



Proliferation of abnormal palynoflora during the end-Devonian biotic crisis

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The dispersed spore assemblage of the *Retispora lepidophyta-Verrucosisporites nitidus* (LN) Zone from the Holy Cross Mountains (Poland) is marked by enrichment (above 4%) in abnormal spore morphotypes during a terrestrial flora turnover close to the Devonian–Carboniferous boundary, recorded just above the Hangenberg Black Shale level. Incomplete and complete tetrads represent mostly *Vallatisporites* spp., supplemented by *Grandispora*, *Retusotriletes* and *Apiculiretusispora*. Additional peculiar morphotypes, marked by anomalous overall shape and ornamentation, are interpreted as mutated varieties of *Vallatisporites* based on intermediate morphological stages, connecting them with this well known genus. This relatively high aberrant palynomorph frequency is accompanied by volcanic ash intercalations, as well as by charcoal debris and polycyclic aromatic biomarkers indicative of forest wildfire. Thus, the anomalous spore morphology could reflect the mutagenic effect of regional acidification due to explosive volcanism. However, palynological literature data from NW France and Canada highlight the possibility of a supra-regional mutated spore signal near the Devonian–Carboniferous boundary, and there is need for high-resolution studies of the LN Zone to examine this. The end-Permian scenario of abnormal floral growth in immensely stressed habitats may therefore apply to other potentially volcanically-induced biotic turnovers.

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INTRODUCTION

The multiphase Devonian–Carboniferous (D–C) biotic turnover, associated with the anoxic Hangenberg Event, is not known as one of the “Big Five” mass extinctions (Walliser, 1996; Hallam and Wignall, 1997; Kaiser, 2005), but its significance has recently been emphasized (e.g., Racki, 2005; Alroy, 2008). During this interval, the glacial episode in the D–C boundary transition is well represented in Gondwana, recorded primarily in a profound sea level fall (Streel *et al.*, 2000; Sandberg *et al.*, 2002; Haq and Schutter, 2008; Isaacson *et al.*, 2008). Thus, the preceding gradual cooling is commonly accepted as the main oceanographic trigger, leading to efficient mixing and increased nutrient inventories that resulted in amplified primary productivity, the spread of benthic anoxia (even to the photic zone; Marynowski and Filipiak, 2007), and a final marine demise (Hallam and Wignall, 1997; Caplan and Bustin, 1999; Brand *et al.*, 2004; Kaiser, 2005; Cramer *et al.*, 2008). The biocrisis is distinctly recorded in many marine groups, and pelagic and hemipelagic faunas (e.g., ammonoids, conodonts,

ostracods) were more strongly influenced than were neritic faunas (with the exception of reef builders; see summary in Kaiser, 2005). According to Riding (2009), the terrestrial and marine ecosystems were impacted by shifts in atmospheric composition (CO₂ fall, O₂ rise) promoted by the expansion of vascular land plants, and this would have restructured phytoplankton, increased marine photosynthesis and bioinduced calcification, and transformed the food supply to benthic habitats. However, in the light of new oxygen isotope and conodont data, environmental changes, including climatic shifts, appear to have been more complex than previously supposed (Kaiser *et al.*, 2006, 2008).

The terminal Devonian timespan was a far more severe crisis for terrestrial plant evolution than the earlier highlighted Frasnian–Famenian (F–F) mass extinction (see review in Hallam and Wignall, 1997). Both the vascular plants and spores show a dramatic turnover close to the D–C boundary, just above the Hangenberg Black Shale (HBS) (Fairon-Demaret, 1996; Streel *et al.*, 2000), to signal the end of the Hangenberg Event *sensu lato* (Brand *et al.*, 2004); note, however, that Kaiser (2005, fig. 2; 2009, fig. 1) prolongs the multiphase Hangenberg crisis interval well into the earliest Carboniferous. Possible causes are connected with strong changes of edaphic

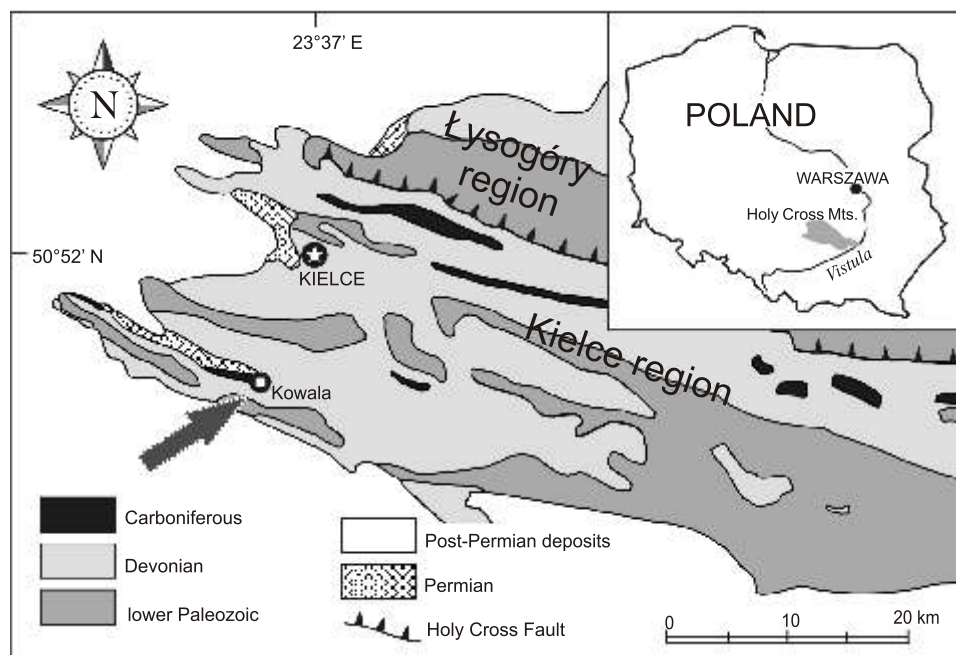


Fig. 1. Simplified geological map showing the study area in Poland and in the Holy Cross Mountains

The arrow indicates the area investigated

factors, caused by global regression coincident with the rapid climate cooling. Collapse of widespread Late Devonian swamp vegetation is directly recorded in the palynostratigraphical succession, for example in the disappearance of such common uppermost Famennian miospore genera as *Retispora* and *Diducites* (Streel *et al.*, 2000; Streel, 2009). The persistence of a cool climate in the Tournaisian resulted in the final establishment of new Carboniferous-type vegetation.

As demonstrated by high-resolution study of a newly-exposed D–C deep-shelf pyroclastics-bearing succession in central Poland (Kowala Quarry in Holy Cross Mountains, Fig. 1; Marynowski and Filipiak, 2007; Trela and Malec, 2007), other stresses may also have contributed to the end-Devonian biotic turnover, particularly for the micro-evolutionary processes of terrestrial, free-sporing vegetation. A noticeable enrichment in spore tetrads and other abnormal palynomorphs is recognized in this locality (see Marynowski and Filipiak, 2007, fig. 9d–g). The significance of this finding is discussed in the context of a possible mutational response to devastating volcanic activity, also via comparison with the anomalous end-Permian palynofloral signature (Visscher *et al.*, 2004).

