



Vegetation history across the Permian–Triassic boundary in Pakistan (Amb section, Salt Range) [☆]



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ABSTRACT

Hypotheses about the Permian–Triassic floral turnover range from a catastrophic extinction of terrestrial plant communities to a gradual change in floral composition punctuated by intervals indicating dramatic changes in the plant communities. The shallow marine Permian–Triassic succession in the Amb Valley, Salt Range, Pakistan, yields palynological suites together with well-preserved cuticle fragments in a stratigraphically well-constrained succession across the Permian–Triassic boundary. Palynology and cuticle analysis indicate a mixed *Glossopteris*–*Dicroidium* flora in the Late Permian. For the first time *Dicroidium* cuticles are documented from age-constrained Upper Permian deposits on the Indian subcontinent. Close to the Permian–Triassic boundary, several sporomorph taxa disappear. However, more than half of these taxa reappear in the overlying Smithian to Spathian succession. The major floral change occurs towards the Dienerian. From the Permian–Triassic boundary up to the middle Dienerian a gradual increase of lycopod spore abundance and a decrease in pteridosperms and conifers are evident. Synchronously, the generic richness of sporomorphs decreases. The middle Dienerian assemblages resemble the previously described spore spikes observed at the end-Permian (Norway) and in the middle Smithian (Pakistan) and might reflect a similar ecological crisis.

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1. Introduction

Whereas in marine environments the extent and chronological course of events of the end-Permian mass extinction has been studied in great detail over recent decades (e.g. Raup and Sepkoski, 1982; Bowring et al., 1999; Jin et al., 2000; Benton and Twitchett, 2003; Haas et al., 2004; Groves et al., 2007; J. Chen et al., 2011), the impact of the mass extinction on continental vegetation remains poorly resolved (e.g. Knoll, 1984; Rees et al., 2002; Bamford, 2004; Utting et al., 2004; Hochuli et al., 2010; Xiong and Wang, 2011).

Despite the unresolved causal mechanism, terrestrial ecosystems changed significantly across the Permian–Triassic boundary. Terrestrial vertebrates, e.g. therapsids (“mammal-like reptiles”) were severely affected by the Permian–Triassic extinction (Kemp, 2005). Several lineages became extinct; others such as the dicynodonts were reduced and recovered in the Middle Triassic (Benton et al., 2004; Ward et al., 2005; Fröbisch, 2008). In contrast, skull morphology of the Cynodontia

shows no significant change across the Permian–Triassic boundary, but changes significantly only in the late Olenekian–Anisian (Abdala and Ribeiro, 2010). A turnover in palaeosol characteristics has been documented from Antarctica in association with the changes in terrestrial vertebrates. Late Permian palaeosols are coal-bearing and coarse-grained compared to the green–red mottled claystones of Early Triassic age. This change has been interpreted to reflect a climatic shift to warmer climates in the Early Triassic (Retallack and Krull, 1999).

Floral records of Late Permian and Early Triassic age have been used as a proxy for migration pathways of newly evolved taxa such as *Dicroidium* (Kerp et al., 2006; Abu Hamad et al., 2008). *Dicroidium* apparently evolved in the Late Permian of the Palaeotropics (Jordan) and migrated to higher southern latitudes probably in association with climatic changes during the Triassic (Kerp et al., 2006; Abu Hamad et al., 2008). However, fossil floral records have also been used as indicators for other environmental signals (stress factors) during the end-Permian biodiversity disruption. The abundant occurrence of unseparated spore tetrads close to the Permian–Triassic boundary has been interpreted to reflect a depletion of the ozone layer (e.g. Visscher et al., 2004; Beerling et al., 2007). As suggested by these authors the ozone layer depletion led to increasing UV-B radiation and mutagenesis in spores, which lost their ability to separate. Another conspicuous

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feature of fossil floral records is brief intervals in which pteridophyte spores became proportionally very abundant. Instead of a long-lasting loss of standing woody biomass (e.g. Looy et al., 1999), palynological data from Norway indicate a rapid succession of spore dominance and immediate recovery of gymnosperms (Hochuli et al., 2010). Reviews of floral records have revealed that faunal mass extinctions are commonly associated with instabilities of terrestrial ecosystems (McElwain and Punyasena, 2007). Such short-term changes, so-called spore spikes or spore peaks, have been observed at the Permian–Triassic boundary (Stemmerik et al., 2001; Hochuli et al., 2010) and during the middle Smithian (Hermann et al., 2011a). Repeated high spore relative abundances close to the Triassic–Jurassic boundary have been interpreted to reflect the vegetation's reaction to environmental changes induced by the Central Atlantic magmatic province. The volcanism caused climatic gradients that led to compositional changes of the regional vegetation (Götz et al., 2009; Bonis and Kürschner, 2012). A distinct fern spike has also been associated with the Cretaceous–Paleogene boundary (Vajda et al., 2001) and compared with the Permian–Triassic floral succession (Vajda and McLoughlin, 2007). In all mentioned instances high spore abundances are associated with environmental change and faunal extinction events.

The end-Permian short-term floral changes reported from the Northern Hemisphere called for a detailed study of the vegetation history across the Permian–Triassic boundary in the Southern Hemisphere, i.e. of a Gondwanan record. The Amb Valley section in the Salt Range (Pakistan), which includes the Chhidru Formation and the Mianwali Formation, offers the opportunity to evaluate palynological data together with well-preserved cuticle fragments to describe the floral succession in a well-constrained temporal framework across the Permian–Triassic boundary.

2. Geological and palaeogeographic setting

The Amb Valley is located in the Salt Range (Pakistan), a low mountain range SSW of Islamabad (Fig. 1B). It is one of numerous valleys that yield fine exposures of the Permian–Triassic marine sedimentary succession in this area. During the Late Permian and Early Triassic, the Salt Range area was part of the southern Tethyan shelf of the Indian subcontinent (Northern Indian Margin); (Fig. 1A) (e.g. Pakistani-Japanese Research Group, 1985; Smith et al., 1994; Golonka and Ford, 2000). The Amb section is located ~20 km SE of Nammal and ~5 km S of the Sakesar mountain (Fig. 1C).

The uppermost part of the Chhidru Formation and the lowermost part of the Mianwali Formation were sampled for the present study.

The uppermost part of the Chhidru Formation was informally named the “white sandstone unit” by Kummel and Teichert (1970). At Amb, the white sandstone unit consists of a 9 m thick succession of alternating white to grey, medium-grained sandstone and dark grey siltstone. In the Salt Range area, the upper part of the Chhidru Formation is of late Changhsingian age based on conodont biostratigraphy (Wardlaw and Mei, 1999; Mei et al., 2002; Shen et al., 2006) and chemostratigraphic correlations of carbon isotope data with the GSSP of Meishan, South China (Schneebeli-Hermann et al., 2013).

The contact between the Chhidru Formation and the overlying Mianwali Formation represents an erosional unconformity interpreted as a sequence boundary (Mertmann, 2003; Hermann et al., 2011b) and representing a temporal hiatus between deposition of the two formations. The extinction of marine biota has been described to coincide with the formational boundary between the two formations (Schindewolf, 1954). The overlying Mianwali Formation has been subdivided into the Kathwai Member, the Mittiwali Member, and the Narmia Member. The present study deals with the basal part of the Mianwali Formation, including the Kathwai Member and the basal part of the Mittiwali Member, namely the Lower Ceratite Limestone and the lowermost interval of the Ceratite Marls (e.g. Waagen, 1895; Kummel and Teichert, 1970; Guex, 1978; Hermann et al., 2011b).

The position of the Permian–Triassic boundary, as defined by the first occurrence of the conodont species *Hindeodus parvus* (Yin et al., 2001) is ambiguous in the Salt Range area, partly because of the diachronicity of lithological boundaries (e.g. Hermann et al., 2011b; Brühwiler et al., 2012). At Nammal, the Pakistani-Japanese Research Group (1985) divided the Kathwai Member into three units and placed the Permian–Triassic boundary in the middle unit, whereas Wardlaw and Mei (1999) documented the occurrence of *H. parvus* near the base of the Kathwai Member in the Salt Range area (without mentioning the exact locality); in some successions the lowermost unit of the Kathwai Member is not preserved (Mertmann, 2003). At Nammal, the negative carbon isotope spike marking the Permian–Triassic boundary sections worldwide occurs in the lowermost part of the Kathwai Member (Baud et al., 1996). Therefore, we use the formational boundary between the Chhidru Formation and the Mianwali Formation as an approximation for the Permian–Triassic boundary at Amb. The overlying Lower Ceratite Limestone is of early Dienerian to earliest middle Dienerian age (Ware et al., 2010, 2011). Ammonoids recovered from the Ceratite Marls indicate middle Dienerian to early Smithian ages; the lowermost 2 m included in this study are of middle Dienerian age (Ware et al., 2010, 2011).

