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Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations

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Abstract

Palynomorph distribution in Euramerica and western Gondwana, from the Latest Givetian to the Latest Famennian, may be explained, to some extent, by climatic changes. Detailed miospore stratigraphy dates accurately the successive steps of these changes. Interpretation is built on three postulates which are discussed: Euramerica at slightly lower latitudes than generally accepted by most paleomagnetic reconstructions; a conodont time-scale accepted as the most used available subdivision of time; and Late Devonian sea-level fluctuations mainly governed by glacio-eustasy. The Frasnian–Famennian timescale is also evaluated.

The comparison, based on conodont correlations, between Givetian and most of the Frasnian miospore assemblages from, respectively, northern and southern Euramerica demonstrates a high taxonomic diversity in the equatorial belt and much difference between supposed equatorial and (sub) tropical vegetations. On the contrary, a similar vegetation pattern and therefore probably compatible climatic conditions were present from tropical to subpolar areas. A rather hot climate culminated during the Latest Frasnian when equatorial miospore assemblages reached their maximum width. The miospore diversity shows also a rather clear global Late Frasnian minimum which is also recorded during the Early and Middle Famennian but only in low latitude regions while, in high latitude, very cold climates without perennial snow may explain the scarcity of miospores and so, of vegetation.

The Early and Middle Famennian conspicuous latitudinal gradient of the vegetation seems to attenuate towards the Late and Latest Famennian but this might be above all the result of the development, of cosmopolitan coastal lowland vegetations (downstream swamps) depending more on the moisture and equable local microclimates than on the probably adverse climates of distant hinterland areas. During that time, periods of cold climate without perennial snow cover and with rare vegetation may have alternated with less cold but wetter climates, thus giving rise to the development of mountain glaciers in high latitudes and explaining the jerking character of the global major marine regression. In high latitude regions, the development of an ice cap reaching sea level is only recorded by the end of the Latest Famennian, immediately below the DCB but, even if glacial evidences are not known at near the FFB, a short (0.1 Ma?) glaciation seems the best reasonable explanation of the major eustatic fall following the Kellwasser Event. The sudden growth and decay of a hypothetical

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Earliest Famennian ice sheet can be explained by the reduction and, later, increase in greenhouse capacity of the atmosphere. These changes in the atmospheric CO_2 might have provoked changes in the mode of ocean-atmosphere operation. It may also be partly controlled by a volcanic paroxysm and/or bolide impacts. The Hony microtektites represent the best known evidence of the impact of extraterrestrial bodies on Earth corresponding to the UKW, and they are immediately followed by a regression, suggested by the quantitative analysis of acritarch assemblages.

In the paleo-tropical Late Famennian, a peat-forming vascular plant community occurs for the first time and makes possible quantitative palynology of autochthonous sediments allowing the recognition of different swamp and near-swamp characteristic miospores. The early Latest Famennian starts with a widespread transgression which could correspond to the melting phases of the hypothetical Late Famennian mountain glaciers. During the end-Famennian, the coastal lowland vegetation has a worldwide distribution from sub-polar to equatorial regions. The climate has become less cold in high latitudes but wetter than before probably because the midlatitude cyclonic activity allows sufficient polar transportation of moisture to form large snow cover. Extensive coastal glaciers developed in different Bolivian and Brazilian basins, well dated by miospores. Rapid climatic changes characterize the onset of glaciation. The cyclic nature of climate allowed even intertropical marine faunas to reach occasionally the subpolar regions.

For the plant kingdom, the crisis which follows the Hangenberg Event was more severe than the Late Frasnian Crisis.

Keywords: Late Frasnian–Famennian climates; palynomorph analyses; Late Devonian glaciations

1. Introduction

The Famennian Stage is bracketed by two main crises and two events in the biosphere: the Late Frasnian Crisis and the Kellwasser Event near the Frasnian/Famennian Boundary (FFB), the end-Famennian Crisis and the Hangenberg Event near the Devonian/Carboniferous Boundary (DCB). We consider a crisis in the biosphere to represent a rather long time interval, during which the biodiversity deteriorates, often resulting in a stepwise loss of taxa. On the contrary, an event is considered to be a geological short-term perturbation compared to preceding and succeeding time intervals (Walliser, 1990; Schindler, 1993). Of course, the abruptness of a short-term perturbation is difficult to establish in the geological past (Van Loon, 1999) and one can consider that crises and events might be only two facets of the same phenomenon.

The proposed causes of crises and events are very diverse, and climate change is only one of them which we intend to focus on (other proposed causes are bolide impacts, tectonism, oceanic overturn, eustatic fluctuations, etc). The Famennian climate itself is often reduced to the question: glaciation or no glaciation? According to Dickins (1993, p. 90), Becker (1993) and House (1996), there was no glaciation during the Famennian and the Earliest Carboniferous. After Boucot (1988, p. 223), the glaciation might be of Early Carboniferous age; after Isaacson et al. (1999), of Late Famennian and Tournaisian ages; after Loboziak et al. (1993), of late Latest Famennian age; after Caputo (1985), of mid-Famennian age. According to Veevers and Powell (1987) and Smith (1997, p. 167), a glaciation might have occurred during the entire Famennian. Too often also, glaciation is confused with global cooling ignoring the fact that, if glaciation requires cold climate, it also does require heavy snowfall.

Few contributions to the understanding of Devonian climates rely on terrestrial vegetation data despite the fact that its impact on the biosphere was very important during that period (Tappan, 1982, 1986; Algeo and Scheckler, 1998). Indeed a massive increase of land plant biomass from Middle Devonian to Early Carboniferous times (Berner, 1990) and the increased rate of organic matter burial during major transgression pulses (Caputo, 1994) is believed to explain the long-term shortage of atmospheric CO_2 at this time. The reason of this scarcity of information has to be found in the scattered and poorly dated occurrences of plant megafossils in the geological record at this time. It is also the result of the continued misconception that even miospores, produced by these land plants, are poorly correlated with marine faunas (see for instance McGhee, 1996, p. 187).

We believe that land plant miospores, which are much more abundant and widespread than land plant megafossils, can supply reliable quantitative data with which to understand climate changes. They are generally found not only in continental deposits but also in marine environments where they are delivered by wind and fluvial systems, and there, mixed with other palynomorphs and also with marine fossils allowing accurate dating. Other palynomorphs include acritarchs, which represent the fossil part of the phytoplankton forming a base of the trophic pyramid of oceanic ecosystems, and chitinozoans, which may represent eggs in the life cycle of a cryptic fossil group: the “chitinozoan animal” (Paris and Nolvak, 1999).

2. Middle Devonian to Frasnian phytogeography and climates, a prerequisite for the interpretation of Late Frasnian–Famennian climates

The entire Devonian was a time of profound change both for terrestrial biotas and the physical environment. However, the Middle Devonian and Frasnian were particularly important epoch and age witnessing to the development of the tree habit in lycophytes and progymnosperms, with changes in the reproductive biology of the latter. *Archaeopteris* is the most representative progymnosperm genus, whereas its iso- or micro-spore, *Geminospora lemurata,* is among the most widespread miospores during this same timespan. They can be used to show the global distribution of this fossil group. Since the end of Middle Devonian, *Archaeopteris* and *G. lemurata* had an apparently wide range of tolerances, ranging from paleo-equatorial to paleo-boreal latitudes and from seasonally dry to wet habitats (Scheckler et al., 1999). This homogeneity is explained by the position of Gondwana relative to North America and Europe which set up potential monsoonal circulation pattern making the climate in the deep tropics more savannah-like than everwet tropical (Bambach et al., 1999).