METHODS AND MATERIAL

Seventeen samples were collected from the lower part of the section, but due to severe weathering, only three contained adequate palynological residues (Fig. 2). Fifteen samples were collected from the upper part of the section, but only seven were palynologically productive (for details see Marynowski and Filipiak, 2007). Rock material was processed using stan-

dard laboratory methods for samples containing mineral matter (e.g., Wood *et al.*, 1996). For statistical analysis, 1000 miospores (including tetrads) were counted from each sample. Over 3000 miospores were determined only for the K3 sample, as well as 500 miospores that were counted for three stratigraphically older H samples, due to the lower concentration of terrestrial particles in this Famennian interval (Fig. 2). In summary, a large collection of well- and very well-preserved palynomorphs, mostly miospores and prasinophytes, was obtained, and more than 100 of them reveal more or less distinctive abnormal characters. For more information concerning detailed palynological investigation, species diversity, recognized phytoplankton taxa and other additional and supporting geochemical data see Marynowski and Filipiak (2007). The palynological slides and residues are housed at the Faculty of Earth Sciences of the University of Silesia in Sosnowiec.

RESULTS

PALYNOSTRATIGRAPHY

Palynostratigraphy of the 10 cm thick claystone layer (K3 sample), from just above the Hangenberg Black Shale (Fig. 2), was primarily based on the joint occurrence of *Retispora lepidophyta* and *Verrucosisporites nitidus* (Fig. 3) and established as the LN miospore Zone (Clayton *et al.*, 1974). More intensive study of organic material from the K3 horizon during the present research revealed the limited presence of *Verrucosisporites nitidus*. This taxon was not observed during the previous palynological review when fewer particles were counted in slides from the same sample

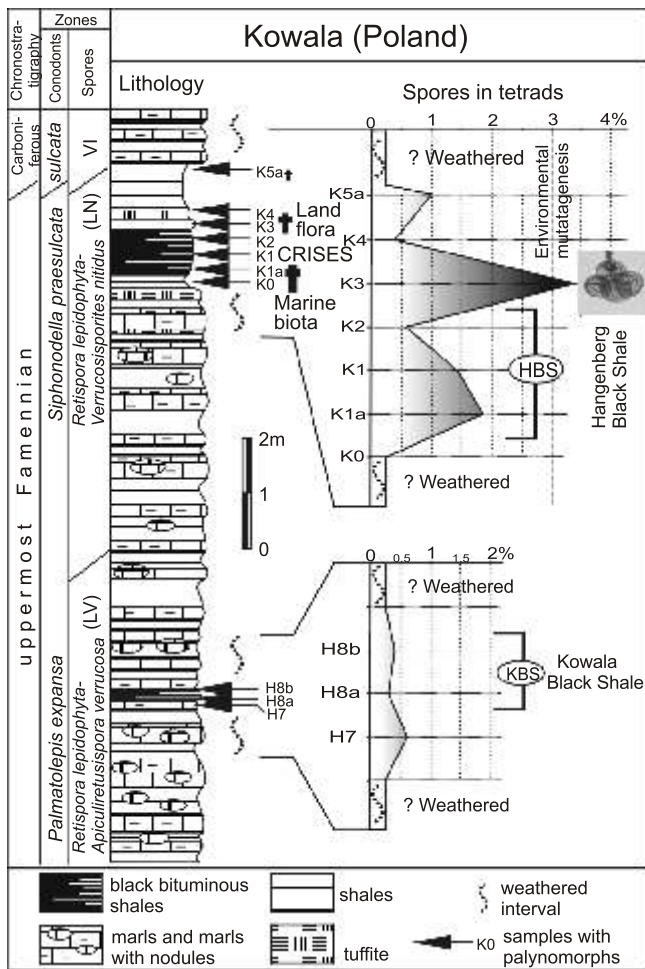


Fig. 2. The uppermost Famennian – basal Carboniferous succession at Kowala Quarry (after Marynowski and Filipiak, 2007), with evolving percentage of miospore tetrads

Extinction steps during the Hangenberg Event *sensu lato* are shown after Brand *et al.* (2004, fig. 9) and Kaiser (2005, fig. 2); note the peak tetrad abundance (above the benchmark of palynomorph abnormality for environmental mutagenesis; Foster and Afonin, 2005) exactly in the floral crisis horizon

(Filipiak in Marynowski and Filipiak, 2007). It is worth mentioning that both eponymous taxa appear in very restricted amounts (< 1%) in the K3 sample, but this does not contradict the previous palynological research from the upper Famennian of the Holy Cross Mountains (e.g., Filipiak, 2004). Besides those guide species, other miospores characteristic of the LN Zone were also recognized in the K3 sample. Very frequent are *Vallatisporites vallatus*, *V. verrucosus* and *V. pusillites* (Fig. 3). According to Clayton *et al.* (1977) in Western Europe *Vallatisporites pusillites* and *V. verrucosus* appear together only in the LN miospore Zone. Furthermore, *V. pusillites* has its upper stratigraphic limit in this zone and is a characteristic species of the LN Zone of the East European Platform (Byvsheva and Umnova, 1993). Additionally, *V. vallatus* appears in the succeeding VI horizon for the first time (e.g., Clayton and Turnau, 1990). Thus, two scenarios are possible to explain the appearance of these three species together in a single horizon: (1) redeposition or (2) an earlier appearance of *V. vallatus* here than in Western Europe. More-

over, in Belarus (Avkhimovitch, 1992; Avkhimovitch *et al.*, 1992) *V. vallatus* is known from the PM local zone which is the stratigraphic equivalent of the upper part of the LN Zone in Western Europe. This may indicate that *V. vallatus*, as in the regions located east of Poland, appears in the uppermost Famennian. This observation constrains the position of the sample investigated, and indicates that the K3 sample is not older than the upper part of the LN miospore Zone. *Diducites versabilis*, an important index for the upper Famennian, is still rarely present in these assemblages. Other species typical of the LN Zone noticed here are: *Apiculiretusispora verrucosa*, *Bascaudaspora submarginata*, *Grandispora echinata*, *G. lupata*, *Kraeuselisporites mitratus*, *Pustulatisporites dolbii*, *Tumulispora malevkensis* and *T. rarituberculata*. In addition, abnormal miospores and miospore tetrads were also observed in the assemblage (see below).

The presently described miospore assemblage, excluding tetrads and abnormal miospores, is similar to those described previously from Eastern Europe (e.g., Byvsheva *et al.*, 1984; Filipiak, 2004). The very uncommon appearance of *Retispora lepidophyta* and *Diducites* spp. indicates a decline phase of the coastal lowland vegetation (= LN transitional *sensu* Higgs *et al.*, 1993). The same floral turnover scenario took place in Western Europe but supposedly somewhat later, just before the D–C boundary (see Streel, 1999, 2009; Streel *et al.*, 2000), although Kaiser (2009) emphasizes wide-ranging correlation errors linked with the system boundary stratotype at La Serre (Montagne Noire, France). Besides the dominant land-derived palynomorphs, marine phytoplankton is present as well, but in the restricted amounts in the succession under study, consisting of rare specimens of poorly differentiated *Leiosphaeridia* spp.