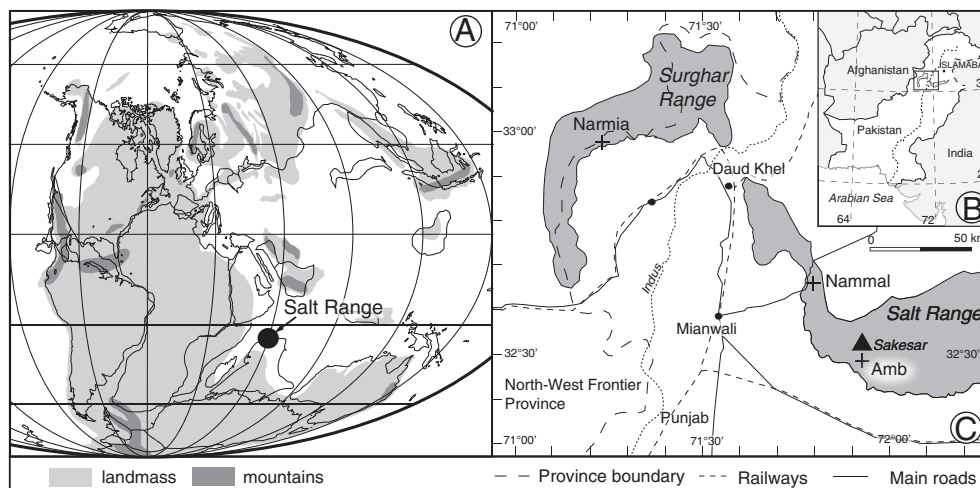


Fig. 1. A: Early Triassic palaeogeographic position of the Salt Range (after Smith et al., 1994 and Golonka and Ford, 2000). B: Location of the Salt Range and Surghar Range in Pakistan. C: Location of the Amb valley in the Salt Range.

3. Methods

Thirty samples were collected from fine-grained siliciclastic intervals of the white sandstone unit (Chhidru Formation) and the basal part of the overlying Mianwali Formation in the Amb section. The samples were crushed and weighed (5–25 g) and subsequently treated with hydrochloric and hydrofluoric acid according to standard palynological preparation techniques (Traverse, 2007). A brief oxidation with nitric acid was performed before the residues were sieved using an 11 µm mesh screen. A minimum of 250 spores and pollen grains per sample were counted from strew mounts. Spores and pollen grains were grouped and classified according to their botanical affinities to aid interpretation of the vegetation history (after Balme, 1995; Lindström et al., 1997; Taylor et al., 2006; Traverse, 2007); (Table 1).

Cuticle fragments were abundant in samples AMB 34, AMB 37, and AMB 45 and were picked and mounted on separate slides for identification. Palynological slides were also screened for identifiable cuticles.

A diversity analysis was performed on the qualitative sporomorph datasets from the Amb Valley section using PAST (Hammer et al., 2001). The number of pollen grains and spore genera per sample was calculated (generic richness). Additionally, the range-through diversity was determined, in which absences between the first and last occurrences were treated as the presence. For comparison, the generic richness and spore/pollen ratios of the previously described palynological record from the Narmia Valley were calculated and illustrated (Hermann et al., 2011a, 2012). Samples are stored in the repository of the Palaeontological Institute and Museum of the University of Zurich (PIMUZ repository numbers A/VI 65 and A/VI 66).

4. The cuticle record

Cuticle fragments were picked from palynological residue samples of AMB 34, AMB 37, and AMB 45, and palynological slides of other samples were scanned for additional cuticle occurrences (see Table 2). The main categories that could be distinguished are: cuticles of *Glossopteris/Gangamopteris* type (Fig. 2); the cordaitalean *Noeggerathiopsis* (Fig. 3A,

Table 2

Stratigraphic distribution of identified cuticle types in the Amb Valley section.

Sample	<i>Lepidopteris</i>	<i>Dicroidium</i> spp.	<i>Glosspteris/Gangamopteris</i>	<i>Noeggerathiopsis</i>
AMB 103				
AMB 26				
AMB 102				
AMB 120				
AMB 101				
AMB 24	x			
AMB 48				
AMB 47		x		
AMB 46				
AMB 45	x	x	x	
AMB 44				
AMB 43				
AMB 42				
AMB 41			x	
AMB 40			x	
AMB 21				
AMB 39			x	
AMB 20				
AMB 38				
AMB 37		x		x
AMB 49				
AMB 36				
AMB 35				
AMB 34	x	x	x	x
AMB 33				
AMB 32				
AMB 31				
AMB 30			x	
AMB 29				
AMB 28				

B), cuticle fragments of the peltasperm *Lepidopteris* (Fig. 3C), and cuticles of the corystosperm *Dicroidium* (Fig. 3D–I). Furthermore cuticles of other indeterminate plant groups (Fig. 3K, L) were encountered.

The identified cuticle types are described below and their stratigraphic distribution is indicated (Table 2).

Table 1

Botanical affinities of relevant sporomorph taxa (after Balme, 1995; Lindström et al., 1997; Taylor et al., 2006; Traverse, 2007).

Bryophytes & Pteridophytes undiff.			Spores undiff and spores of uncertain affinity such as: <i>Didecitriletes</i> spp., <i>Limatulasporites</i> spp., <i>Lunulasporites</i> spp., <i>Playfordiaporina</i> spp., <i>Punctatisporites</i> spp., <i>Punctatosporites</i> spp., and <i>Triplexisporites</i> spp.
Pteridophytes	Ferns		<i>Acanthotriletes</i> spp., <i>Apiculatisporites</i> spp., <i>Baculatisporites</i> spp., <i>Convolutisporites</i> spp., <i>Dictyophyllidites</i> spp., <i>Grandispora</i> spp., <i>Granulatisporites</i> spp., <i>Horriditriletes</i> spp., <i>Laevigatosporites</i> spp., <i>Leiotriletes</i> spp., <i>Lophotriletes</i> spp., <i>Osmundacidites</i> spp., <i>Polypodiisporites</i> spp., <i>Triquirites</i> spp., <i>Verrucosporites</i> spp.
	Lycopodiopsida		<i>Endosporites papillatus</i> <i>Densoisporites</i> spp. <i>Kraeuselisporites</i> spp. <i>Lundbladispora</i> spp. <i>Calamospora</i> spp.
Gymnosperms	Equisetopsida		<i>Ephredipites</i> spp., <i>Gnetaceapollenites</i> spp.
	Gnetopsida		<i>Cycadopites</i> spp., <i>Pretricolpipollenites</i> spp.
	Cycadopsida		<i>Falcisporites</i> spp., <i>Vitreisporites</i> spp., <i>Weylandites</i> spp.
	Pteridospermae and probable seed ferns	Corystospermales, Caytoniales, Peltaspermales	
		Glossopteridales	<i>Protohaploxypinus</i> spp., <i>Striatopodocarpites</i> spp.
	Conifers		<i>Bisaccates taen</i> <i>Chordasporites</i> spp., <i>Florinites</i> spp., <i>Klausipollenites</i> spp., <i>Lueckisporites</i> spp., <i>Pinuspollenites</i> spp., <i>Platysaccus</i> spp., <i>Protodiploxypinus</i> spp., <i>Sulcatisporites</i> spp.
	Conifers + Pteridospermae		<i>Bisaccates undiff</i> <i>Lunatisporites</i> spp. <i>Alisporites</i> spp. <i>Bisaccates non-taen</i>
	Gymnosperms undiff		<i>Cordaitina</i> spp., <i>Corisaccites</i> spp., <i>Densipollenites</i> spp., <i>Guttulapollenites hannonicus</i> , <i>Inaperturopollenites</i> spp., <i>Marsupipollenites</i> spp., undiff monosaccate and monosulcate pollen

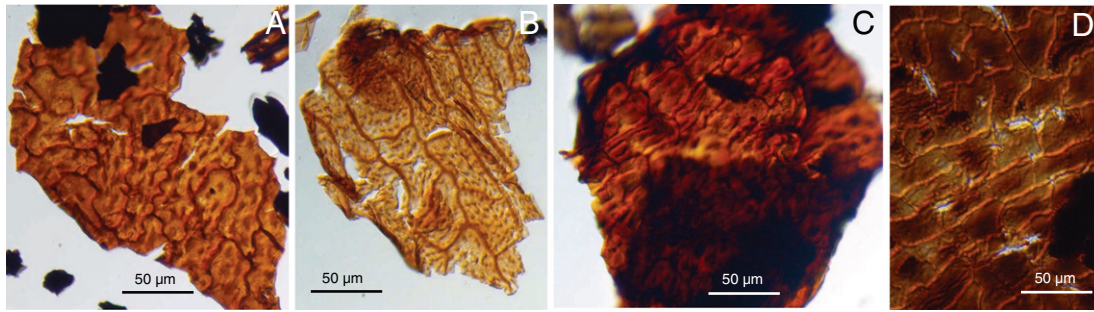


Fig. 2. *Glossopteris/Gangamopteris* cuticle types from the Amb section. Sample number is followed by England Finder coordinates. PIMUZ repository number A/VI 65: A: AMB 34a, Q14/3–4. B: AMB 40a E27/1–3. C: AMB 30a, N7/0. PIMUZ repository number A/VI 66: D: AMB 34C, Z11/1–3.