The display of these data needs a suitable paleogeographic frame. We have to choose among many published maps based either on paleomagnetic or on nonpaleomagnetic data.

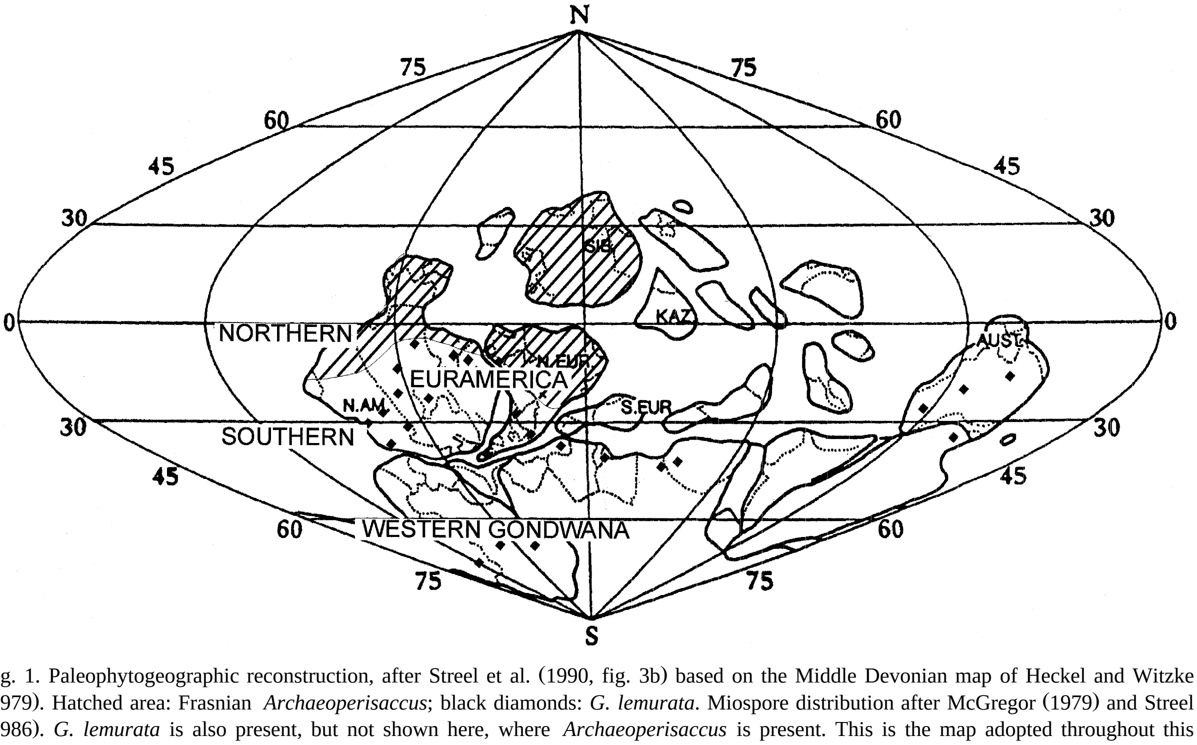


Fig. 1. Paleophytogeographic reconstruction, after Streel et al. (1990, fig. 3b) based on the Middle Devonian map of Heckel and Witzke (1979). Hatched area: Frasnian *Archaeoperisaccus*; black diamonds: *G. lemurata*. Miospore distribution after McGregor (1979) and Streel (1986). *G. lemurata* is also present, but not shown here, where *Archaeoperisaccus* is present. This is the map adopted throughout this paper. *Geminospora* has a worldwide distribution, *Archaeoperisaccus* distribution being centered on the equatorial belt.

Miospores can help in selecting such a map by using, for instance, the geographic distribution of *Archaeoperisaccus,* a very distinct monolete microspore, which was produced, during the Frasnian, by a heterosporous plant that produced also the distinctive megaspore *Nikitinsporites* (McGregor, 1969). By comparison with the near-global distribution of *Geminospora*, *Archaeoperisaccus* has a restricted distribution, a major control on its geographic distribution being likely to have been the limited transportation potential of the megaspore within the limits of the corresponding ecological domain (Marshall, 1996, p. 1136).

Heckel and Witzke's (1979) Middle Devonian nonpaleomagnetic reconstruction (Fig. 1) seems to be the most appropriate map for displaying the *Archaeoperisaccus* distribution. It restricts the location of *Archaeoperisaccus* microspores to a paleo-intertropical belt situated between 35°N and 20°S, the paleo-equator crossing western North America near the Alaskan border and eastern Europe near the Urals (Streel et al., 1990, fig. 3). This reconstruction is based on the distribution of paleoclimatically sensitive rocks (Witzke, 1990) and assumes a paleomagnetic pole which is slightly different from the rotational pole, a hypothesis, however, considered improbable by Smith (1997, p. 177). Of course, the reliability of some paleomagnetic data may need to be reevaluated. This reconstruction is partially matched by Boucot's (1988) Late Devonian nonpaleomagnetic reconstruction and is used by Vavrdova and Isaacson (1999) to display late Famennian acritarch bioprovinces.

These maps differ from Scotese and McKerrow's (1990) paleomagnetic map (Fig. 2) where the paleoequator crosses through Hudson Bay and the western/eastern border of Europe. The inadequacy of the latter reconstruction is obvious. A comparison with late Quaternary vegetation maps shows that the modern-day vegetation is distributed more or less equally on both sides of the equator, even during the LGM (Late Glacial Maximum) time (Adams et al., 1990). This is mainly the result of a similar thermoperiodism in the equatorial belt (Went, 1953; Streel, 1962). Indeed, the key characteristic of this belt today is not warmth or humidity, which can vary

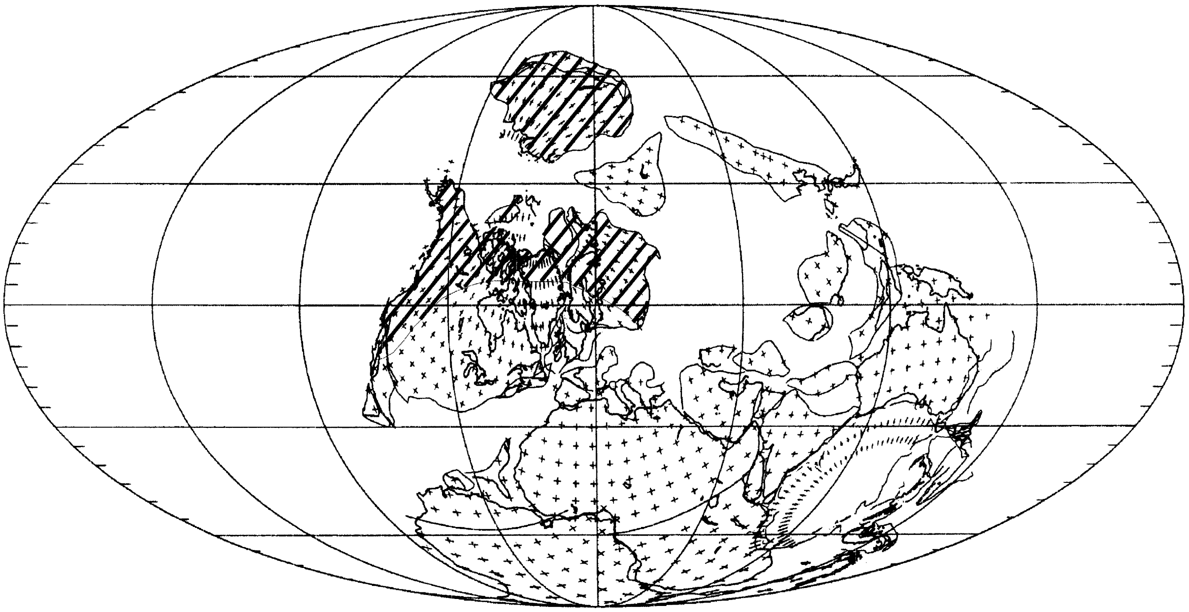


Fig. 2. Paleophytogeographic reconstruction based on the Late Devonian map of Scotese and McKerrow (1990, fig. 16). Hatched area: Frasnian *Archaeoperisaccus* distribution as in Fig. 1. This map is not used because the *Archaeoperisaccus* distribution is shown to be limited by the equator line on its southern side, which is unlikely.