ABNORMAL PALYNOFACIES CHARACTERISTICS

The present palynological investigation reveals that miospores in the Kowala samples studied were relatively frequently released in unseparated tetrads (Fig. 4). The nearby D–C borehole section was studied previously but without such surprising results due to a low sampling density (Turnau, 1985, 1990; Table 1). Only three samples were assigned to the critical Devonian–Carboniferous interval by Turnau (1990): two of them were assigned to the LN and the one to the VI miospore Zones (see Turnau, 1990). In this study, the number of miospore tetrads in the HBS is between 0.5% and 2%, and reaches over 3% in a thin (10 cm) claystone layer, just above the HBS (sample K3 in Fig. 2). Although different microfloral genera are represented by tetrads, the most frequent are *Vallatisporites* spp., supplemented by incomplete and complete tetrads of *Grandispora*, *Retusotriletes* and *Apiculiretusispora* as well (Fig. 4).

Together with relatively abundant tetrads, additional peculiar palynomorph morphotypes in the K3 sample are marked by anomalous overall shape and ornamentation, probably belonging to abnormal specimens of *Vallatisporites* (Fig. 5) or *Cristatisporites*(?), although they are not as frequent as are tetrads. There is a problem with exact frequency estimation, because some part of the population appears in an intermediate stage, and therefore it was difficult to classify them either to known genera or as abnormal taxa (see Fig. 5). Generally, in fi-

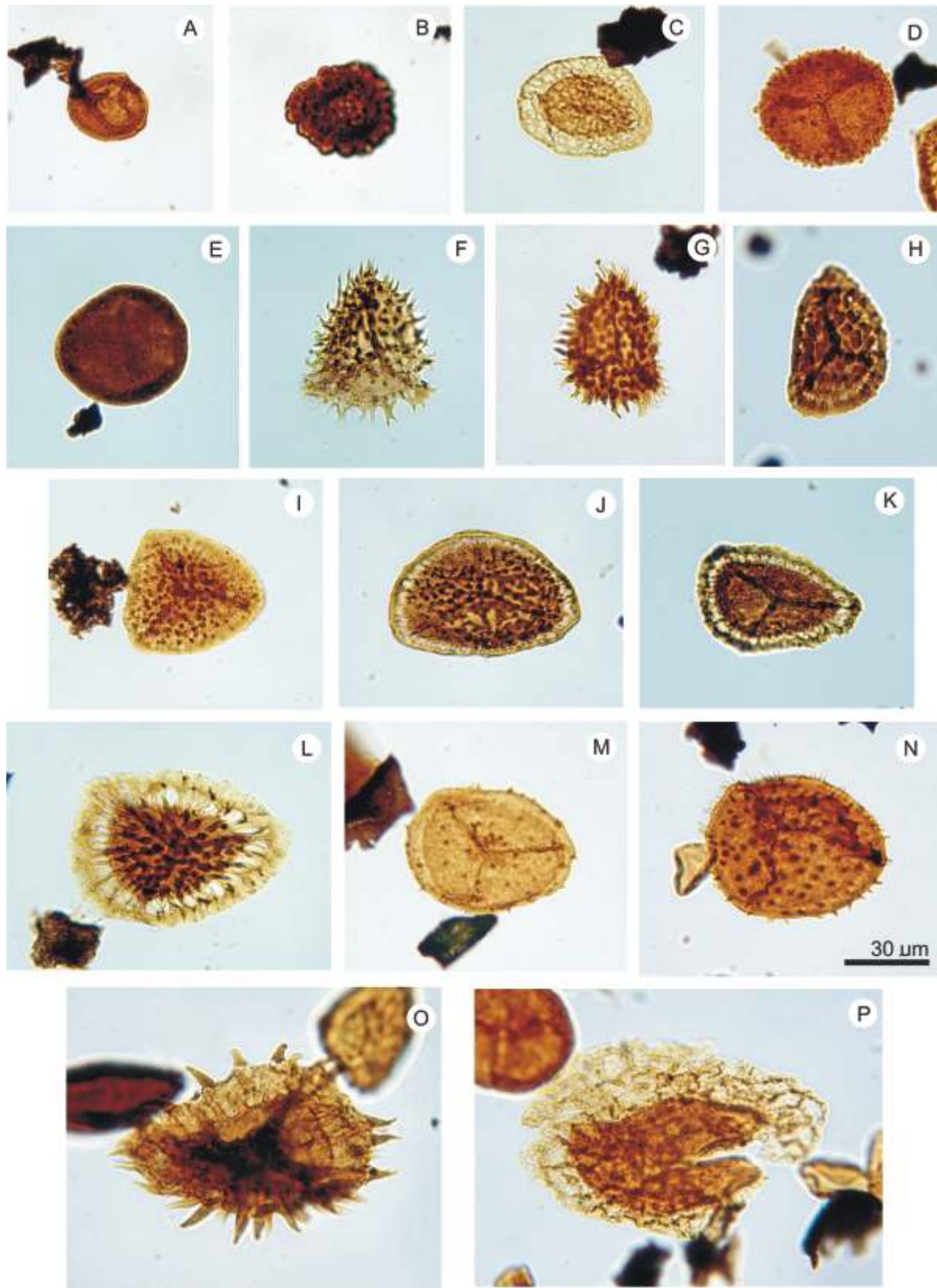


Fig. 3. The typical miospore assemblage for the LN miospore Zone in sample K3 from the uppermost Famennian of Kowala Quarry

A – unrecognized *Archaeozonotrites*-type of trilete miospore with very little echinate ornamentation; B – *Verrucosporites nitidus* Playford, 1964; C – *Retispora lepidophyta* (Kedo) Playford, 1976; D – *Apiculiretusispora verrucosa* (Caro Moniez) Streeel in Becker *et al.*, 1974; E – *Retusotrites incohatus* Sullivan, 1964; F, G – *Kraeuselisporites mitratus* Higgs, 1975; H – *Vallatisporites verrucosus* Hacquebard, 1957; I–K – *Vallatisporites vallatus* Hacquebard, 1957; L – *Vallatisporites pusillites* (Kedo) Dolby and Neves, 1970; M – *Grandispora echinata* Hacquebard, 1957; N – *Grandispora micronulata* (Kedo) Avkhimovitch, 2000; O – *Spinozonotrites uncatius* Hacquebard, 1957; P – *Retispora macroreticulata* (Kedo) Byvsheva, 1985. Magnification for all pictures is shown in N