4.1. Cuticle type 1 (*Glossopteridales*) (Fig. 2)

4.1.1. Description

Cuticle moderately thick; epidermal cell pattern differentiated into costal and intercostal fields (Fig. 2A, C). Cells irregularly arranged and with variable outlines in intercostal fields (Fig. 2A), tending to longitudinal alignment and elongation in costal fields (Fig. 2B, upper part of Fig. 2C, D); anticlinal cell walls curved to highly sinuous (Fig. 2A, B). Outer cuticle surface smooth or with a characteristic microstructure composed of evenly distributed, small, solid papillate projections with a density of about five to more than 20 per cell (Fig. 2A–C).

4.1.2. Remarks

Cuticle and epidermal characters of the *Glossopteridales* have been studied extensively (see, e.g. Zeiller, 1896; Sahni, 1923; Pant, 1958; Chandra, 1974; Pant and Gupta, 1968; Pant and Singh, 1968; Singh and Maheshwari, 2000); they show a remarkable variability between genera and species, but also within individual species (e.g. Surange and Srivastava, 1956; Chandra, 1974; Singh, 2000). It is, therefore, difficult to accurately delimit this plant group based on cuticle and epidermal features alone (e.g. Singh, 2000). However, some species of *Glossopteris*, including *Glossopteris colpodes*, *Glossopteris fibrosa*, *Glossopteris hispida*, *Glossopteris petiolata*, *Glossopteris tenuifolia* and *Glossopteris waltonii*, possess cuticles that are characterised by a particular surface microstructure of numerous small, solid papillae, as described above (see, e.g. Pant, 1958; Pant and Gupta, 1968; Maheshwari and Tewari, 1992). Similar structures have also been described to occur on the cuticle of some *Gangamopteris* species (Srivastava, 1957). This particular type of ornamentation is not known to occur in other plant groups of that time. Together with the characteristically sinuous anticlinal walls of epidermal cells, it forms a reliable diagnostic feature for at least certain species of *Glossopteris* and *Gangamopteris*.

4.2. Cuticle type 2 (*Noeggerathiopsis*) (Fig. 3A, B)

4.2.1. Description

Cuticle thick. Epidermal cells arranged in nearly regular longitudinal files, oriented longitudinally; epidermis differentiated into alternating, parallel longitudinal rows of stomata-bearing and stomata-free zones. Epidermal cells in stomata-free (costal) rows longitudinally elongate, with straight or slightly curving anticlinal walls, and smooth anticlinal wall cutinisations; periclinal walls smooth or with up to three diffuse papilla-like thickenings with circular outline. Epidermal cells in stomata-bearing (intercostal) rows with overall similar features but smaller, less elongate, and more variably oriented. Stomata occurring in one or several ill-defined longitudinal files per intercostal row, each with about five to eight (usually seven) subsidiary cells that are similar, but more heavily cutinised than surrounding regular epidermal cells; subsidiary cells lacking papillae; stomatal aperture narrow oval or

rectangular, longitudinally oriented; guard cells superficial or only little sunken.

4.2.2. Remarks

The material agrees well with the epidermal and cuticular structure of some species of *Noeggerathiopsis* (e.g. Lele and Maithy, 1964; Pant and Verma, 1964); the presence of only few, ill-defined papillae and more or less superficial guard cells show close similarity to the cuticles of *Noeggerathiopsis bunburyana* (Pant and Verma, 1964) and *Noeggerathiopsis hislopii* of Zeiller (1896).

It is important to note, however, that other species of *Noeggerathiopsis* from Gondwana, including forms that are known in remarkable detail based on anatomically preserved material from Antarctica (McLoughlin and Drinnan, 1996), show a very different epidermal morphology with trichome-lined stomatal grooves. Similar epidermal structures are characteristic features also of the rufloiriacean Cordaitales typical of Angara (see, e.g., Gluchova, 2009). Indeed, we encountered a few cuticle fragments in sample AMB 34 that show such trichome-lined depressions, possibly stomatal chambers or grooves, in the epidermal surface (Fig. 3J). Even though these specimens are only small fragments, they appear remarkably similar to the cuticles of *Rufloiria gondwanensis* Guerra Sommer from the Permian of Rio Grande do Sul (Guerra Sommer, 1989), which together with co-occurring *Nephropsis*-type bracts (Corrêa da Silva and Arrondo, 1977) form the so far only known Gondwanan representatives of rufloiriacean Cordaitales. Although we cannot identify these dispersed cuticle fragments as belonging to the Rufloiriaceae with certainty at present, it may be possible that the composition of cordaitalean plants in the Permian peri-Tethyan realm was more complex than previously thought, combining typical Gondwanan *Noeggerathiopsis* plants as well as additional taxa that are usually considered characteristic elements of the Angaran vegetation.

4.3. Cuticle type 3 (*Lepidopteris*) (Fig. 3C)

4.3.1. Description

Cuticles moderately thick to thick. Epidermal cells arranged irregularly and without preferred orientation, small, of relatively uniform size and shape, polygonal with mostly four to six sides, with straight anticlinal walls and smooth, even anticlinal wall cutinisation; each regular epidermal cell bearing a distinct, centrally positioned, hemispherical, solid papillate thickening. Stomatal complexes evenly distributed, irregularly oriented, (sub)circular in outline and essentially radially symmetrical, with four to seven (usually five or six) subsidiary cells that are similarly or less cutinised than surrounding regular epidermal cells; subsidiary-cell papillae positioned close to and usually overarching the stomatal pit; guard cells conspicuously sunken.

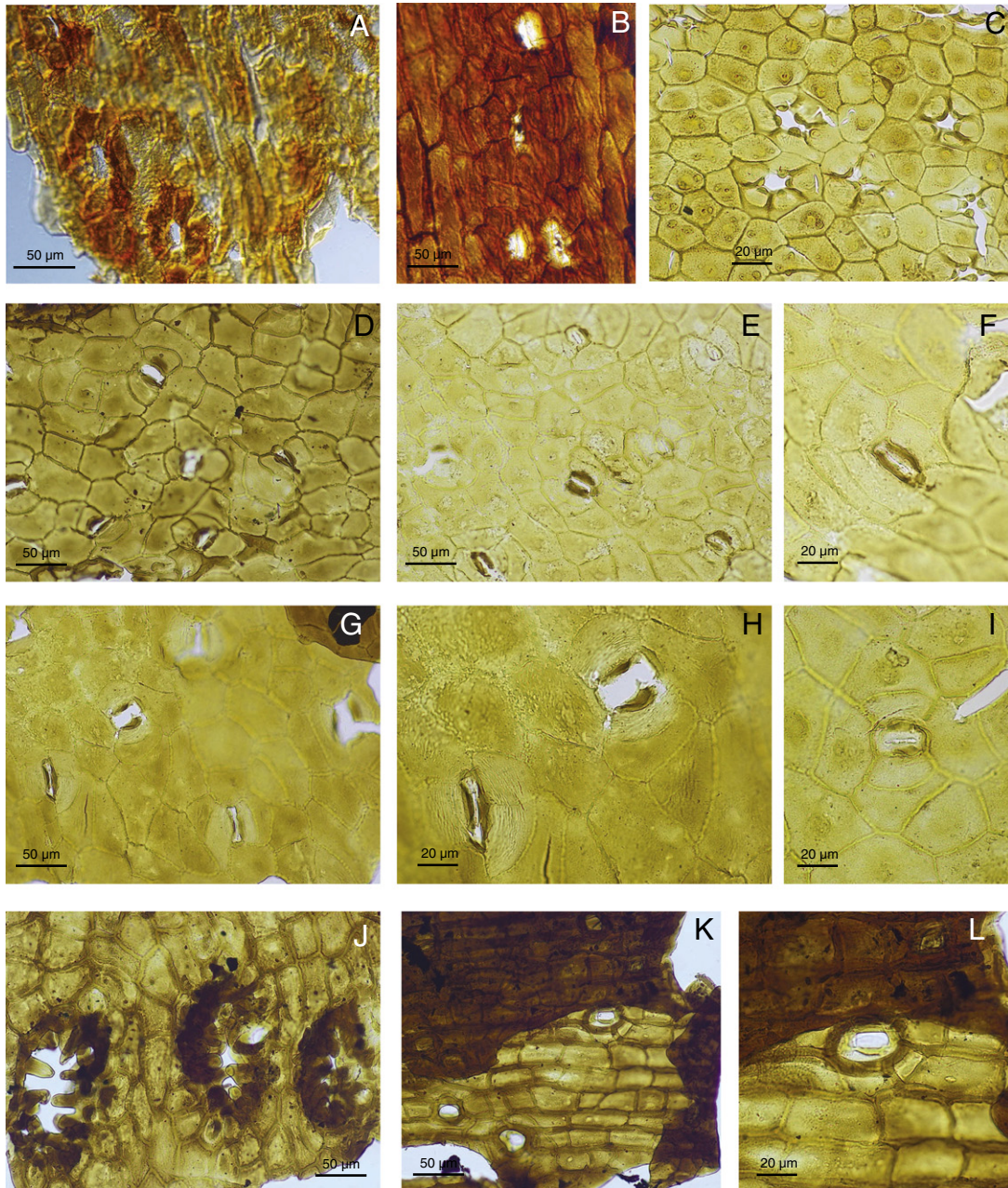


Fig. 3. Cuticles from the Amb section. Identified cuticle is followed by sample number and England Finder coordinates. All PIMUZ repository number A/VI 66. A: *Noeggerathiopsis* sp., AMB 34CO, P26/4. B: *Noeggerathiopsis* sp., AMB 34CO, T26/0. C: *Lepidopteris* sp., AMB 24 2.Präp. a, H21/4. D: *Dicroidium* sp., AMB 34C, S22/4. E, F, I: *Dicroidium* sp., AMB 45CO, X26/4. G, H: *Dicroidium* sp., AMB 45CO, P23/4. J: *Ruffloria/Noeggerathiopsis* sp., AMB 34C, M41/1. K, L: Unidentified cuticle, AMB 34C, E33/3–4.