considerably from tropical savannahs to rainforests; rather, it is the relative constancy of conditions, i.e., the comparatively low level of environmental fluctuations (Meyerhoff et al., 1996, p. 3). If the Frasnian *Archaeoperisaccus* distribution was dependent on the same climatic factors, its location (Fig. 2) only on the northern side of the equatorial line (implied by Scotese and McKerrow's (1990) map) is unlikely. Of course, during no time interval of the past there is evidence for a perfect latitudinal biotic distribution owing to the complex interactions of varied longitudinal barriers (Meyerhoff et al., 1996, p. 5). However, the bipolar distribution of various biotas normally appears as at least three distinct zones, including two polar-centered biotic units, one boreal and one austral, and at least one unit lying between the polar units. Of course, the absence of a boreal belt in Heckel and Witzke's (1979) reconstruction results from the absence of northerly continents. The inadequacy of Scotese and McKerrow's (1990) map is also obvious from the distribution of Famennian and lowermost Tournaisian marine deposits yielding Rugosa (Poty, 1999, fig. 1), which is not centered on the equator of this map but rather on a parallel some 15° to the north. According to Heckel and Witzke's (1979) reconstruction, the equatorial belt was thus centered on northwestern Canada and western USA, as well as on eastern Europe, a single province called here northern Euramerica. Southern Euramerica was centered on eastern Canada and USA and on western Europe, representing a tropical belt (a subtropical belt on northern Africa).

Avkhimovitch et al. (1993) show the correlation (Fig. 3), based on conodonts, between Givetian and most of the Frasnian miospore assemblages from, respectively, northern and southern Euramerica. These assemblages are poorly correlatable on the basis of miospores themselves (Loboziak and Streel, 1981; Streel and Loboziak, 1996) because these miospore assemblages are rather different. On the contrary, the presence of 12 Givetian-Frasnian miospore-events in the same order of occurrence in western Europe (southern Euramerica), Northern Africa and Brazil (western Gondwana) indicates (Fig. 4) similar changes in vegetation composition and therefore probably similar climatic conditions ranging from tropical to subpolar areas (Streel et al., 1990, fig. 1). It contradicts (as did also Paris and Robardet, 1990, p. 206) Van der Voo's (1988) Late Devonian paleomagnetic reconstruction which esti-

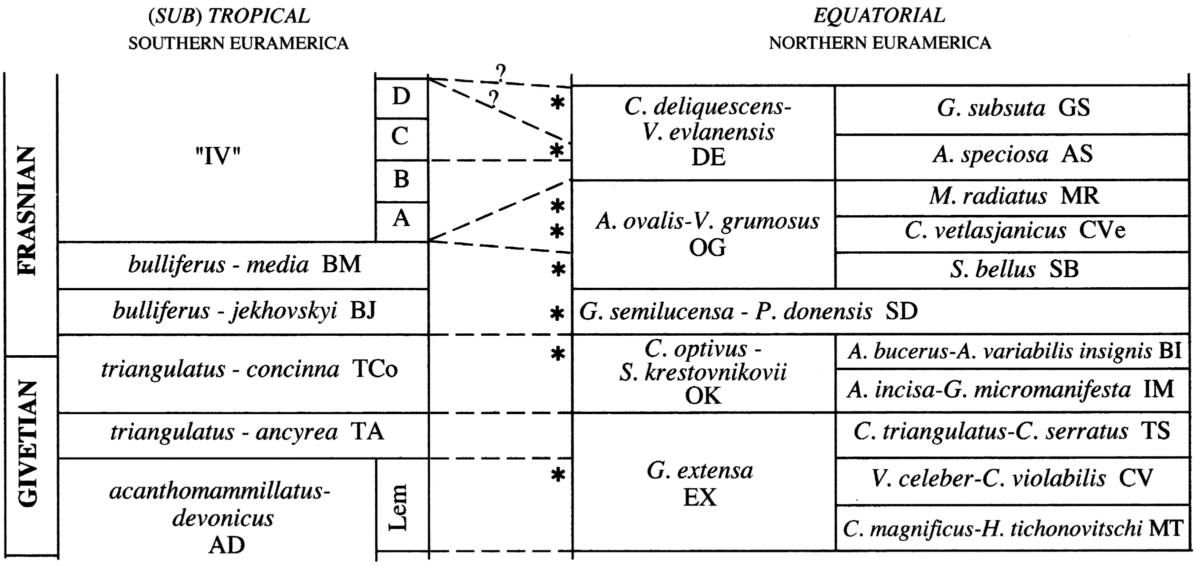


Fig. 3. Correlation chart between southern and northern Euramerican miospore zonations after Avkhimovitch et al. (1993, fig. 4 modified). * = conodont data in northern Euramerica; for conodont data in southern Euramerica, see correlation conodont-miospore in Streel et al. (1987). The detailed correlation is possible by conodonts, not really by miospore assemblages, which are different in southern and northern Euramerica.