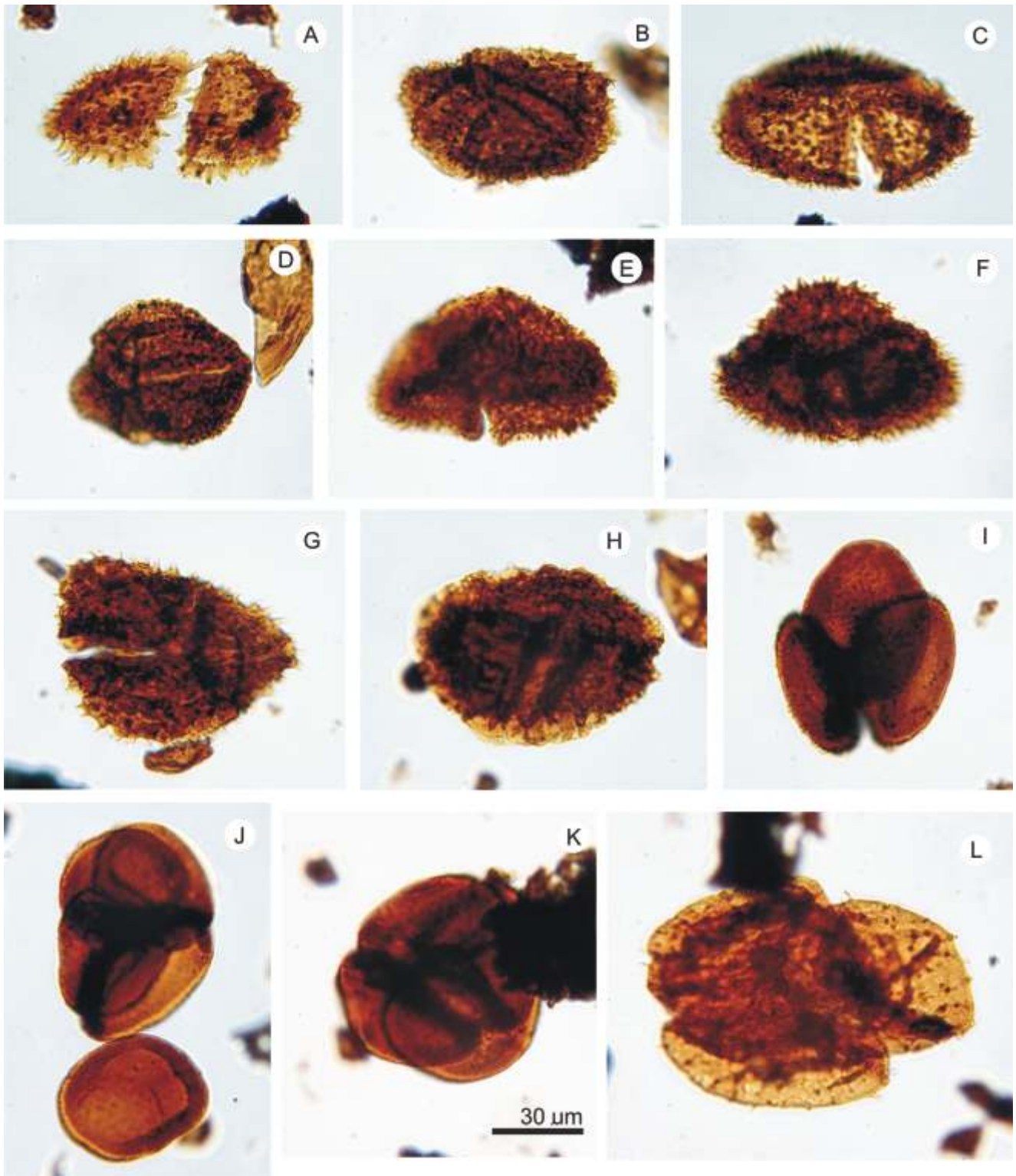


Fig. 4. Different types of miospore tetrads from sample K3 (LN Zone, Kowala Quarry)

A – separate, not complete tetrad of *Vallatisporites*; B–H – tetrad variety of *Vallatisporites* sp.; I – tetrad of *Apiculiretusispora verrucosa* (Caro Moniez) Strel in Becker *et al.*, 1974; J, K – tetrad and single taxa of *Retusotriletes incohatus* Sullivan, 1964; L – tetrad of *Grandispora* sp. Magnification for all pictures is shown in K

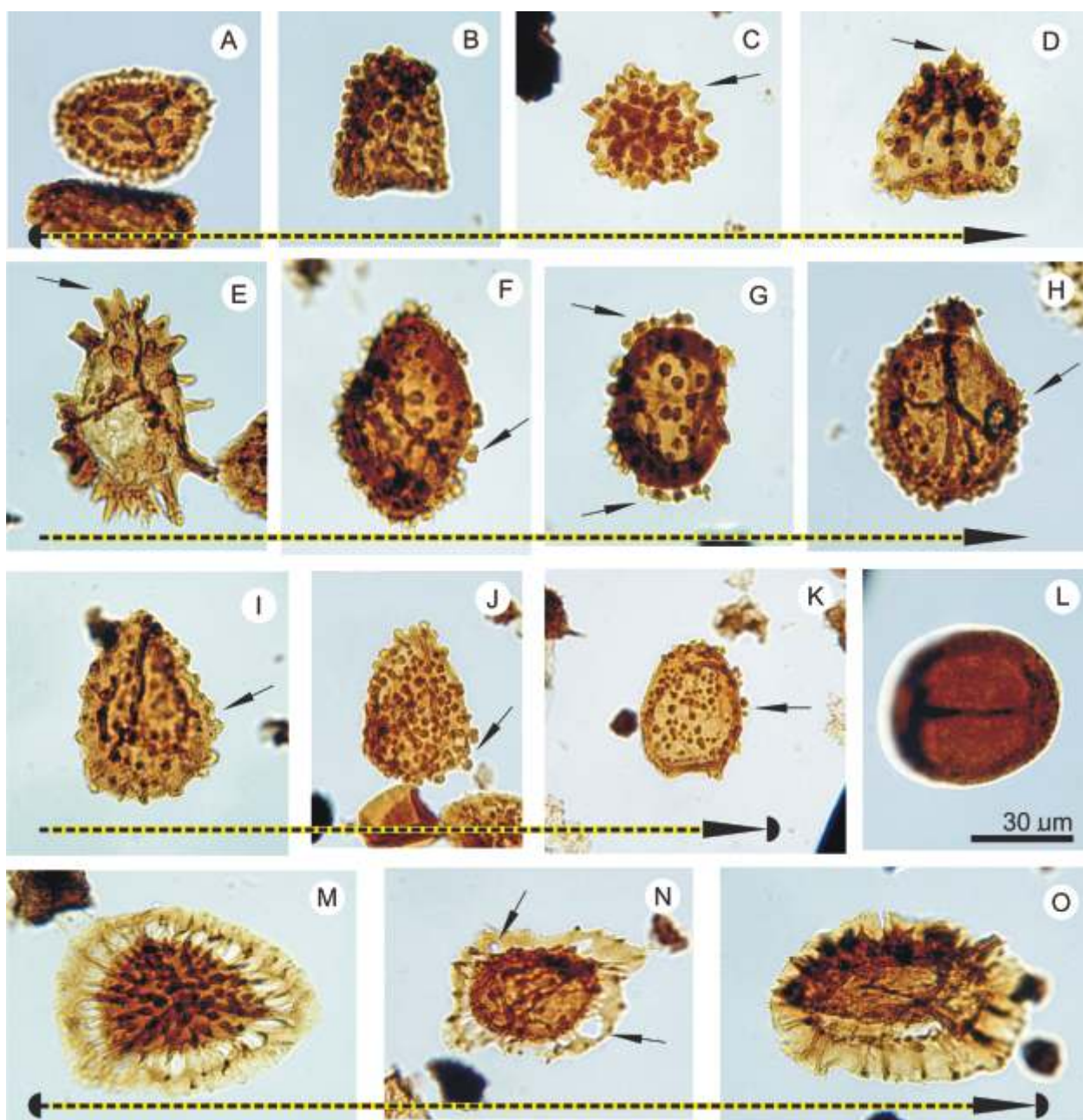


Fig. 5. Abnormal, mutated(?) and untypical miospores from sample K3 (LN Zone, Kowala Quarry)