4.3.2. Remarks

Cuticle and epidermal features of these fragments are typical of the peltasperm *Lepidopteris/Peltaspermum* in having (1) a homogeneous epidermal cell pattern, with irregularly arranged cells of rather uniform size and shape, (2) irregular and roughly even distribution of stomata, (3) stomatal complexes that are randomly oriented, almost circular in outline, and radially symmetrical, (4) usually five or six subsidiary cells, (5) conspicuously sunken guard cells, and (6) papillae overarching the stomatal pit (e.g. Townrow, 1960; Meyen and Migdissova, 1969; Bose and Srivastava, 1972; Anderson and Anderson, 1989; Poort and Kerp, 1990; Retallack, 2002; Zhang et al., 2012). With the subsidiary cells being similarly or even less cutinised than the surrounding regular epidermal cells, the present material is similar to *Lepidopteris* species reported from the Lower Triassic of India (e.g. Bose and Srivastava, 1972; Bose and Banerji, 1976).

4.4. Cuticle type 4 (*Dicroidium*) (Fig. 3D–I)

4.4.1. Description

Cuticles thin or only moderately thick. Regular epidermal cells with straight or slightly curving anticlinal walls and smooth (Fig. 3I), finely buttressed, or interrupted (Fig. 3D) cutinisation; periclinal wall surface either smooth, or with a single circular, low, diffuse thickening or hollow papilla (Fig. 3E), or showing ornamentation of fine longitudinal striae (see Fig. 3H). Epidermal cells of costal fields rounded rectangular or elongate polygonal, arranged in longitudinal rows, mostly oriented longitudinally; cells of free lamina irregularly arranged, of variable size, rounded polygonal, roughly isodiametric or slightly elongated (Fig. 3D, E, G). Stomata evenly distributed across the entire epidermis, oriented mostly either longitudinally or transversely to adjacent vein courses (Fig. 3D, E, G); few stomata oriented obliquely. Longitudinally

and transversely oriented stomatal complexes usually hourglass- or butterfly-shaped, i.e. with two to rarely four differentiated lateral subsidiary cells that are small, rounded-trapezoid, without papillae, and commonly less cutinised than surrounding regular epidermal cells (Fig. 3D, G–I); some obliquely oriented stomata surrounded by an incomplete to complete ring of up to seven subsidiary cells that are similarly differentiated; encircling cells common (Fig. 3H). Stomatal pit rectangular or spindle-shaped, commonly bordered by thickened proximal anticlinal walls of lateral subsidiary cells (Fig. 3D–I); guard cells only little sunken, feebly cutinised (Fig. 3F, I).

4.4.2. Remarks

Epidermal and cuticular features of the corystosperm foliage *Dicroidium* have been studied in great detail (e.g. Gothan, 1912; Jacob and Jacob, 1950; Archangelsky, 1968; Baldoni, 1980; Anderson and Anderson, 1983; Abu Hamad et al., 2008; Bomfleur and Kerp, 2010). Of special importance is the characteristic stomatal organisation that distinguishes *Dicroidium* from other gymnosperm groups (e.g. Lele, 1962; Rao and Lele, 1963; Retallack, 1977; Anderson and Anderson, 1983; Bomfleur and Kerp, 2010). With generally thin cuticle, weakly developed papillae, and relatively thin subsidiary-cell cuticle, the present material most closely resembles the cuticle morphology of *Dicroidium irnensis* Abu Hamad et Kerp (Abu Hamad, 2004) and *Dicroidium jordanensis* Abu Hamad et Kerp (Abu Hamad, 2004), which were recently described from the Upper Permian of Jordan (Abu Hamad et al., 2008).

5. The palynological record

The well-preserved spore–pollen assemblages from the Amb Valley section in the Salt Range provided a palynofloral signal across the Permian–Triassic boundary. The assemblages derive from the uppermost Permian Chhidru Formation, the so-called white sandstone unit, to the lowermost Triassic basal Mianwali Formation, including the Kathwai Member, the Lower Ceratite Sandstone and the basal part of the Ceratite Marls. Within the corresponding time interval, the flora underwent several quantitative changes, categorized here as floral phases (I to IV) (Fig. 4); palynological assemblages from the uppermost Permian white sandstone unit (phase I, 24 samples) are dominated by taeniate and non-taeniate bisaccate pollen grains such as *Protohaploxypinus* spp., *Falcisporites* spp. and *Sulcatisporites* spp. *Kraeuselisporites* spp. (lycophyte spores) occur consistently in low abundances. Ornamented trilete spores and monolete spores are present throughout. Their abundance increases slightly towards the top of the interval. The Griesbachian assemblage (phase II) is represented by a single sample. Gymnosperm pollen grains are still the dominant component, but compared to the underlying Permian assemblage, the non-taeniate bisaccate pollen proportion is reduced. *Densoisporites* spp. (lycophyte spores) and *Cycadopites* spp. (ginkgoalean or cycadophyte pollen) occur regularly. The Griesbachian to earliest middle Dienerian assemblage (phase III, three samples) shows a pronounced increase in *Densoisporites* spp. abundance. Taeniate and non-taeniate pollen grains are reduced in relative abundance or even absent (e.g. *Falcisporites*