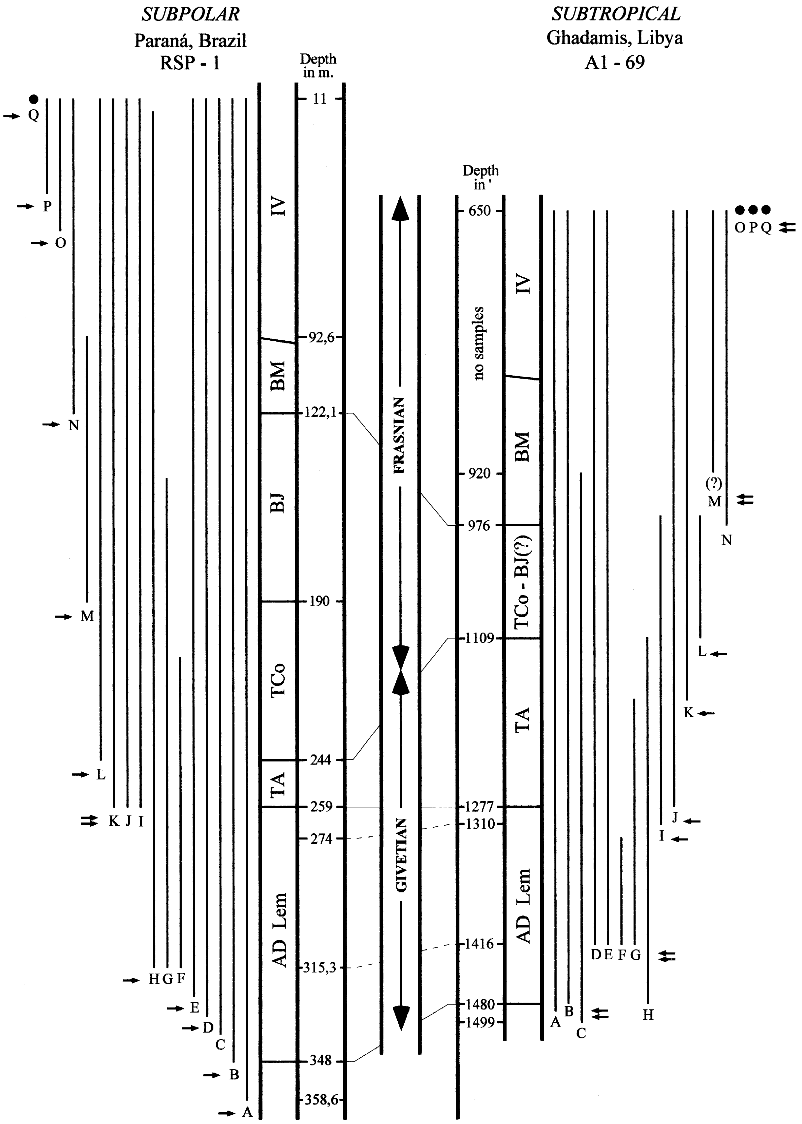


Fig. 4. Correlation, within western Gondwana, between two boreholes, respectively, from subpolar (Brazil) and subtropical (Libya) regions, after Streel et al. (1990, fig. 1. Used with the permission of the Geological Society Publishing House). Seventeen species are designated by capital letter. Miospore zonation from tropical southern Euramerica (western Europe) after Streel et al. (1987). Single arrows indicate the miospore-events, which have the same order of occurrence in western Europe, Libya and Brazil. Double arrows indicate condensed portions of the sections.

mates an ocean 3000 km wide between Euramerica and Gondwana.

The homogeneity of miospore assemblages from paleo-tropical to paleo-subpolar regions was even more obvious during the Frasnian than during the Givetian (Streel et al., 1990, fig. 2). Tropical (non-equatorial) vegetations seem to have extended their range into higher latitudes from Givetian to Frasnian (Fig. 5). Morphologically elaborate miospores characteristic of western Gondwana almost disappear at the end of the Givetian, paralleling the faunal trend towards cosmopolitanism which had started in the

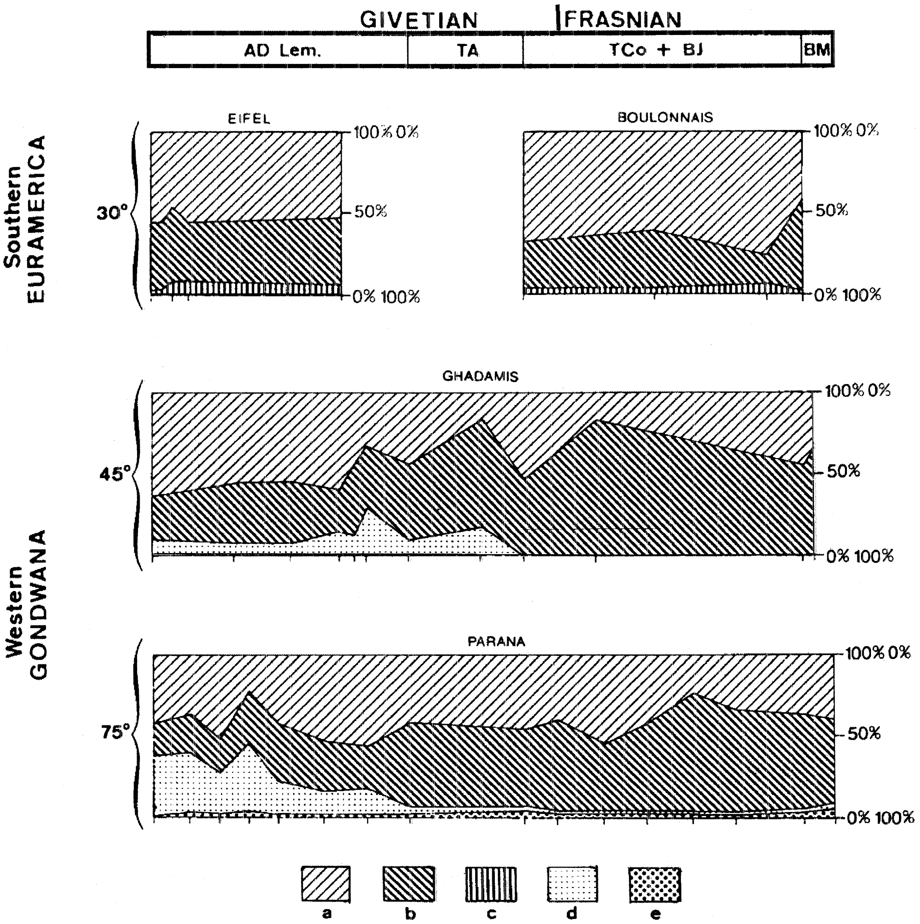


Fig. 5. Quantitative distribution of various miospore classes in different regions of western Gondwana and southern Euramerica, after Streel et al. (1990, fig. 2. Used with the permission of the Geological Society Publishing House). Note that percentages are of specimens, not of species. (a) Morphologically simple (smooth or finely sculptured, one-layered) miospores, (b–e) morphologically elaborate miospores, (b) occurring in all regions, (c) never found in Gondwana, (d) only found in Gondwana, (e) only found in Brazil (Paraná Basin). In western Gondwana, the amount of Gondwanan taxa (d) is decreasing (Brazil) or disappearing (North Africa) from the Late Givetian upwards.

Givetian (Boucot, 1988; Sablock, 1993) and corresponded to the development of a rather hot climate and an extended carbonate platform belt which reached paleolatitudes up to 45°S (Heckel and Witzke, 1979) during the Frasnian (the “warm mode” of Frakes et al., 1992).

Miospores are known also in regions other than Euramerica and western Gondwana, e.g., China and Australia, but these have their own history that is beyond the scope of the present contribution. For instance, during the Late Devonian, the Indo–Australian–Antarctic region of Gondwana moved rapidly from a subtropical to polar position (Scotese et al., 1999, p. 100).