A – *Vallatisporites verrucosus* Hacquebard, 1957 common miospore in the uppermost Famennian; B–K – some variations of general body construction and ornamentation changes of *Vallatisporites verrucosus*(?); see long broken line arrows (A–K). Stages on B–D show taxa very similar to *V. verrucosus*; E shows an example with solid, long ornamentation with small spines at free end and without cingulum with vacuoles; F–I show next stages not so strongly connected with *V. verrucosus*. Miospores are differentially built, possessing this same type of ornamentation: a bulbous appendages with thin echinae spines (see small black arrows). Generally, from F to K they possess different types of body construction, not typical of *Vallatisporites*. J and K show specimens possessing finer ornamentation but of the same kind as previously shown (compare F and G with J and K). All these forms perhaps represent abnormal types and/or mutations of *Vallatisporites* spp.(?); L – miospore similar to *Retusotriletes*(?) but possessing a monolete laesure mark; M – *Vallatisporites pusillites* (Kedo) Dolby and Neves, 1970; N, O – variation in body construction of *V. pusillites* leading to absolute vacuole reduction in the cingulum; see other long broken line arrows (M–O). N shows intermediate stage with irregular vacuoles (small black arrows); O shows a specimen possessing similar ornamentation on the central body to *V. pusillites* but with a cingulum free of vacuoles (perhaps representing different genera?). Magnification for all pictures is shown in L

nal mutant stages, their morphology exceeds the established morphological boundary of normalcy within a population. In other circumstances, excluding mutation, the morphological changes are so profound that a new genus might be established.

For mutant-enriched sample K3 from the claystone layer (Fig. 2), almost 100% of countable kerogen components is of terrestrial origin. Also the absence of amorphous organic matter indicates generally normal oxic conditions at the bottom (see Marynowski and Filipiak, 2007).

SUMMARY OF PALYNOLOGICAL DATA
AROUND THE D–C BOUNDARY

The uppermost Famennian strata, corresponding to the Hangenberg Event and younger than the D–C boundary strata, have been intensely studied in many natural exposures (Higgs and Strel, 1984), trenches (Higgs and Strel, 1984; Higgs *et al.*, 1993; Strel, 1999; Filipiak, 2004) and boreholes (Turnau, 1978; Higgs and Strel, 1984, 1994; Byvsheva *et al.*, 1988; Davies *et al.*, 1991; Filipiak, 2004; González *et al.*, 2005). Al-

most all these papers concern only palynostratigraphy and some bio-correlations based on microflora. We report herein the exceptional occurrence of miospore tetrads over the broad D–C boundary, and the crucial successions are reviewed below in this intriguing context (see summary in Table 1).

The most detailed palyno-environmental study has been done by Strel (1999), who summarized sedimentological and palaeoclimatological data together with refined palynological quantitative analysis and proposed complex environmental scenarios for the latest Famennian based on samples taken from the Ourthe Valley (Belgium) and Sauerland (Germany), with-

Table 1

Eighteen selected papers, dealing with the uppermost Devonian to Devonian–Carboniferous transition palynostratigraphy from different parts of the world, analyzed in the context of tetrad record and possible causes of their absence

Author(s)	Country/region	Palynostratigraphy/ chronostratigraphy	The main goal of paper	Tetrads: noticed (+) or not (-), and probably why?
Avkhimovitch <i>et al.</i> (1988)	European part of former USSR	LV–VI (Famennian–Tournaisian)	correlation of eastern and western zones	(-) not mentioned in text
Becker <i>et al.</i> (1974)	Belgium	upper Famennian– Lower Carboniferous	palaeoecological	(+) noticed
Davies <i>et al.</i> (1991)	Wales, Glamorgan Vale	LN–PC (Famennian–Tournaisian)	palaeoenvironmental, palynostratigraphical	(+) noticed
Filipiak (2004)	Poland, Holy Cross Mountains	CVa–CM (Famennian–Tournaisian)	palynostratigraphy	(-) weathered samples, stratigraphical gap and not frequent sampling
González <i>et al.</i> (2005)	S Spain, Iberian Pyrite Belt	VCo, LN (Famennian)	palynostratigraphy, miospores description	(-) palynoflora overheated
Hartkopf–Fröder (2004)	Germany, Ardennes–Rhenish Massif – Refrath 1 borehole	LL (Famennian)	palynostratigraphy	(+) noticed
Hartkopf–Fröder and Strel (1994)	Germany, Ardennes–Rhenish Massif, Paffrath Syncline	LV (Famennian)	palynostratigraphy	(+) noticed
Higgs and Strel (1984)	Germany, northern “Rheinisches Schiefergebirge”	LL–HD (Famennian–Tournaisian)	palynostratigraphy	(-) stratigraphical gap and/or not frequent sampling
Higgs <i>et al.</i> (1988)	Ireland	LL–CM (Famennian–Tournaisian)	palynostratigraphy, systematic, stratigraphic distribution, zonal scheme creating	(-) not frequent sampling
Higgs <i>et al.</i> (1993)	Germany, Rhenish Massif Stockum trench II, Hasselbachtal borehole	LN/VI (Famennian/Tournaisian)	palynostratigraphy	(-) most probable interesting beds (Stockum – 161, 151) omitted in sampling
Loboziak <i>et al.</i> (1994)	Belgium, Namur Synclorium Menen borehole	GF, LN, PC (Famennian, Tournaisian)	palynostratigraphy	(-) not frequent sampling
Maziane <i>et al.</i> (1999)	Belgium, Ourthe Valley	VCo–LE (Famennian)	miospore zonation – revision	(-) very detailed investigation, but not sufficiently stratigraphically extended
Melo and Loboziak (2003)	Brazil, Amazon Basin	wildely zonation including LN/VI interval (Devonian–Carboniferous)	palynostratigraphy, local zonal scheme creating (summarizing paper)	(-) not mentioned in text
Stempień–Satek (2002) and partly Turnau (1978)	Poland, Western Pomerania	RD–Cl (Famennian–Tournaisian)	palynostratigraphy, systematic, local zonal scheme creating	(-) stratigraphical gap
Strel (1999)	Belgium, Ourthe Valley; Germany, Stockum trench II	LN/VI (Famennian/Tournaisian)	palaeogeographical, palaeoclimatological, palaeoenvironmental	(-) most probable interesting beds (Stockum – 161, 151) omitted in sampling
Turnau (1985, 1990)	Poland, Holy Cross Mountains	LN/VI (Famennian/Tournaisian)	palynostratigraphy	(-) not frequent sampling