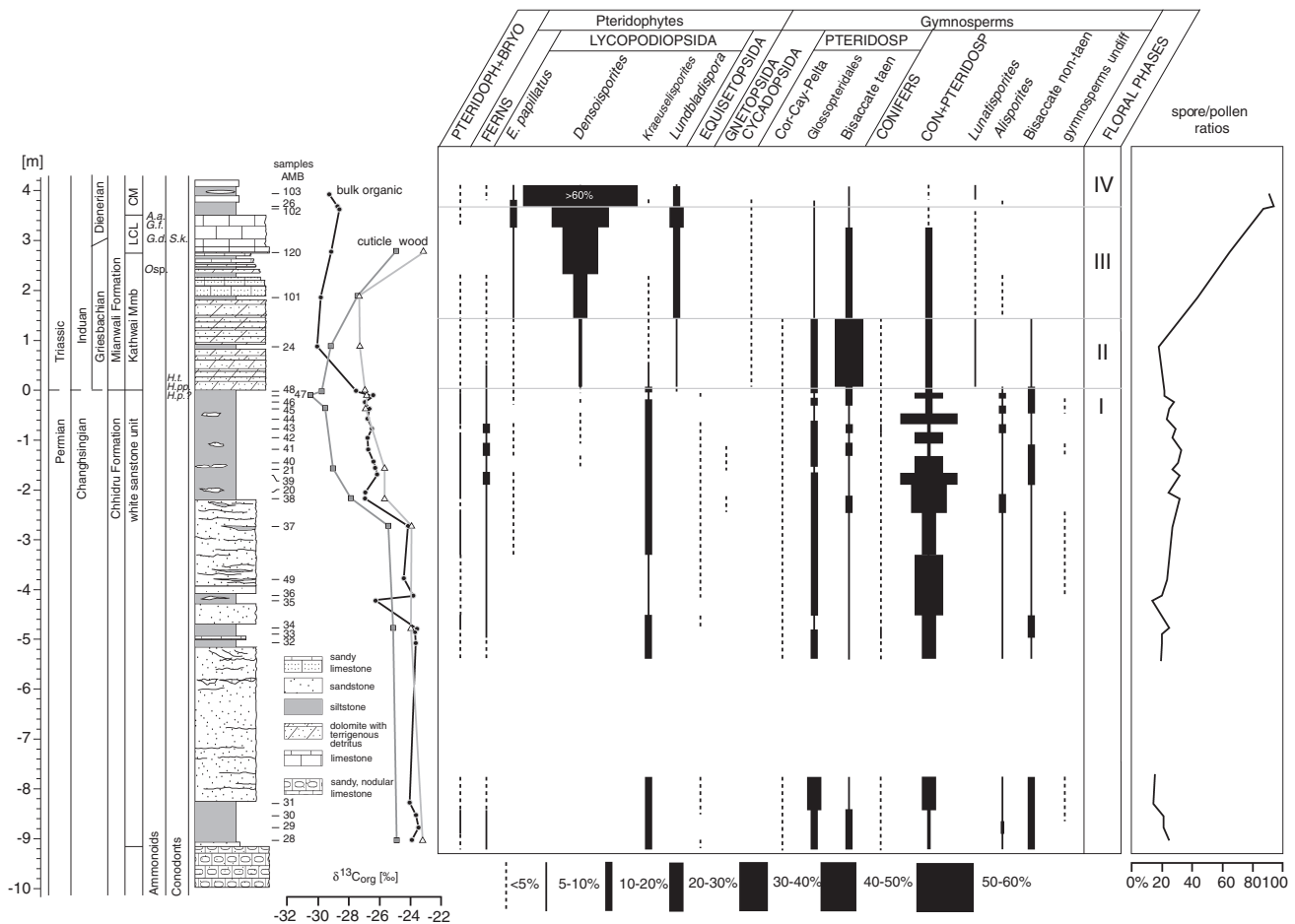


Fig. 4. Permian–Triassic lithology, biostratigraphy, C-isotopes, and floral phases. LCL = Lower Ceratite Limestone, CM = Ceratite Marls. Ammonoid and conodont biostratigraphy: A.a. *Ambites atavus*, G.f. *Gyronites frequens*, G.d. *Gyronites dubius*, O.sp., ?*Ophiceras* sp., S.k. *Sweetospathodus kummeli*, H.t. *Hindeodus typicalis*, H.pp. *Hindeodus praeparvus*, H.p.? ambiguous *H. parvus*. Organic carbon isotopes after Schneebeli-Hermann et al. (2013). Permian–Triassic vegetation succession of the Amb Valley section with floral phase (I–IV) and spore/pollen ratios. Cor = Corystospermales, Cay = Caytoniales, Pelta = Peltaspermales, CON + PTERIDOSP = Conifers and Pteridosperms undifferentiated.

spp., *Weylandites* spp., and *Vitreisporites* spp.). In the middle Dienerian assemblages of the basal Ceratite Marls (IV) *Densoisporites* spp. relative abundance exceeds 60% and the total spore component reaches 95%.

The trends evident in the range-through diversity and the generic richness (number of genera) across the Permian–Triassic boundary are similar (Fig. 5). The highest diversity is reached in the uppermost part of the Chhidru Formation, in an interval of 2 m below the formational boundary. Diversity markedly decreases in the Kathwai Member where 14 genera disappear between the samples AMB 48 and AMB 24. Diversity decreases further towards the Dienerian. Nine of the 14 genera that disappear at the formational boundary, have been observed in the overlying Lower Triassic strata (eight in the lower Smithian and one in the Spathian according to Hermann et al., 2012). Considering these Smithian and Spathian occurrences, the drop in range-through diversity is less severe (grey line and dots in Fig. 5).

Compared to Amb, the palynological data from Narmia are of low resolution (Fig. 6). The main differences between the two records are the high spore abundance in the uppermost Permian and the lack of appropriate Griesbachian samples. Spore abundances in the uppermost Permian (phase I) range between 50 and 60%, compared to maximum of 33% at Amb. Diversity in the Upper Permian is similar to that at Amb. However, the drop in diversity occurs only in the Dienerian, together with an increase in spore abundance (phase IV; Fig. 5). Due to the low sampling resolution, floral phases II and III are missing.

6. Discussion

6.1. 'Mesozoic' pteridosperms in the Upper Permian of Pakistan

The pteridosperm *Dicroidium* (Corystospermales) has been historically considered to be restricted to the Triassic of Gondwana (e.g. Gothan, 1912). Recent reports of *Dicroidium* from the Upper Permian Um Irna Formation of Jordan, however, indicate that this genus probably evolved in the palaeotropics during the Late Permian and migrated southward with the decline of the Gondwanan *Glossopteris* flora, eventually colonising the entire Gondwanan realm during the Middle and Late Triassic (Kerp et al., 2006; Abu Hamad et al., 2008). *Umkomasia*, the female fructification of *Dicroidium* has been reported from the Late Permian Raniganj Formation (Chandra et al., 2008). The age assignment is based on the co-occurring megafloora that contains elements of typical Late Permian *Glossopteris* flora and palynological assemblages. An independent proof, i.e. biostratigraphically or chemostratigraphically calibrated occurrence, for the existence of *Dicroidium* in the Late Permian of the Indian subcontinent is missing so far. The present finds of abundant *Dicroidium* cuticles in the Upper Permian Chhidru Formation fill an important gap in the stratigraphic and geographic range of corystosperm fossils; they demonstrate that corystosperms already co-occurred with typical Permian taxa (*Glossopteris*/*Gangamopteris*, *Noeggerathiopsis*) along the Tethyan margin of Gondwana during the Changhsingian. This extends the geographic distribution of the

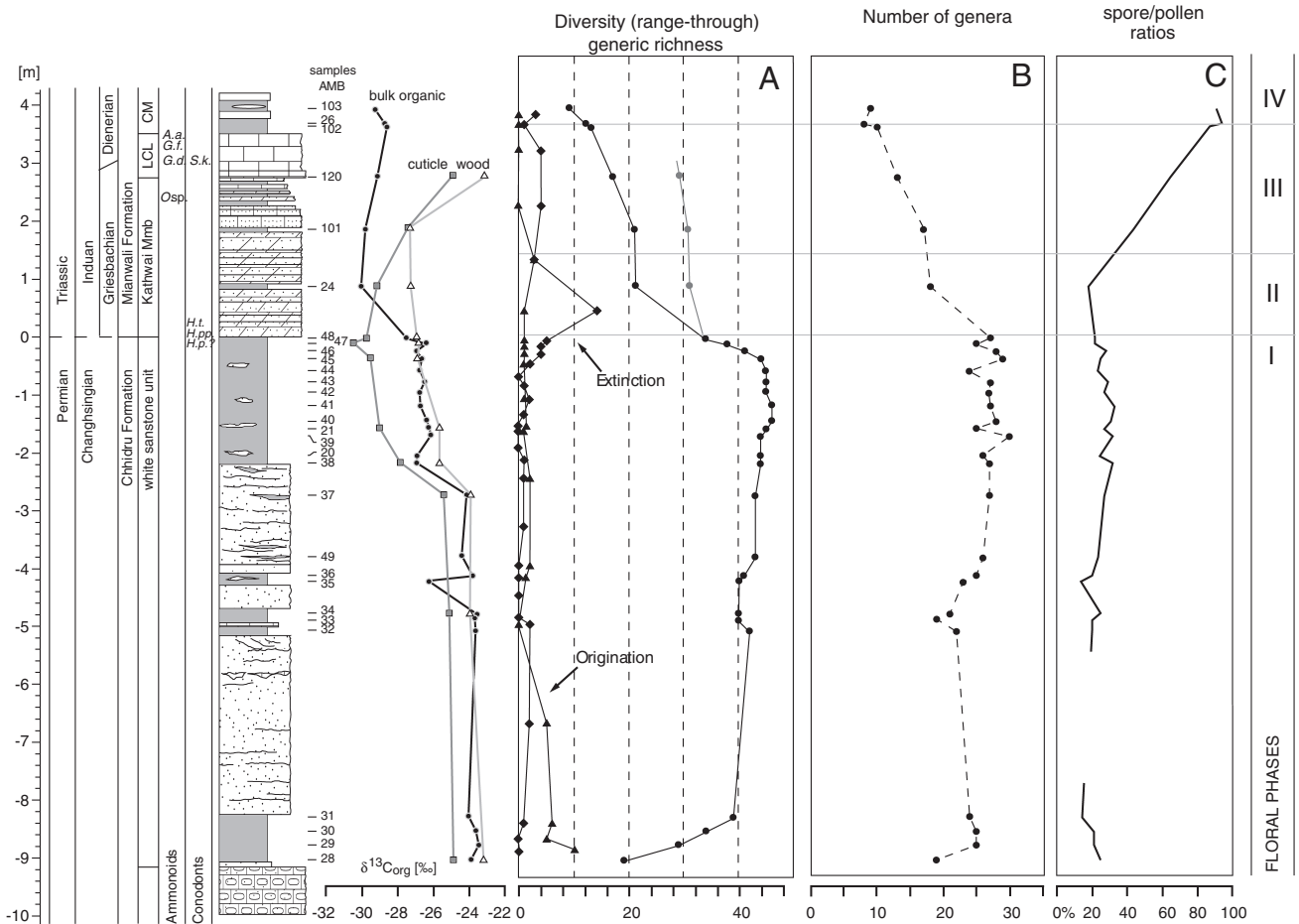


Fig. 5. Palynological generic diversity from the Amb Valley section. A: range-through diversity, with origination, and extinction records. Grey line and dots show the range through diversity considering palynomorph occurrences of Smithian and Spathian age after Hermann et al. (2012). B: generic richness. C: spore/pollen ratios. Ammonoid and conodont biostratigraphy: *A.a.* *A. atavus*, *G.f.* *G. frequens*, *G.d.* *G. dubius*, *O.sp.* *Ophiceras* sp., *S.k.* *S. kummeli*, *H.t.* *H. typicalis*, *H.pp.* *H. praeparvus*, *H.p.?* ambiguous *H. parvus*. Organic carbon isotopes after Schneebeli-Hermann et al. (2013). LCL = Lower Ceratite Limestone, CM = Ceratite Marls, see Fig. 4 for lithological legend.

