctica. Implications for palynofloristic turnover across Gondwana. *Rev. Palaeobot. Palyno.* 145, 89–122.
 Looy, C.V., Brugman, W.A., Dilcher, D.L., Visscher, H., 1999. The delayed resurgence of equatorial forests after the Permian–Triassic ecologic crisis. *Proc. Natl. Acad. Sci. USA* 96 (24), 13857–13862.

- Looy, C.V., Twitchett, R.J., Dilcher, D.L., van Konijnenburg-van Cittert, J.H.A., Visscher, H., 2001. Life in the end-Permian dead zone. *Proc. Natl Acad. Sci. USA* 98 (14), 7879–7883.
- MacLeod, N., 2003. The causes of Phanerozoic extinctions. In: Rothschild, L.J., Lister, A.M. (Eds.), *Evolution of Planet Earth*. Academic Press, Amsterdam, pp. 253–277.
- Mangerud, G., 1994. Palynostratigraphy of the Permian and lowermost Triassic succession, Finnmark Platform, Barents Sea. *Rev. Palaeobot. Palyno.* 82, 317–349.
- McElwain, J.C., Punyasena, S.W., 2007. Mass extinction and the plant fossil record. *Trends Ecol. Evol.* 22 (10), 548–557.
- Metcalfe, I., Foster, C.B., Afonin, S.A., Nicoll, R.S., Mundil, R., Xiaofeng, W., et al., 2009. Stratigraphy, biostratigraphy and C-isotopes of the Permian–Triassic non-marine sequence at Dalong and Lucaogou, Xinjiang Province, China. *J. Asian Earth Sci.* 36, 503–520.
- Morante, R., 1996. Permian and Early Triassic isotopic records of carbon and strontium in Australia and a scenario of events about the Permian–Triassic boundary. *Hist. Biol.* 11, 289–310.
- Mundil, R., Metcalfe, I., Ludwig, K.R., Renne, P.R., Oberli, F., Nicoll, R.S., 2001. Timing of the Permian–Triassic biotic crisis: implications from new zircon U/Pb age data (and their limitations). *Earth Planet. Sci. Lett.* 187, 131–145.
- Mundil, K.R., Ludwig, I., Metcalfe, P.R., Renne, P.R., 2004. Age and timing of the Permian mass extinction: U/Pb dating of close-system zircons. *Science* 305, 1760–1763.
- Ouyang, S., Utting, J., 1990. Palynology of Upper Permian and Lower Triassic rocks, Meishan, Changxing County, Zhejiang Province, China. *Rev. Palaeobot. Palyno.* 66, 65–103.
- Page, C.N., 2002. Ecological strategies in fern evolution: a neopteridological overview. *Rev. Palaeobot. Palyno.* 119, 1–33.
- Payne, J.L., Lehrmann, D.J., Wei, J.Y., Orchard, M.J., Schrag, D.P., Knoll, A.H., 2004. Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* 305, 506–509.
- Peng, Y., Shi, G.R., 2009. Life crises on land across the Permian–Triassic boundary in South China. *Glob. Planet. Change* 65, 155–165.
- Peng, Y., Zhang, S., Yu, T., Yang, F., Gao, Y., Shi, G.R., 2005. High-resolution terrestrial Permian–Triassic eventostratigraphic boundary in western Guizhou and eastern Yunnan, southwestern China. *Palaeogeogr. Palaeoclim. Palaeoecol.* 215, 285–295.
- Peng, Y., Yu, J., Gao, Y., Yang, F., 2006. Palynological assemblages of non-marine rocks at the Permian–Triassic boundary, western Guizhou and eastern Yunnan, South China. *J. Asian Earth Sci.* 28, 291–305.
- Retallack, G.J., 1995. Permian–Triassic life crisis on land. *Science* 267, 77–80.
- Retallack, G.J., 1999. Postapocalyptic greenhouse paleoclimate revealed by earliest Triassic paleosols in the Sydney Basin, Australia. *Geol. Soc. Am. B.* 111 (1), 52–70.
- Retallack, G.J., Smith, R.M.H., Ward, P.D., 2003. Vertebrate extinction across Permian–Triassic boundary in Karoo Basin, South Africa. *Geol. Soc. Am. B.* 15 (9), 1133–1152.
- Shevryev, A.A., 2006. Triassic biochronology: state of the art and main problems. *Stratigr. Geol. Correl.* 14, 6, 629–641.
- Stemmerik, L., Bendix-Almgreen, S.E., Piasecki, S., 2001. The Permian–Triassic boundary in East Greenland: past and present views. *B. Geol. Soc. Denmark* 48, 159–167.
- Svensen, H., Planke, S., Polozov, A.G., Schmidbauer, N., Corfu, F., Podladchikov, Y., et al., 2009. Siberian gas venting and the end-Permian environmental crisis. *Earth Planet. Sci. Lett.* 277, 490–500.
- Tozer, E.T., 1994. Canadian Triassic ammonoid faunas. *Geol. Surv. Can. B.* 467, 1–663.
- Tozer, E.T., Parker, J.R., 1968. Notes on the Triassic biostratigraphy of Svalbard. *Geol. Mag.* 105 (6), 526–542.
- Traverse, A., 2007. *Paleopalynology* 2nd ed. Springer Verlag, Dordrecht.
- Twitchett, R.J., Looy, C.V., Morante, R., Visscher, H., Wignall, P.B., 2001. Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology* 29, 4, 351–354.
- Utting, J., Spina, A., Jansonius, J., McGregor, D.C., Marshall, J.E.A., 2004. Reworked miospores in the upper Paleozoic and lower Triassic of the Northern circum-polar area and selected localities. *Palynology* 28, 75–119.
- Vajda, V., Raine, J.I., Hollis, C.J., 2001. Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. *Science* 294, 1700–1702.
- Van de Schootbrugge, B., Quan, T.M., Lindström, S., Püttmann, W., Heunisch, C., Pross, J., et al., 2009. Floral changes across the Triassic/Jurassic boundary linked to flood basalt volcanism. *Nat. Geosci.* 2, 589–594.
- Visscher, H., Brugman, W.A., 1986. The Permian–Triassic boundary in the southern Alps: a palynological approach. *Mem. Soc. Geol. Ital.* 34, 121–128.
- Visscher, H., Brinkhuis, H., Dilcher, D.L., Elsik, W.C., Eshet, Y., Looy, C.V., et al., 1996. The terminal Paleozoic fungal event: evidence of terrestrial ecosystem destabilization and collapse. *Proc. Natl Acad. Sci. USA* 93, 2155–2158.
- Visscher, H., Looy, C.V., Collison, M.E., Brinkhuis, H., van Konijnenburg-van Cittert, J.H.A., Kürschner, W., et al., 2004. Environmental mutagenesis during the end-Permian ecological crisis. *Proc. Natl Acad. Sci. USA* 101 35, 12952–12956.
- Yin, H., Zhang, K., Tong, J., Yang, Z., Wu, S., 2001. The global stratotype section and point (GSSP) of the Permian–Triassic boundary. *Episodes* 24 (2), 102–114.
- Zhang, K., Tong, J., Shi, G.R., Lai, X., Yu, J., He, W., et al., 2007. Early Triassic conodont-palynological biostratigraphy of the Meishan D Section in Changxing, Zhejiang Province, South China. *Palaeogeogr. Palaeoclim. Palaeoecol.* 252, 4–23.