out mentioning tetrads in this high-resolution analysis. Higgs *et al.* (1993) presented a refined palynostratigraphy of the D–C transitional interval from the Stockum trench II (Germany). They obtained palynological organic material from 21 samples but the critical stratigraphical interval, in our opinion [i.e., layers 161 and 151, just above the black(?) shale; see fig. 1, p. 552 in Higgs *et al.*, 1993], was omitted in the sampling. Similar data from the Hasselbachtal borehole (Higgs *et al.*, 1993) came from the Hangenberg shale interval, indicating the LN miospore Zone, but the section was not so densely sampled (see fig. 2, p. 555 in Higgs *et al.*, 1993). Moreover, also not so densely sampled were the boreholes described by Higgs and Streeel (1994) from the key D–C intervals from the Rhenish Slate Mountains in Germany. On the other hand, another higher-resolution palynological investigation by Maziane *et al.* (1999) reached only the LE Zone, just below the LN level due to unfavorable facies (limestone).

Detailed palynological analyses have been made in Southern Spain, in the Iberian Pyrite Belt (González *et al.*, 2005; Sáez *et al.*, 2008). In the Gondwanan region there are two black shale horizons dated as the LN Zone (see fig. 2 in González *et al.*, 2005), but unfortunately the palynomorphs have been overheated, and miospore tetrads were not noticed.

Meanwhile, in other palaeoenvironmental and palynofacies papers, miospore tetrads have been reported from the broader D–C boundary interval. Davies *et al.* (1991) observed the constant but low-frequency occurrences of tetrads in south-east Wales. Hartkopf-Fröder and Streeel (1994) also noticed more abundant tetrads in the LV Zone in the Bergisch Gladbach–Paffrath Syncline of the Rhenish Slate Mountains (Germany). From the same region, Hartkopf-Fröder (2004), in samples from the Refrath 1 borehole has found complete and incomplete miospore tetrads, dated palynologically to the LL Zone (*sensu* Maziane *et al.*, 1999). Significantly, based on the occurrence of the diverse acanthomorph acritarch assemblage and accompanying typical marine fauna, normal marine conditions were postulated for this palynofacies (Hartkopf-Fröder, 2004). This is in opposition to the common view that a profusion of miospore tetrads indicates a near-shore environment (e.g., Batten, 1996; see below). Taking into account the hitherto reported frequency of miospore tetrads, it seems that the Rhenish Slate Mountains area is the most promising region, where refined sampling, bed by bed, would help constrain the uppermost Famennian palaeoenvironmental history.

However, older palynostratigraphic data from other regions are also noteworthy because Combaz and Streeel (1971) described a remarkable assemblage from the D–C boundary (Hangenberg shale) interval in the Brévillers borehole (Pas-de-Calais, NW France) including *Raistrickia variabilis*, distinguished by overgrown and deformed ornamentations of spines, ridges and thickened tubercles (see Combaz and Streeel, 1971, p. 229, pl. 3: 3–9). The authors suggest that similar “quasi teratological” features characterize the coeval Famennian palynofloras from Canada illustrated by McGregor and Owens (1966, pl. 28: 26–27, pl. 29: 9–10). Also, Streeel (2009, p. 173) in discussing the Upper Devonian miospores of western Europe, reported the occurrence of *Verrucosiporites*

nitidus with atypically small verrucate ornamentation. Those rare morphotypes were noticed just above the HBS (Hasselbachtal section, Sauerland, Germany; see also Higgs and Streeel, 1994).

In summary, mutated palynomorphs have rarely been reported from the critical D–C interval for many reasons (Table 1), but according to our observations from Kowala, their maximum concentration is directly above the HBS, and this horizon should be preferentially examined in future high-resolution studies of the LN miospore Zone.

DISCUSSION

Among the spore-producing plants recorded in the end-Devonian palynofacies from Kowala, *Vallatisporites* belongs to lepidophyte cones, whereas *Retusotriletes* and *Apiculiretusispora* could be produced by a number of other pteridophyte groups such as sphenopsids (Traverse, 2007). These plants are probably most common in the parental coastal (“coal”) swamp vegetation (Streeel *et al.*, 2000; Streeel, 2009).

Tetrads are treated as a palaeoenvironmental indicator (Tyson, 1993). Their exceptional enrichment in sediments is rather common in shallow, palaeoshore-proximal and/or prodelta environments (e.g., Batten, 1996), near to the parent flora (they are four times bigger than single trilete spores). Judging from the dark, clayey-carbonate sediment type (Fig. 2) and mostly pelagic biota, it is obvious that a critical part of the Kowala succession was deposited in a deep-shelf environment (Marynowski and Filipiak, 2007). Unfortunately, the samples from the intervals just below and above the HBS horizon in the locality are weathered, organic-poor marls not useful for palynology, but the quantity of miospores in tetrads is “normal”, close to 0.5%, in the underlying bituminous level (Fig. 2). As shown by extensive study of Upper Devonian and lower Carboniferous sites in the region (above 200 samples; see Filipiak, 2004), the typical abundance of spore tetrads is very low, essentially below 1%. Such normal tetrad concentrations has been observed in Famennian samples from the *annulata* and Dasberg Black Shales, studied recently by the first author from the same Kowala succession (Filipiak in Marynowski *et al.*, 2010). Davies *et al.* (1991) noticed similarly infrequent tetrads (below 1%) in all coeval 37 investigated samples from south-east Wales. Accordingly, this percentage reflects an approximate palynofacies signature of background intraspecific variation among Devonian spore-bearing plants in an offshore sedimentary setting, as also seen in representative palynofloras from the Permian–Triassic (P–T) transition (Foster and Afonin, 2005). When combined with the exclusive co-occurrence of aberrant spore varieties (Fig. 5), the highest tetrad abundance only just above the HBS level, i.e., during the highlighted “miospore events” very near the D–C boundary (Streeel *et al.*, 2000, 2009; Fig. 2), is accepted as a real ecological phenomenon, and not as a trivial taphonomic effect of variable sorting.