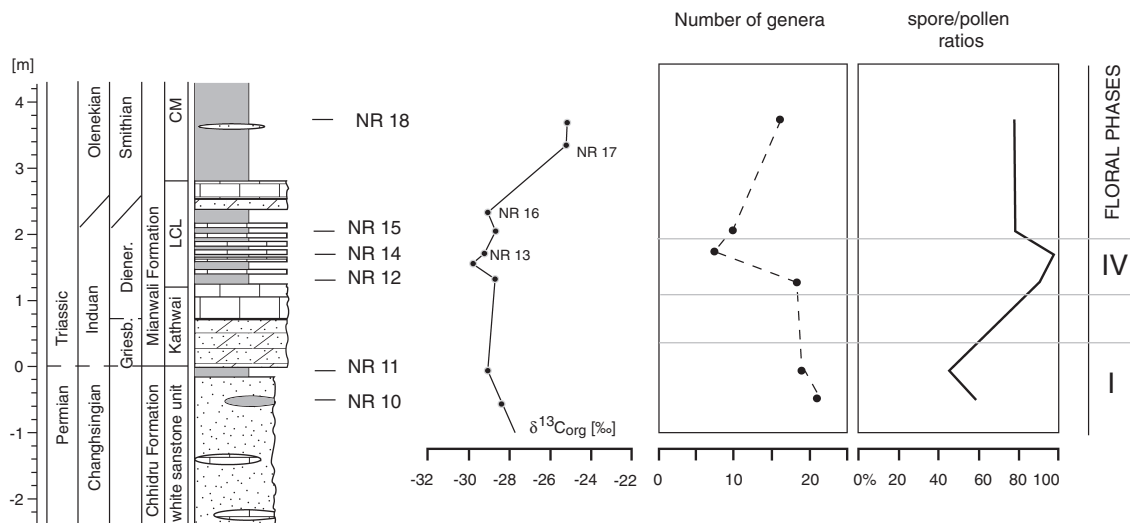


Fig. 6. Permian–Triassic lithology, C-isotopes, sporomorph generic richness and spore/pollen ratios at Narmia. Bulk organic carbon isotopes after Hermann et al. (2011b). LCL = Lower Ceratite Limestone, CM = Ceratite Marls, see Fig. 4 for lithological legend.

earliest, Palaeozoic occurrences of the pteridosperm *Dicroidium* from palaeotropical latitudes in modern Jordan (Kerp et al., 2006; Abu Hamad et al., 2008) into the mid-latitude regions (~30°S) in the southern circum-Tethys realm.

The biostratigraphy of the continental strata of the Indian subcontinent is based on palynology and macrofloral records (e.g. Sarbadhikari, 1974; Tiwari and Tripathi, 1992; Tiwari and Kumar, 2002). Stratigraphic uncertainties in these continental sequences, such as the identification of the Permian–Triassic boundary, are probably based on assumptions relating to the stratigraphic ranges of plant megafossils (Dutta, 1987). The Permian–Triassic transition has traditionally been identified by the disappearance of *Glossopteris* and the appearance of *Dicroidium* as a stratigraphic marker for the Triassic (e.g. Pant, 1996; Goswami, 2006).

The co-existence of *Glossopteris* and *Dicroidium* in the lower beds of the Indian Panchet Formation (Sarbadhikari, 1974) has been interpreted to represent an uppermost Permian sequence (based on the last occurrence of *Glossopteris*). The usefulness of the last occurrence of *Glossopteris* to define the top of the Permian has been questioned by several workers, who proposed *Glossopteris* to range into the Triassic (e.g. Acharyya et al., 1977; Dutta, 1987; Pant and Pant, 1987; McManus et al., 2002). In a recent study, the presence of *Glossopteris* together with the absence of *Dicroidium* has been used to define Permian strata in the Raniganj Basin, an important coalfield in India (Pal et al., 2010). Additionally, microfloral records from the same basin have been used to define the Permian–Triassic boundary (Fig. 7C, after Sarkar et al., 2003). Comparing the bulk organic carbon isotope record of the Raniganj Basin succession with the Amb valley record (Fig. 7), a different position of the Permian–Triassic boundary is suggested for the Raniganj Basin succession (Fig. 7D). In both sections (Amb and Raniganj) the bulk organic carbon isotope records show values of ~−23‰ at their base, followed by a first drop to values of ~−27‰ in the white sandstone unit at Amb and the Raniganj Formation in India, respectively. The minimum of the bulk organic carbon isotope excursion at Amb is probably corrupted by a sedimentary gap between the Chhidru and the Mianwali Formation (e.g. Schneebeli-Hermann et al., 2012b). However, the negative shift of carbonate carbon isotope at Nammal indicates that the carbon isotope minimum is close the formational boundary (Fig. 7A). The correlation of the carbon isotope minimum in the Salt Range with the carbon isotope minimum of the Raniganj Basin suggests a latest Permian age for the mixed *Glossopteris*–*Dicroidium* flora of the basal Panchet Formation supporting the interpretation of Sarbadhikari (1974) (Fig. 7D). In contrast, other recent assessments have assigned an Early Triassic age to the basal Panchet Formation based on macroflora

and microflora (Sarkar et al., 2003; Pal et al., 2010) (Fig. 7C). The presence of *Dicroidium* in the latest Permian of the Amb section on the Indian subcontinent thus provides further support for a Late Permian age of *Umkomasia* finds from the Raniganj Formation (Chandra et al., 2008).

6.2. The flora across the Permian–Triassic boundary in Pakistan

For the reconstruction of the vegetation history, palynological data have been translated into a parent plant record (Fig. 4, Table 1). Palaeopalynological assemblages reflect the flora of the hinterland of the basin (Muller, 1959; Traverse, 2007). However, there are some obvious taphonomic effects that need to be considered (Chaloner and Muir, 1968; Traverse, 2007), since the diverse morphologies of sporomorph taxa are subject to different buoyancy and transportation modes. Sporomorphs with higher buoyancy, e.g. bisaccate pollen grains, are bound to be transported over longer distances, and are generally more abundant in distal settings (e.g. highstand system tracts; Tyson, 1995 and references therein). For the proximal–distal trends in the present study see below.

Phase (1) The Late Permian flora is characterised by conifers and pteridosperms. Relative abundance of *Protohaploxylinus* spp. and *Striatopodocarpites* spp. indicate that Glossopteridales were an important constituent of the vegetation (Lindström et al., 1997). Conifers represented by pollen taxa such as *Sulcatisporites* spp. are a minor component of the vegetation. Suggested parent plants of *Falcisporites* spp. include peltasperms or early ginkgophytes, and specifically corystosperms (Balme, 1970; Taylor et al., 2006; Naugholnykh, 2013). Its presence in the Late Permian suggests that *Dicroidium*, a typical Mesozoic corystosperm, grew in the catchment area (Balme, 1970; Balme, 1995; Taylor et al., 2006). The shallow depositional setting of the white sandstone unit favoured the deposition and preservation of numerous land plant cuticles. Cuticles unequivocally assigned to *Dicroidium* prove the presence of corystosperms in the Late Permian of Pakistan (see also Section 6.1.). Therefore, the Late Permian flora of the Amb Valley represents a mixed *Glossopteris*–*Dicroidium* flora. Northern Hemisphere records (from Norway and Greenland) reveal a distinct spore spike in the uppermost Permian (Stemmerik et al., 2001; Hochuli et al., 2010). Hermann