3. Evaluation of an accurate Late Frasnian–Famennian timescale

Palynomorphs cannot help much in defining a timescale because their biozones are rarely based on evolutionary lineages. Ziegler and Sandberg (1990, 1994); Sandberg and Ziegler (1996) and Ziegler and Weddige (1999) have proposed that conodonts can be used for that purpose, each conodont zone averag-

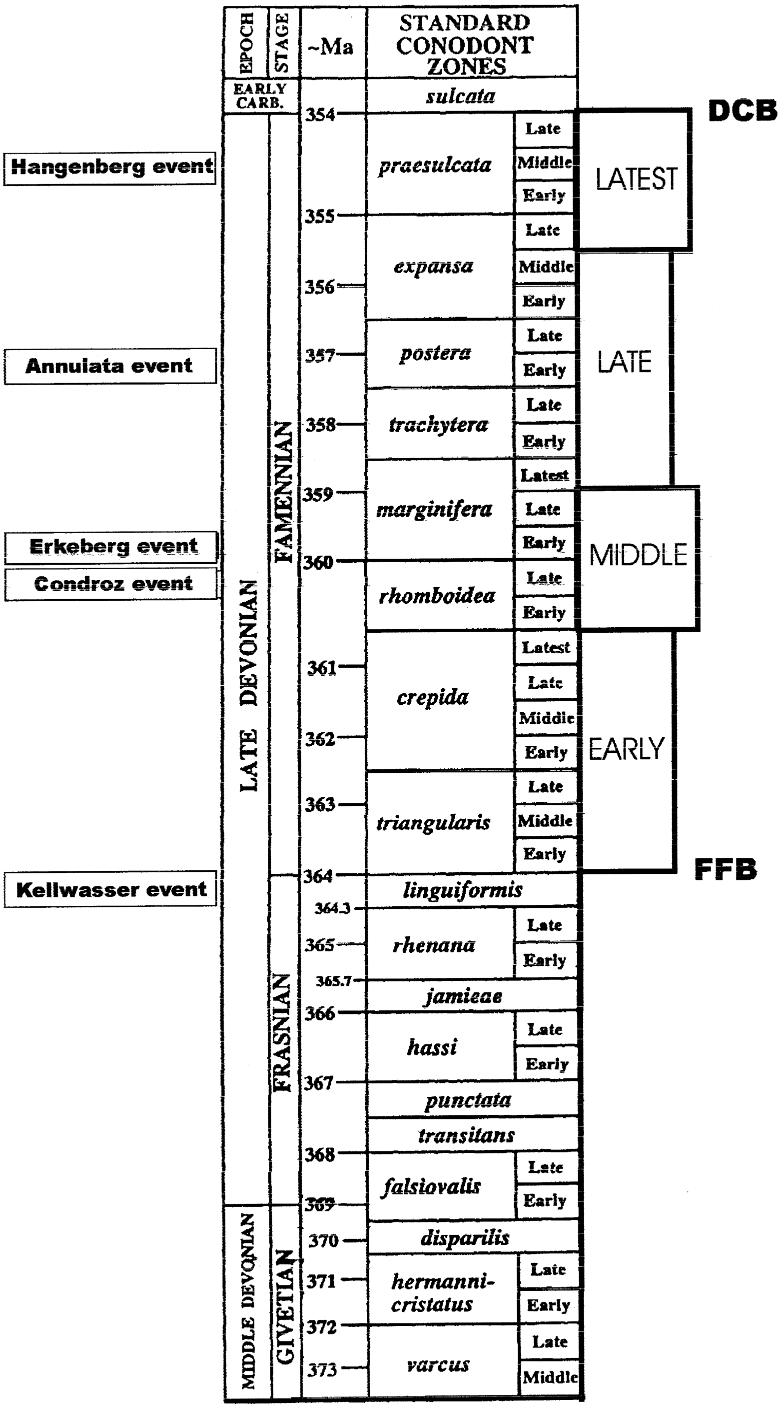


Fig. 6. Chronostratigraphy, geochronology and standard conodont zones of Givetian to Early Carboniferous, after Sandberg et al. (1997, fig. 2. Used with the permission of the first author). Sub-ages of the Famennian after Streel et al. (1999). Only the Kellwasser and the Hangenberg events are concerned by this paper. The other events, which do not correspond to major biotic crises, are only shown to help correlation.

ing about a half million years in duration. We are aware of course that evolutionary events cannot be demonstrated to occur at the same rate in any stratigraphic interval (see also Fordham, 1992 for discussion). But in order to subdivide the Late Devonian Epochs, the conodont-based scale is the most often used and, moreover, its subdivision in time units makes the calibration of events easier (Fig. 6).

Originally, Late Devonian conodont zonal boundaries were dated backwards from a starting point of 0 Ma at the DCB. Ties to the radiometric time scale were avoided because of the often controversial datings (McGhee, 1996, p. 7) proposed for the DCB (Sandberg et al., 1997). The finding, by Claoué-Long et al. (1992, 1993), of a new, biostratigraphically controlled zircon fission-track date of 353.2 Ma from a bentonite layer deposited just above the base of the Earliest Carboniferous *sulcata* Zone led Sandberg and Ziegler (1996) to redate the DCB to 354 Ma.

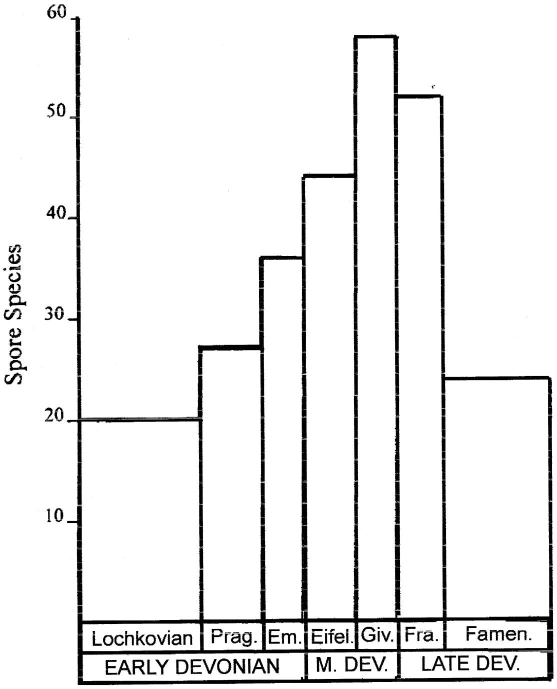


Fig. 7. Diversity of miospore species in the Devonian. Data from Richardson and McGregor (1986). Modified from Boulter et al. (1988), after McGhee (1996, fig. 4.24 redrawn. Used with the permission of the author). The diversity of miospore species shows a maximum during the Givetian and the Frasnian and a rather dramatic drop between the Frasnian and the Famennian.

Recently, Tucker et al. (1998) claimed to have obtained new U–Pb zircon dates from a series of volcanic ashes closely tied (supposed better than before) to biostratigraphic zones. (1) The Late Famennian new data, which are assumed by Tucker et al. (1998) to date the Fa2d part of the Belgian scale, i.e., the Late *expansa* conodont Zone, are not confirmed by facts. They are based on a palynological analysis of the Carrow Formation of the Piskahegan Group in southern New Brunswick made by McGregor and McCutcheon (1988). However, these authors could not really distinguish between their *pusillites–lepidophyta* Zone (Fa2d) and *flexuosa–cornuta* Zone (Fa2c). Indeed, one single specimen of one species only (*Retispora lepidophyta?*, pl. 2, figs. 15, 16) has been found which might indicate the *pusillites–lepidophyta* Zone. But, with our present experience of the *R. lepidophyta* Morphon (Steemans et al., 1996), we believe that this specimen most probably belongs to *R. cassicula* (now *R. macroreticulata*) which first occurs in the Latest *marginifera* conodont Zone in Belgium (Streel and Loboziak, 1996, text-fig. 3). In the absence of *R. lepidophyta*, the single specimen of *V. pusillites* (*V. pusillites sensu lato*, pl. 3, fig. 7) might belong to the *pusillites–fructicosa* Zone of Richardson and Ahmed (1988), the base of which is in the uppermost part of the Ellicott Formation or in the lowermost part of the Cattaraugus Formation in New York State (USA), i.e., within the Latest *marginifera* Zone, thus 4 to 5 millions years older than the DCB. (2) The new Early Frasnian data are claimed by Tucker et al. (1998) to characterize the *punctata* to Late *hassi* conodont Zones. It is based on an unpublished determination by them of *P. punctata* from the Chattanooga Shale at Little War Gap, east Tennessee (USA), formerly attributed by Dennison and Boucot (1974) to the Eifelian on the basis of brachiopod data. However, the presence of the brachiopod *Leiorhynchus limitare* in the Tioga tuffaceous beds at the base of the Chattanooga Shale still supports an Eifelian age (a late Eifelian age according to P. Sartenaer, personal communication, December 1999). Consequently, we believe that the Late Famennian (363.6 ± 1.6 Ma) and Early Frasnian (381.1 ± 1.3 Ma) dates given by Tucker et al. (1998) are poorly constrained biostratigraphically and, thus, for the time being, we prefer to adopt Sandberg and Ziegler's

(1996) chronology, that is 354 Ma for the DCB, 364 Ma for the FFB and 369 Ma for the base of the Frasnian Stage. This is in line with Gradstein and Oggs (1996) age and duration of the Famennian Stage.