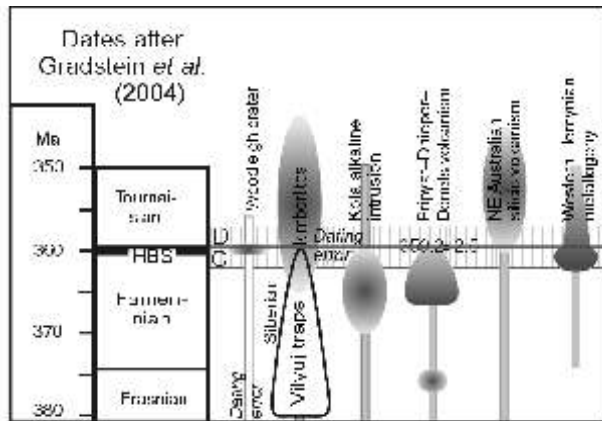


Fig. 6. Selected Earth-bound and extraterrestrial event signatures around the D–C boundary, showing their poorly documented correlation with the global biotic crisis (Hangenberg Black Shale – HBS) because of radiometric age errors and the long-lasting multiphase nature of igneous activity (partly based on fig. 4 in Racki, 2005, and references therein; Wilson and Lyashkevich, 1996; Lescuyer *et al.*, 1998; Courtillot and Renne, 2003; Bryan *et al.*, 2004; Downes *et al.*, 2005; Keller, 2005; González *et al.*, 2006); for the Siberian volcanism alternative dating of flood basalt volcanism and diamondiferous kimberlite explosive activity is shown, respectively after Pirajno *et al.* (2009) and Agashev *et al.* (2004)

ENVIRONMENTAL STRESS AND SPORE/POLLEN MUTATION PHENOMENA

In recent pollen grains, an anomalously large morphological variation is a proxy for a high mutation rate in stressful life conditions, induced by either environmental pollutants, or primarily by intense ionizing and ultraviolet (UV–B) radiation due to a stratospheric ozone collapse caused by a diversity of processes (e.g., Dzyuba, 1998; Ries *et al.* 2000; Visscher *et al.*, 2004; Koti *et al.*, 2005; Lomax *et al.*, 2008). In fact, plants are exposed to multiple environmental disturbances concurrently, and their reproductive processes are highly susceptible to global climate change factors such as CO₂, temperature, and UV radiation, although there were no positive feedbacks between these lethal driving forces (Koti *et al.*, 2005). On the other hand, extant *Pinus* pollen grains, studied by Miñeta and Murín (1998), demonstrate clearly that heavy industrial pollution and/or acidification (fluorides and SO₂) can strongly influence local tree populations, recorded in aberrant varieties (see other examples in Dzyuba, 1998, 2006; Foster and Afonin, 2005). The mutational symptoms are recorded mostly by the occurrence of permanent tetrad configurations, a grouping of four embryophytic spores that result from atypical meiotic division of one mother cell (e.g., Dzyuba and Tarasevich, 2001; Visscher *et al.*, 2004).

Several studies have highlighted dramatic ecosystem consequences of sulphur-rich volatiles outgassed into the stratosphere during volcanic explosive activity, which are progressively converted into sulphate aerosols that eventually formed acid rains (e.g., Chenet *et al.*, 2005; Grattan, 2005; Dzyuba 2006). The ecological trauma, as displayed by the Icelandic 1783 Laki basaltic eruption, may be continental in extent, and plant life is seriously disturbed, together with fruiting (Grattan,

2005). Most recent results imply that huge volumes of S and Cl volatiles were released from even single lava flows in some ancient flood basalt provinces, and their environmental impact was probably far more disastrous than hitherto assumed (Scaillet, 2008). Thus, anomalous spore morphology could certainly also reflect the mutagenic effect of environmental change due to explosive volcanism, on a geographical scale at least comparable to major industrial SO₂ pollution (see review of volcanically induced stresses in Dale *et al.*, 2005). Humid domains, marked by weakly buffered soils, are particularly susceptible to volcanogenic and anthropogenic acidification (Kilian *et al.*, 2006).

As summarized by Foster and Afonin (2005), percentages above 3% of abnormal pollen are commonly used as a proxy to monitor recent air pollution, and therefore, a comparable abundance of mutated pollen and spores is a signal of fertilization failure in stressed ancient habitats. In the fossil record, however, such a specifically anomalous palynofacies (tetrads and aberrant morphotypes) has been exclusively associated with the end-Permian event (Marynowski and Filipiak, 2007). Common teratologies in lycopod spores and more frequently in gymnosperm pollen, and other deformed varieties, occurred around the P–T boundary worldwide (Visscher *et al.*, 2004; Foster and Afonin, 2005), with the exception of the Antarctic domain (Collinson *et al.*, 2006). Aberrant spores and pollen are found at between 3 and 15%, but occasionally reaching even 40–60% of all palynomorphs. Visscher *et al.* (2004) and Foster and Afonin (2005) hypothesized that frequent abnormal palynomorphs provides evidence for chronic environmental mutagenesis in the surviving end-Permian terrestrial floras. The land vegetation is hence a sensitive proxy for identifying the biotic response to major environmental stress (Visscher *et al.*, 2004; McElwain and Punyasena, 2007), and a central component of volcanism-extinction scenarios (Wignall, 2005, 2007; van de Schootbrugge *et al.*, 2009). Excessive subaerial emission of hydrothermal organohalogens in vast areas affected by the Siberian Traps eruption, coupled with thermogenic production of the pollutants, led to raised UV stress as a result of ongoing stratospheric Cl and Br increase and ozone collapse (Visscher *et al.*, 2004). As simulated by Beerling *et al.* (2007), protracted exposures to harmful radiation during a 100–200 kA eruptive phase, combined with other deleterious factors (such as acid rain from SO₂, high CO₂ and H₂S fluxes, rapidly rising temperatures; Kump *et al.*, 2005; Racki and Wignall, 2005; Scaillet, 2008), may have played a decisive role in floral destruction (e.g., Visscher *et al.*, 2004; Wignall, 2007).

IMPLICATIONS FOR THE END-DEVONIAN BIOTIC CRISIS

More frequent tetrads have been reported mainly from late Famennian alluvial-lagoonal to proximal-marine facies in the Ardennes–Rhenish Massif (Streel in Becker *et al.*, 1974; Hartkopf-Fröder *et al.*, 2007). The quantitatively undefined enrichments are simply explained by hydrodynamic sorting in shallow-water settings, especially since contemporaneous distal environments are characterized by decreased tetrad frequencies (Hartkopf-Fröder, 2004, p. 81). Notably, the offshore

Rhenish “abnormal” (tetrad-rich) palynofacies is limited to the LL miospore Zone (*sensu* Maziane *et al.*, 1999), below the HBS, and therefore approximately coeval with “background” tetrad frequencies in the Polish succession (Fig. 2).

This tetrad enrichment is accompanied by volcanic ash levels at Kowala, and, as recently recognized, by a large amount of charcoal debris and polycyclic aromatic biomarkers indicative of forest wildfire (Marynowski and Filipiak, 2007). The latter compounds have been interpreted by van de Schootbrugge *et al.* (2009) as a record of incomplete combustion of plant matter by outpouring lavas. Anomalous spore morphology could certainly reflect the mutagenic effect of regional environmental acidification and other stresses due to volcanic eruptions, as reviewed above (?also extremely toxic polycyclic aromatic hydrocarbons; see van de Schootbrugge *et al.*, 2009). A similar case may be, for example, abundant undissociated spore tetrads (8.5 to 16%) in Old Red Sandstone fluvial deposits associated with lava piles, interpreted by Lavender and Wellman (2002) as reflecting primitive reproductive strategies. This explanation is certainly irrelevant in the Late Devonian lycopsid plants, because only pre-Mid Devonian land-derived microfloras were marked by functional tetrads of spore-like palynomorphs (Strother, 2000).