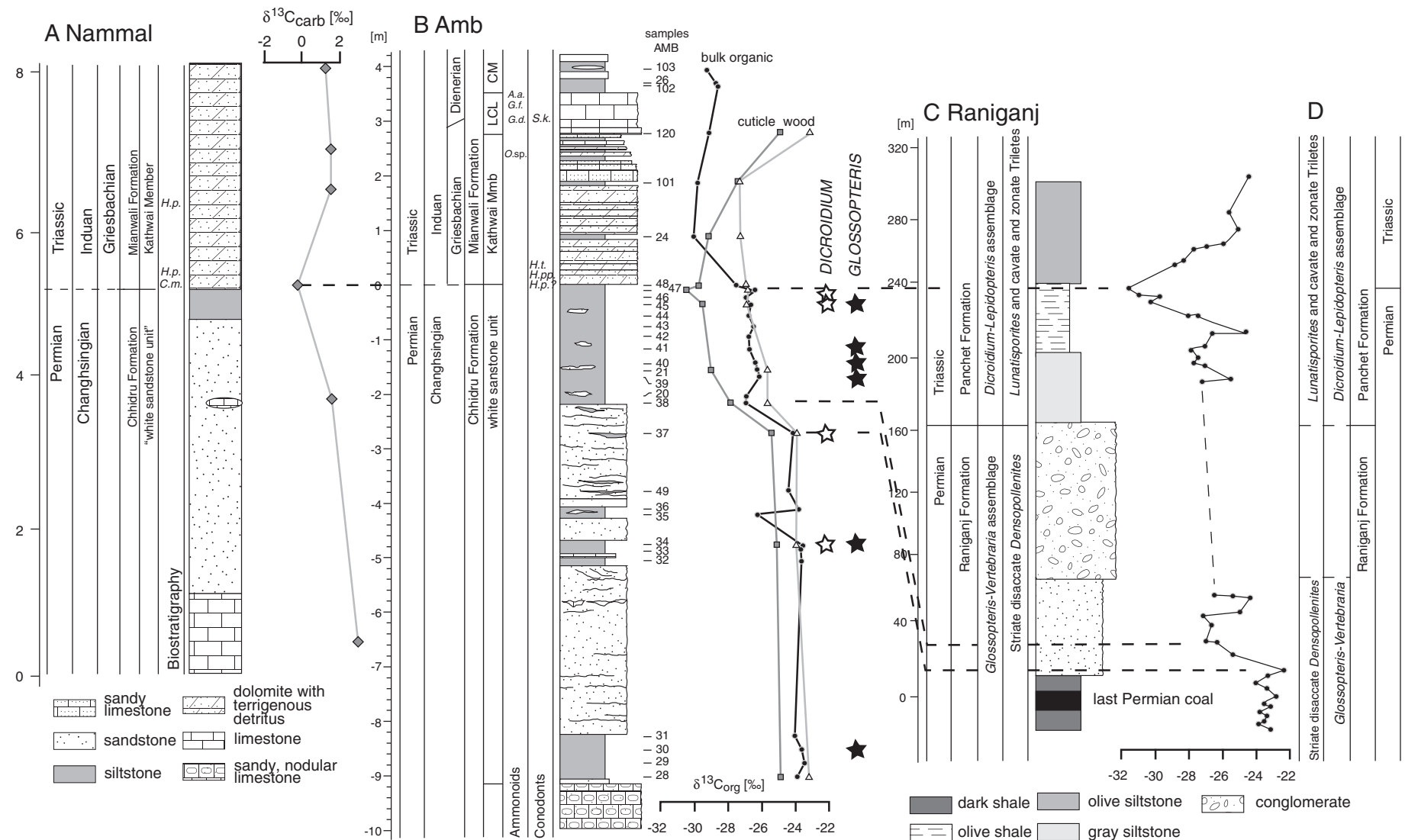


Fig. 7. A: Generalised lithology and biostratigraphy of the Chhidru Formation and Mianwali Formation and correlation with the Raniganj Basin. A: Carbonate $\delta^{13}C$ record from Nammal (Baud et al., 1996) together with extrapolated stratigraphic markers from other Salt Range sections H.p. = *H. parvus*, C. m. = *Clarkina meishanensis* (after Pakistani-Japanese Research Group, 1985; Wardlaw and Mei, 1999). B: The Amb valley section, organic carbon isotopes after Schnebeli-Herrmann et al. (2013). Upper Permian *Dicroidium* findings are indicated by stars. Ammonoid and conodont biostratigraphy: A.a. *A. atavus*, G.f. *G. frequens*, G.d. *G. dubius*, O.sp. *Ophiceras* sp., S.k. *S. kummeli*, H.t. *H. typicalis*, H.pp. *H. praeparvus*, H.p.? ambiguous *H. parvus*. C: Record of the continental series of the Indian Raniganj Basin, lithology, stratigraphy, and bulk organic carbon isotopes after Sarkar et al. (2003). D: Suggested new position of the Permian-Triassic boundary in the Raniganj Basin.

et al. (2012) noted similar high spore abundances (up to 60%) in the uppermost Permian of the Narmia section, Pakistan. Balme (1970) also described spore abundances of up to 60% from the uppermost part of the white sandstone unit at Wargal (about 15 km SE of Amb). These spore abundances were not observed in the Amb section. However, in the Australian Bowen Basin sequences, spore abundances of ~80% (*Lundbladispora brevicula*) are known from the lower part of Rewan Formation (de Jersey, 1979). Foster (1982) also reported cavate trilete spore abundances of 44–80% in the *Protohaploxylinus microcorpus* Zone of the lower Rewan Formation, which can be correlated with the palynological assemblages of the Chhidru Formation in Pakistan (Hermann et al., 2012). The Lower Triassic Kockatea Shale in Western Australia is also known for its high lycopod spore abundances (Balme, 1963). Its basal part is now considered to be of very latest Permian age (Shi et al., 2010). However, the exact stratigraphic position of these high spore abundances remains enigmatic and synchronicity with the Northern Hemisphere spore spike speculative. The absence of high spore abundances in the uppermost Permian at Amb might be due to regional variability of sedimentation rates and completeness of the late Permian strata (Mertmann, 2003). Sedimentary gaps at the 2.2 m level at Amb and at the formation boundary between the white sandstone unit and the Kathwai Member are likely.

Phase (II) Although the diversity decreases towards the Griesbachian, gymnosperms remained the dominant constituent of the vegetation. The increased relative abundance of taeniata bisaccates (excluding *Lueckisporites* spp.) indicates dominance of pteridosperms. Other changes are the appearance of *Lunatisporites* spp. and *Cycadopites* spp. The botanical affinity of *Lunatisporites* spp. is unclear. It has been assigned to conifers (Clement-Westerhof, 1974) and to pteridosperms (Townrow, 1962). The monosulcate pollen *Cycadopites* spp. has been associated not only with Cycadopsida but also with Ginkgopsida and the Peltaspermales (Balme, 1995). Cuticles recovered from the underlying white sandstone unit resemble those of the peltasperm *Lepidopteris*, which also had been associated with *Cycadopites* and other younger groups (Bennettiales and Pentoxylales) (Balme, 1995).

Phase (III) The main changes in the composition of the vegetation occur in floral phase III. Gymnosperm abundance decreases continuously whilst lycopod abundance increases. Cuticles are generally rare in these samples. This is due to the deepening (more distal) depositional environment and probably also due to the increasing dominance of pteridophytes, whose cuticles have a lower preservation potential. Palynofacies data and the lithology indicate that the sea level changed significantly within the studied interval (Schneebeli-Hermann et al., 2012b). Although the sediments of floral phase I were deposited under shallow-water conditions, those of floral phases II to IV were deposited in more open marine settings. A short interval of slight shallowing at the boundary between floral phase III and IV is indicated by the palynofacies data. According to the taphonomic effects described above, increasing pollen abundance can be expected with deepening of the depositional environment. Here, we observe that spores increase with deepening and the establishment of more distal depositional environments. The representative spores are predominantly cavate and the exospores may have induced a hydrological behaviour similar to that of bisaccate pollen grains sacci. However, cavate trilete spores even increase during the short interval of shallowing (AMB 26 and AMB 103) demonstrating that their relative

abundance is essentially independent of eustatic influence and primarily reflects the composition of the vegetation in the basin hinterland.

Phase (IV) Lycopods dominate the flora of the middle Dienerian with abundances of up to 90%. These spore abundances are comparable to the end-Permian and middle Smithian spore spikes reported from Norway and Pakistan, respectively (Hochuli et al., 2010; Hermann et al., 2011a). Similarly high lycopod spore abundances are also present in the Dienerian assemblages from Narmia (Fig. 6). High lycopod spore abundances is also characteristic for the *Kraeuselisporites saeptatus* Zone in Western Australia (uppermost Permian–Smithian Kockatea Shale, Perth Basin, Balme, 1963; Dienerian–Smithian Locker Shale, Carnarvon Basin, Dolby and Balme, 1976). On the other hand the records from Narmia and Nammal demonstrate that lycopod abundance decreases in the lower Smithian (Hermann et al., 2012). *Densoisporites* spp. has been described from cones of various species of *Pleuromeia* (Balme, 1995). Its dominance in the middle Dienerian assemblages (exceeding 60%) indicates that the vegetation was characterised by a remarkably high proportion of *Pleuromeia*. *Pleuromeia* has been considered to be an opportunistic plant occurring in monospecific stands especially in coastal habitats in Gondwana (Retallack, 1975, 1977).

The short term dominance of spores in the middle Dienerian of up to 90% is striking but not a singular event during Permian and Triassic times or even Earth history. Similar phenomena have been described to occur in the late Permian of Norway and Greenland (Stemmerik et al., 2001; Hochuli et al., 2010), in the middle Smithian of Pakistan (Hermann et al., 2011a), and in association with the Triassic–Jurassic boundary (Slovakia, Ruckwied and Götze, 2009; Hungary, Ruckwied et al., 2008; St. Audrey's Bay, UK, Bonis and Kürschner, 2012) and the Cretaceous–Paleogene boundary (New Zealand, Vajda et al., 2001). During these intervals lycopod and fern spores are exceedingly abundant due to extreme changes in vegetation structure (e.g. McElwain and Punyasena, 2007), involving a transient minimum in plant diversity. These intervals have been interpreted to reflect the reaction of plant communities to sharply changing environmental conditions (e.g. McElwain and Punyasena, 2007; Bonis and Kürschner, 2012). In the Amb record, sporomorph diversity decreases toward the middle Dienerian (Fig. 5) and lycopod spores become very abundant (Figs. 4, 6). Hence, the middle Dienerian sporomorph association shows the same features as those previously described intervals of high spore abundance.