Since formal subdivisions of the Famennian age have not yet been defined by the IUGS Subcommission on Devonian Stratigraphy, we will use here the following four sub-ages (Streel et al., 1999): Early Famennian, defined at the base of the Early *triangularis* Zone and composed of seven conodont zones; Middle Famennian, defined at the base of the Early *rhomboidea* Zone and composed of four conodont zones; Late Famennian, defined at the base of the Latest *marginifera* Zone and composed of seven conodont zones, and Latest Famennian (or Strunian), defined at the base of the Late *expansa* Zone and composed of four conodont zones (Fig. 6).

4. The Late Frasnian Crisis

The Late Frasnian Crisis is often cited as one of the major crises in the history of life on Earth. Probably three-quarters of all animal species, more than half of all the genera (Sepkoski, 1986), more than a fifth of all the families (Sepkoski, 1982) did not survive this crisis. The temporal duration of the Late Frasnian Crisis has been, and still is, the subject of considerable hot debate. However, a careful analysis of available data (McGhee, 1996) demonstrates that the Late Frasnian diversity crisis is clearly not a single instantaneous event as it occurs over 3.0 Ma at least, the main pulse of the extinction spanning about 2.0 Ma, from the base of the Early *rhenana* Zone to the base of the Middle *triangularis* Zone. Often mentioned is the mass extinction of rugose corals (Sorauf and Pedder, 1986) and brachiopods (Balinski, 1996; Copper, 1998; Racki, 1998a,b). However, the most devastating diversity loss occurs in the *linguiformis* Zone, which might be of 0.3 Ma in duration (Sandberg et al., 1988) and is herein referred to (see below) as the Kellwasser Event.

4.1. Miospores

Considering undifferentiated northern and southern Euramerican data from Richardson and McGregor (1986), the diversity of characteristic miospore species computed to the Stage level (McGhee, 1996, fig. 4.24) clearly shows a maximum during the Givetian and the Frasnian and a rather dramatic drop from the Frasnian to the Famennian (Fig. 7). However, according to Boulter et al. (1988) and Raymond and Metz (1995, fig. 3), also based on Richardson and McGregor's (1986) data, but considering genera rather than species at a substage level, miospore diversity shows a rather clear Late Frasnian-Middle Famennian minimum (Fig. 8).

More recent northern Euramerican data from northwestern Canada (Braman and Hills, 1992) and eastern Europe (Avchimovitch et al., 1993) clearly confirm a diversity crisis during the Late Frasnian to Middle Famennian timespan. The northwestern Canadian data (Fig. 9) are the most interesting because the complete miospore assemblage is given (including morphologically simple, smooth or finely sculptured, one-layered species which are seldom used to characterize assemblages). Eighty-five taxa have last occurrences (LO taxa) and only 14 first occurrences (FO taxa) in the Late Frasnian to Middle Famennian interval (46 LO against 5 FO in the Late Frasnian, less than 2 Ma in duration, and 39 LO against 9 FO in the Early and Middle Famennian, altogether 5 Ma in duration). The eastern European data (Fig. 10) only concern the biostratigraphically characteristic miospores and, therefore probably, the diversity loss across the FFB is much less obvious (42 taxa have last occurrences and 39 first occurrences in the Late Frasnian to Middle Famennian timespan: 20 LO against 10 FO in the less than 2 Ma-long Late Frasnian and 22 LO against 29 FO in the 5 Ma-long Early and Middle Famennian). The diversity minimum seems to be on the Frasnian side rather than on the Famennian side of the transitional timespan.

McLaren (1988, p. 2), when invoking an "instantaneous event" at the FFB, mentioned a major break in miospore development at that time. He cited Richardson and McGregor (1986) in support of his view, clearly referring to the *ovalis–bulliferus/ torquata–gracilis* Assemblage Zone boundary illustrated by these authors (Richardson and McGregor, 1986, fig. 3) in the Latest Frasnian strata of New York State (USA), and where at least 10 species seem to have first occurrences at the same time

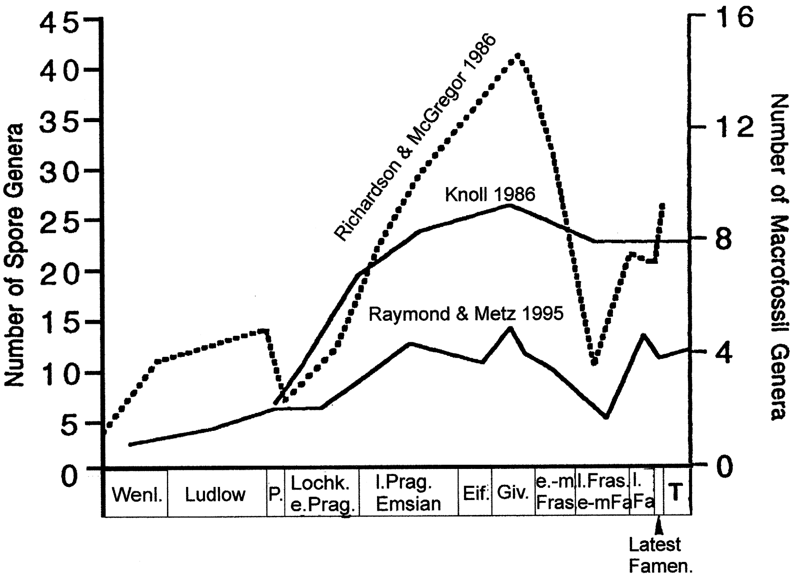


Fig. 8. Diversity of Middle Silurian through Late Devonian land plants using various diversity measurements: the dotted line represents the standing diversity of miospore genera at interval boundaries, taken from data by Richardson and McGregor (1986); the solid lines represent the mean generic richness of plant megafossil genera in each interval after Knoll (1986) or data compiled by Raymond and Metz (1995). After Raymond and Metz (1995, fig. 3 redrawn). The use of a sub-stage scale allows showing that the drop in miospore and plant megafossil taxa starts within the Frasnian.

immediately below the FFB (Fig. 11). But more recently, it became evident through the conodont study by Over (1997) that the *torquata–gracilis* Assemblage Zone first occurs in the lower part of the Hanover Shale below the entry of the conodont *Palmatolepis linguiformis* (likely within the range of *Palmatolepis juntianensis* comparable with the Frasnian Montagne Noire conodont zonation of Klapper and Foster, 1993). Besides, there was a large sampling gap in the New York State section below this level because the *ovalis–bulliferus* Assemblage Zone last occurs in the Rhinestreet Shale, three lithostratigraphic units below the Hanover Shale, i.e., in the *hassi* or *jamieae* conodont Zones (Fig. 12). The dramatic end Frasnian change in New York State section is a sampling, and maybe also a fossil preservation, artifact, the younger assemblage starting with poorly preserved material (Richardson and Ahmed, 1988, p. 545).