The maximum proportion of abnormal miospores (mostly tetrads) is over 4%, which therefore may be considered, after Foster and Afonin (2005), as an indication of environmental mutagenesis, though this threshold refers essentially to mutated gymnosperms. The data altogether imply that volcanism could regionally have caused soil acidification from sulphuric acid deposition and/or atmospheric stress on land vegetation before and especially just after the Hangenberg Event. In addition, however, the present paper provides the first indication of an increased mutation signal during a significant floral turnover close to the D–C boundary that succeeded the major marine extinction (Fig. 2).

The Famennian age, and especially the broadly defined D–C transition is overall distinguished by intensive Eovariscan tectono-thermal and magmatic activity in many regions during an overall plate convergence (e.g., Khain and Seslavinsky, 1996; Nikishin *et al.*, 1996; Lescuyer *et al.*, 1998; Racki, 1998; Pracht, 2000; Han and Zhao, 2003; Mazur *et al.*, 2006; Kaiser *et al.*, 2007, 2008; Kroner *et al.*, 2007; Sasseville *et al.*, 2008). By analogy with the end-Permian crisis, volcanism may have been responsible for the D–C terrestrial crisis.

Evidence of such large-scale igneous activity remains rather conjectural near the D–C boundary, because imprecise dating is the main obstacle to general interpretation (Fig. 6; see also fig. 4 in Racki, 1998). In fact, outside the Holy Cross Mts. (for regional summary of the “Strunian” volcanism see Kowala, 1967), well-dated lava flows and volcanic ashes from the D–C transition have until now only been known from Europe (e.g., Rhenish Mountains – Korn and Weyer, 2003; Thuringia – Rösler 1960, p. 209; the Dnieper rift – Nikishin *et al.*, 1996, fig. 10; SW Ireland – Pracht and Batchelor, 1999; the Iberian domain – Oliveira *et al.*, 2004), some Asiatic regions (southern China – Bai, 2001; Alazeja-Oloj area in the Kolyma Basin – Gagiev, 1997, fig. 3; the Kuznetsk Basin – Karaulov and Gretschnikova, 1997, fig. 4; the Minusinsk Basin – Karaulov and Gretschnikova, 1988, p. 240; see also

Simakov, 1993, figs. 1–3)), and from the New England fold belt, Eastern Australia (Claoue-Long *et al.*, 1992; see also Bryan *et al.*, 2003, 2004). For example, the tuff horizon in the Hasselbachtal borehole (Rhenish Mountains) and Zr-rich Hangenberg Sandstone in the Bohlen section (Thuringia) are correlative with the critical Kowala pyroclastic level (see fig. 4 in Piecha *et al.*, 2008 and fig. 8 in Bartzsch *et al.*, 1998, respectively). The supra-regional exhalative mineralization peak (a global pulse?), recorded primarily within the western North American, Chinese (e.g., Tianshan) and West Hercynian belts, also took place near the D–C boundary (Lescuyer *et al.*, 1998; Fang *et al.*, 2001; Han and Zhao, 2003; Dergachev and Eremin, 2008; Piercey *et al.*, 2008), as recorded in the largest geochemical anomaly on Earth, linked to the Almadén mercury ore deposits in Spain (*ca.* 360 Ma; Higuera *et al.*, 2005). The black shale (LN Zone) succession, which includes the massive sulfides, stockworks and acidic volcanic rocks of the giant Iberian Pyrite Belt (Oliveira *et al.*, 2004; Sáez *et al.*, 2008), is the starting point for the concept by González *et al.* (2006) of a volcanically-associated Hangenberg anoxic episode. The data seem to point mostly to subaqueous igneous activity, but Late Devonian to early Carboniferous (*ca.* 360–350 Ma) subaerial explosive volcanism was widespread (>250 000 km²) across the shallow marine, partly emergent “back-arc” basin system along the Eastern Australian continental margin (Bryan *et al.*, 2003, 2004).

On the other hand, a poorly-dated Siberian (North Asian) and/or East European Craton (super)plume violent eruptive episode, encompassing extremely explosive kimberlite explosions, may have been the required worldwide trigger (Wilson and Lyashkevich, 1996; Yarmolyuk *et al.*, 2000; Ernst and Buchan, 2001; Courtillot and Renne, 2003; Kononova *et al.*, 2006; Khain and Filatova, 2008; see Fig. 6). In addition, Cather *et al.* (2009) causally linked the D–C Gondwanan glaciations with major protracted silicic volcanism in Eastern Australia. Although still speculative, this accumulation of more or less reliable data on magmatic activation may appear to finally be a key to volcanically-influenced deteriorating atmospheric conditions near the D–C boundary.

Alternatively, new biomarker evidence (isorenieratane; Marynowski and Filipiak, 2007) is consistent with the hypothesis of euxinic surface-water conditions and the catastrophic release of oceanic hydrogen sulfide as an atmospheric factor that disastrously affected terrestrial life (Kump *et al.*, 2005; see also discussion in Harfoot *et al.*, 2008).

CONCLUSIONS

1. The mutated end-Devonian palynofloral event may have been related to a variety of local or regional stress sources (e.g., soil acidification and atmospheric pollution). However, as shown above, palynological records across the D–C boundary should be re-visited in the context of the distinct Polish signature, as supported by some older records from France and Canada. As emphasized by Lavender and Wellman (2002), until now there has been little attention paid to Devonian miospore tetrads, which have rarely been reported in the literature, and, because of this, have escaped the interest of palaeobotanists.

If it is confirmed that the spore tetrad acme occurs in widely separated D–C localities, especially close to magmatic centres, the hypothesis of an episode of global atmospheric stress triggered by volcanism, analogous to the end-Permian event, may be further developed.

2. The overall hypothesis that Phanerozoic mass extinctions have coincided with volatile-induced climate response due to massive flood basalt eruptions, and feedback greenhouse mechanisms has been comprehensively developed (Courtilot and Renne, 2003; Wignall, 2005, 2007; Racki and Wignall, 2005; Hough *et al.*, 2006; Scaillet, 2008, among others), although a supplementary icehouse – silicic large igneous province hypothesis has recently been proposed by Cather *et al.* (2009). Even if we consider volcanism acting on a local scale only, as an additional deleterious factor operating in the terminal Devonian interval, our intriguing palaeobotanical finding suggests that the end-Permian model of increased mutation rate in highly stressed habitats apply to other biotic crises (facultative spore tetrads from the Triassic–Jurassic transition have been discussed in this context: Visscher *et al.*, 2004).

Testing this hypothesis requires detailed study of other volcanically-triggered extinction intervals at various atmospheric oxygen levels (Berner, 2006), significant as regards stratospheric ozone stability.

3. Such results emphasized the need for comprehensive elucidation of the role of floral change in global biodiversity crises, as expressed by McElwain and Punyasena (2007), above all to gain a better understanding of vegetational response to current environmental perturbation. Remarkably, the terrestrial flora shift occurred after the marine crisis not only during the Hangenberg crisis, but also during other extinction events, notably the end-Permian (Wignall, 2007), suggestive a similar phased pattern.

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