Recent modern global empirical studies of dryland habitats, supported by experimental studies of the last two decades, suggest that plant biodiversity enhances the ability of ecosystems to maintain multiple functions, such as carbon storage, productivity, and the build-up of nutrient pools (called multifunctionality by Maestre et al., 2012). Intact plant biodiversity is interpreted to be the major driver in buffering negative effects of environmental changes that are harmful for animal life such as climate change and desertification (Maestre et al., 2012). It has even been proposed that plant diversity and multifunctionality of ecosystems positively correlate in stressed habitats. Hence, the consequences of biodiversity loss would be worse in harsh environments (Jucker and Coomes, 2012).

Assuming that ancient plant communities provided the same or very similar functions for animal life as they do today, the relationship between plant biodiversity and intact ecosystem would imply that during times of extreme spore abundance with reduced floral diversity, ecological support for fauna was reduced in a similar way.

A recent study on marine biodiversity and carbon cycling during the Triassic suggested that long-term reduced biodiversity led to changes in the biological pump efficacy and destabilized ecosystems (Whiteside

and Ward, 2011). It has been suggested that destabilized ecosystems affect the food web and hence the mode of carbon burial. Destabilized ecosystems have been proposed as one of the drivers for the huge carbon cycle perturbation during the Early Triassic (Whiteside and Ward, 2011).

The aforementioned ancient continental perturbations of floral biodiversity (global or regional changes in plant communities during the end-Permian, middle Smithian, Triassic–Jurassic, Cretaceous–Paleogene) are associated with extinction events. The end-Permian mass extinction has been characterised by catastrophic decimation of marine and terrestrial fauna (e.g. Raup and Sepkoski, 1982; Benton and Twitchett, 2003) and a delayed recovery of ~5 Myrs for benthic organisms (e.g. Fraiser and Bottjer, 2005). In recent studies the delayed recovery of the marine fauna has been challenged. Instead, several studies have documented that intervals of recovery were reset by renewed environmental perturbations (Brühwiler et al., 2010; Z.Q. Chen et al., 2011; Hautmann et al., 2011; Hofmann et al., 2011; Wu et al., 2012). Similar pictures have been drawn for the continental floras, with a catastrophic reduction in standing biomass and the demise of forests (e.g. Eshet et al., 1995; Steiner et al., 2003), followed by a long-lasting (5 Myr) recovery interval (Looy et al., 1999). In a recent review on the effects of the end-Permian extinction on terrestrial plants Benton and Newell (2014) still conclude that a fungal spike (high abundance of *Reduviasporonites*) represents the dieback of gymnosperms and initiates the Early Triassic dominance of pioneering plants. However, recent studies proved that floral dynamics around the Permian–Triassic boundary and during the Early Triassic were far more complex. High resolution records have shown that the relative abundances of floral components changed rapidly. A short interval in the end-Permian succession in Norway is dominated to 95% by lycopod spores but gymnosperm recovery followed within some 10 kyrs (Hochuli et al., 2010). From the Antarctic Prince Charles Mountains Lindström and McLoughlin (2007) reported an increase in spore–pollen diversity in the basal Triassic due to composite flora of lingering Permian taxa, transient pioneer taxa

and recovering floral elements. The correlation of the microfungal succession from the Maji ya Chumvi Formation, Kenya with Australian palynozonation suggests that these floras span the Permian–Triassic transition. This transition is marked there by a decrease in spores, especially lycopod spores and an increase in bisaccate pollen (Hankel, 1992).

The chronology of events for the Smithian was analysed in the succession from Pakistan. The lycopod spore spike (middle Smithian, not to be confused with the fungal spike consisting of *Reduviasporonites*!) precedes the marine extinction event in the late Smithian (Brühwiler et al., 2010; Hermann et al., 2011a). The reduced floral biodiversity probably reflects the environmental changes leading to the faunal extinction. Data on plant–insect associations (plant hosts and their insect herbivores) could be the mean to study trophic changes in deep time, however, available data is still too coarse to infer detailed patterns (Labandeira and Currano, 2013). The situation for the middle Dienerian is rather enigmatic, a late Dienerian or early Smithian extinction event in the marine realm has been suggested (Brayard et al., 2006; Galfetti et al., 2007a) but is not confirmed. The conclusion that the end-Permian mass extinction was less profound for plants (Benton and Newell, 2014) might be correct in taxonomical terms. Plant extinction rates might have been not as high as in the marine fauna, however, terrestrial ecosystems very well responded distinctly to environmental changes during and after the end-Permian mass extinction event.

Together with earlier studies (Hochuli et al., 2010; Hermann et al., 2011a) the recent palynological results show that the picture of the “delayed recovery” of the terrestrial vegetation has to be revised in a similar way as the supposed delayed recovery of marine fauna. The end-Permian and Early Triassic time was marked by repeated ecological crises as reflected in successive episodes of spore abundance (end-Permian, middle–late? Dienerian, middle Smithian) and corresponding recovery phases (end-Permian, early Smithian, late Smithian–early Spathian; Fig. 8) reflecting the unstable environmental conditions during that time.

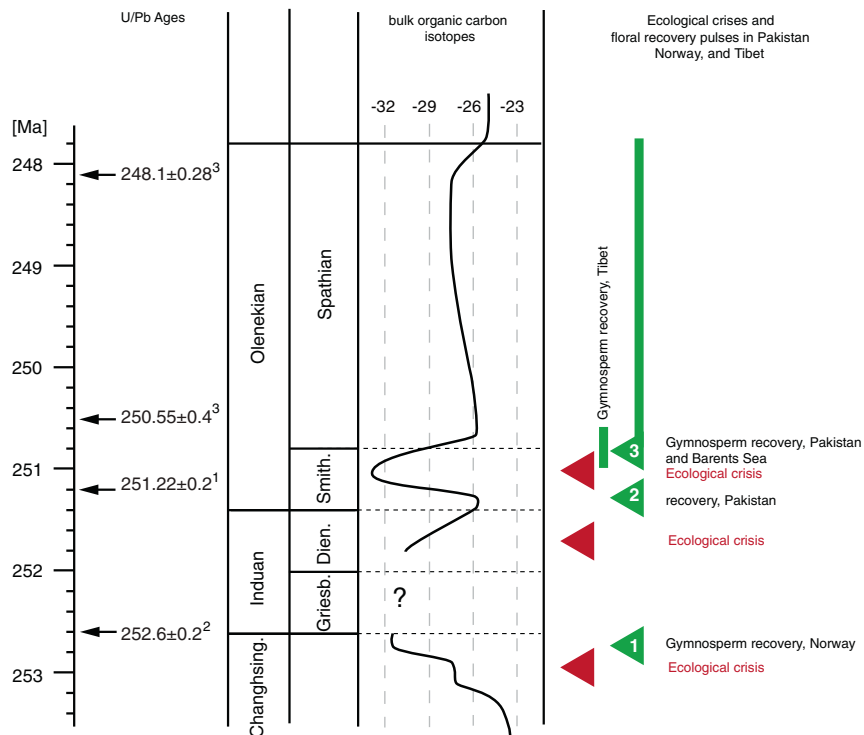


Fig. 8. Successive ecological crises and recoveries in terrestrial vegetation from the end-Permian to the Early Triassic. Floral recovery pulses as recorded in the end-Permian to Lower Triassic successions from the northern mid-latitudes (Norway: Hochuli et al., 2010) and the southern subtropics (Pakistan and Tibet: Hermann et al., 2011a; Schneebeli-Hermann et al., 2012a and this study). U/Pb ages after 1) Galfetti et al. (2007b), 2) Mundil et al. (2004), and 3) Ovtcharova et al. (2006). Schematic bulk organic carbon isotopes after Hermann et al. (2011b) (Early Triassic, Pakistan) and Schneebeli-Hermann et al. (2013) (Permian–Triassic boundary, Pakistan).

7. Conclusions

The Permian–Triassic palynofloral record from Amb, Salt Range, Pakistan has a rather low resolution due the shallow depositional environment that included hiatuses in the Upper Permian and a rather condensed Griesbachian. Therefore, the short-term changes as documented in other Permian–Triassic sections were not observed at Amb and a rather gradual floral change across the Permian–Triassic boundary is observed. The Late Permian flora is marked by a mixed *Glossopteris*–*Dicroidium* association. The findings of *Dicroidium* cuticles in the Chhidru Formation prove the presence of this typically Triassic corystosperm genus in the Late Permian of the Indian subcontinent. They further imply new age constraints on the Indian continental successions. Based on our new data we suggest a Late Permian age for the lowermost part of the Indian Panchet Formation in the Raniganj Basin. Close to the formational boundary between the Chhidru and the Mianwali formations, which has been used as approximation for the Permian–Triassic boundary, several sporomorph genera disappear. However, most of them reappear in the overlying Lower Triassic Mianwali Formation (after Hermann et al., 2012). The lower part of the Mianwali Formation up to the middle Dienerian is characterised by an increase in lycopod spores and a continued loss in diversity. The high spore abundances in the Dienerian assemblages might reflect a similar ecological crisis as previously proposed for other spore spikes associated with biodiversity crises (e.g. Permian–Triassic, middle Smithian, Triassic–Jurassic, and Cretaceous–Paleogene). Despite the biodiversity crises in Earth history might have had different causes (asteroid impacts, large igneous province emissions, etc.) the responses of terrestrial ecosystems (vegetation) seem to be similar.

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