In the Hydrequent Formation (Boulonnais, northern France), the Late Frasnian does not show any major break in the succession of corresponding assemblages. Samples with abundant and well-preserved miospores have been collected from the Briquetterie de Beaulieu section. This section displays a rather detailed miospore zonal subdivision (Loboziak et al., 1983) within Zone "IV" and shows the base of the succeeding Zone "V" (Fig. 13). Zone "IV" has some similarity, in miospore composition, with the Latest Frasnian *C. deliquescens–V. evlanensis* Zone (the DE Zone comprising the AS and GS Subzones, after Avkhimovitch et al., 1993), described in eastern Europe, which characterizes the equatorial belt at that same time (Fig. 3). The base of this zone, starting with the entry of *Cymbosporites acanthaceus,* corresponds to the Late *rhenana* conodont Zone in eastern Europe (Obukhovskaya et al., in press). The uppermost part of Zone "IV" is dated with acritarchs (Loboziak et al., 1983) known from the transitional Late *rhenana–linguiformis* Zones (Martin, 1993, fig. 9; Bultynck and Martin, 1995, Fig. 2). Zone "V" is characterized by the first entry of three species (*Knoxisporites dedaleus, K.* cf. *hederatus and Diducites versabilis*) of which only one (*K. dedaleus*) starts at the base of the *torquata-gracilis* Assemblage Zone of Richardson and Mc-

Gregor (1986). Eighteen species gradually disappear and 25 gradually appear in the interval spanning from Zone “IV” to the beginning of Zone “V”. Two species (*Diducites poljessicus* and *Grandispora gracilis*) marking the base of the *torquata-gracilis* Assemblage Zone of Richardson and McGregor (1986) occur within Zone “IV”. Therefore, the sharp turnover (Fig. 11) illustrated by Richardson and McGregor (1986, fig. 3) cannot be observed in the Boulonnais area. The Latest Frasnian is characterized by a miospore assemblage (the *C. deliquescens–V. evlanensis* Zone) from eastern Europe which, exceptionally during the Frasnian, is rather similar both in equatorial and tropical regions suggesting that the equatorial climatic belts had reached a maximum width in the Latest Frasnian.

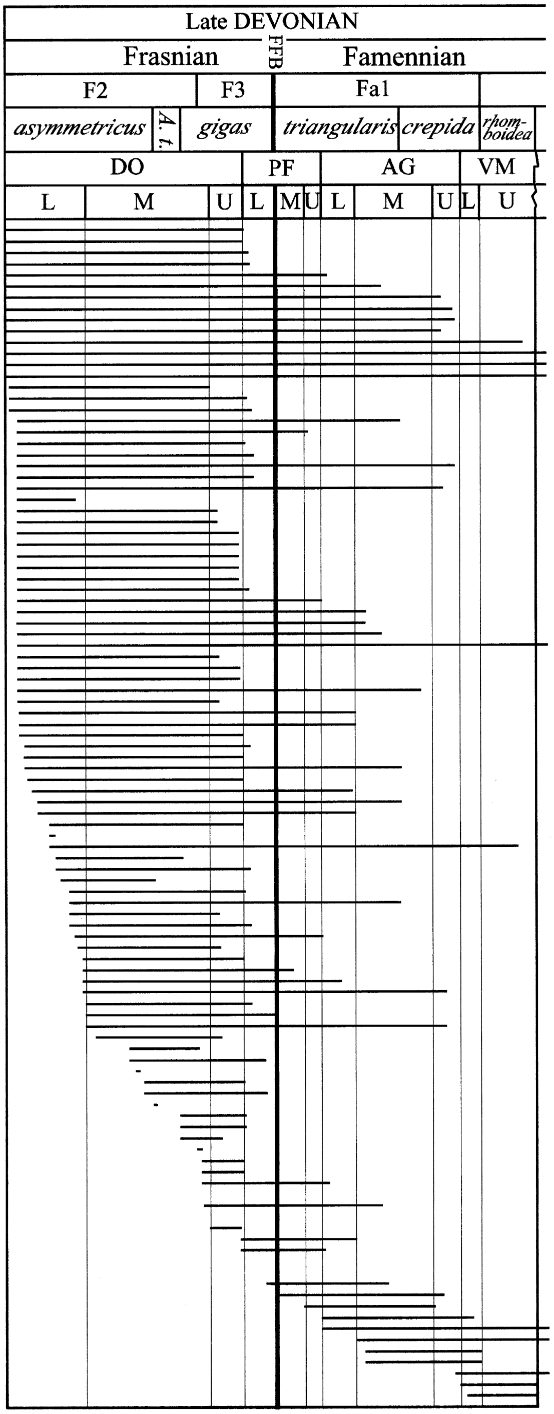


Fig. 9. Composite stratigraphic ranges of miospores across the FFB, conodont and miospore Zonation, from western Canada, after Braman and Hills (1992, text-fig. 5 modified). The loss in miospore diversity obviously starts in the Late Frasnian. Eighty-five taxa have last occurrences (LO taxa) and only 14 first occurrences (FO taxa) in the Late Frasnian to Middle Famennian interval (46 LO against 5 FO in the Late Frasnian which has less than 2 Ma in duration, and 39 LO against 9 FO in the Early and Middle Famennian which have altogether 5 Ma in duration).

4.2. Land plants

According to Boulter et al. (1988) and Raymond and Metz (1995, figs. 2 and 3), the diversity of land plant genera at substage boundaries also shows a clear Late Frasnian–Middle Famennian minimum (Fig. 8). The number of genera and number of investigated localities are rather low for this interval but statistical tests suggest that poor sampling does not cause the observed diversity minimum (Raymond and Metz, 1995, table 6). It is not possible, however, to discriminate between the Late Frasnian and the Early–Middle Famennian data so that no conclusion can be drawn for the time being.

4.3. Acritarchs

Although Tappan (1971, fig. 1) clearly shows that acritarch diversity collapses at the DCB, and not at the FFB, McGhee (1996) used the diversity evaluation of acritarchs (including Prasinophycean green algae) at a poor resolution level, i.e., the Epoch (see

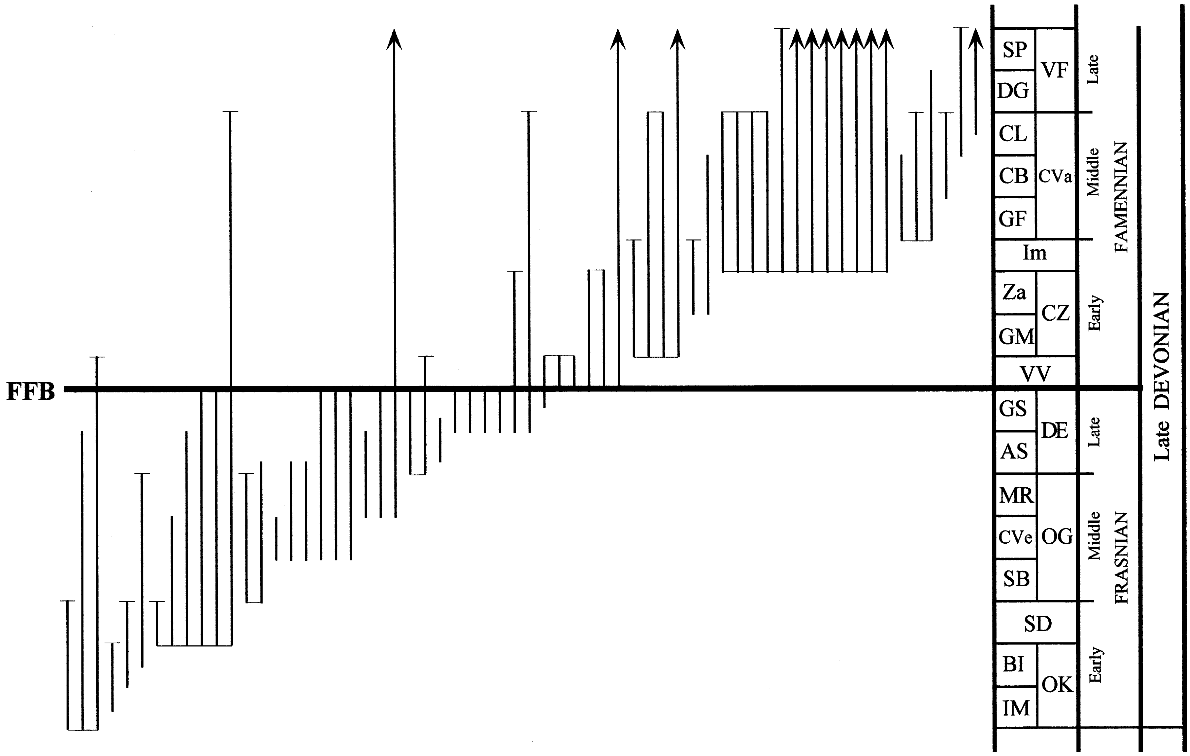


Fig. 10. Composite stratigraphic ranges of selected miospores across the FFB and miospore Zonation from eastern Europe, after Avkhimovitch et al. (1993, fig. 3 modified). These eastern European data only concern the biostratigraphically characteristic miospores and, therefore, the diversity loss across the FFB is less obvious than in Fig. 9. Forty-two taxa have last occurrences and 39 first occurrences in the Late Frasnian to Middle Famennian timespan (20 LO against 10 FO in the less than 2 Ma-long Late Frasnian and 22 LO against 29 FO in the 5 Ma-long Early and Middle Famennian).

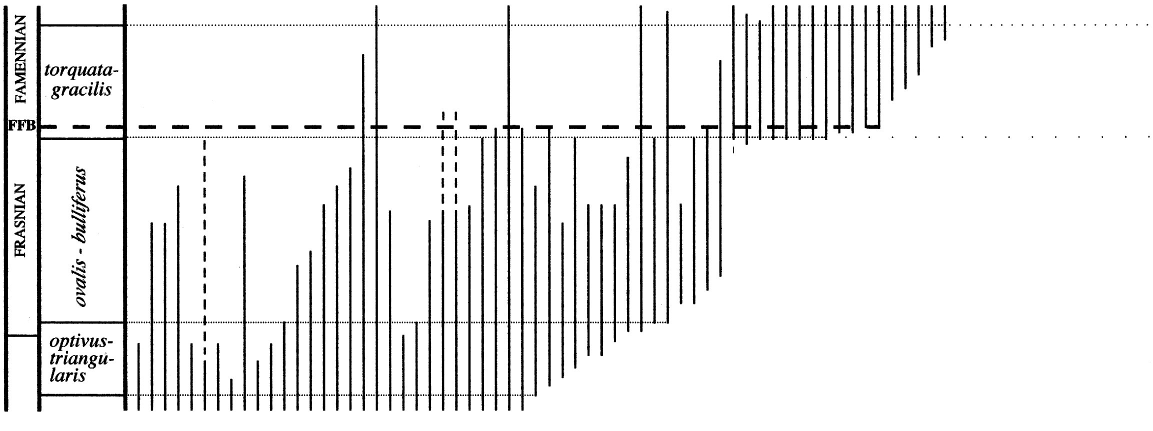
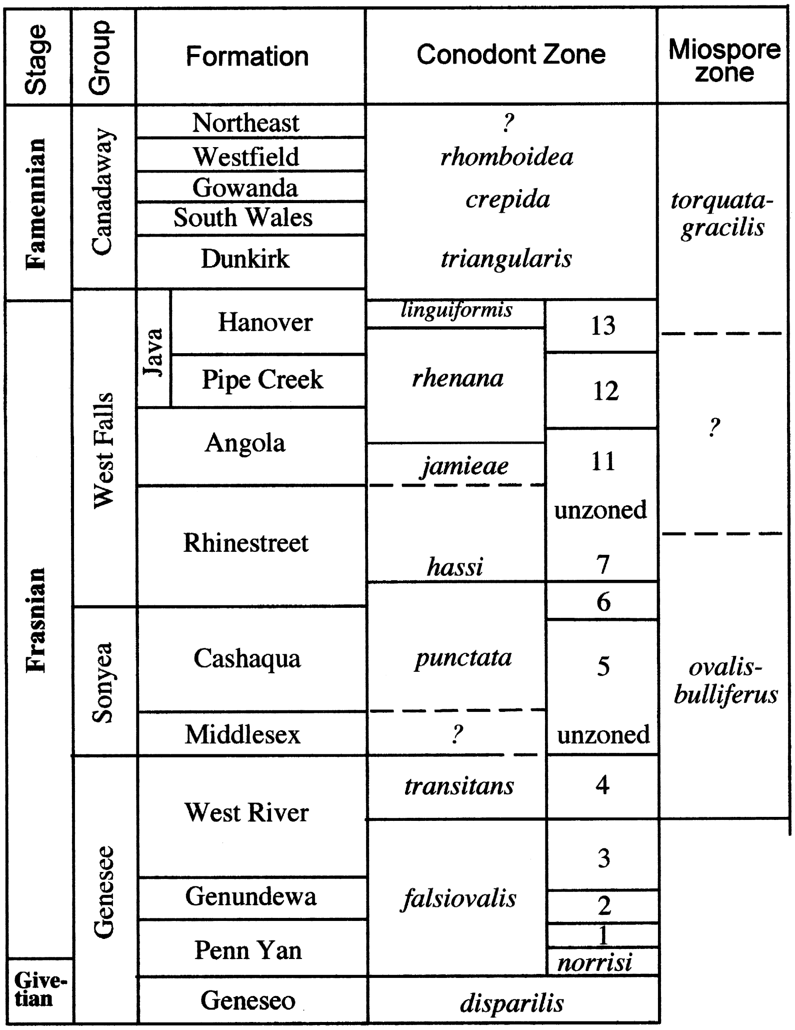


Fig. 11. Distribution of characteristic miospores across the FFB from the Old Red Sandstone Continent and adjacent regions, after Richardson and McGregor (1986, fig. 3 modified). Ten taxa seem to have first occurrences, at the same time, immediately below the FFB. This is a sampling, and maybe also a fossil preservation, artifact.



Stage	Group		Formation	Conodont Zone		Miospore zone
Famennian	Canadaway		Northeast	?		*torquata-gracilis*
			Westfield	*rhomboidea*		
			Gowanda	*crepida*		
			South Wales			
			Dunkirk	*triangularis*		
Frasnian	West Falls	Java	Hanover	*linguiformis*	13	
		Java	Pipe Creek	*rhenana*	12	?
			Angola	*jamieae*	11	
			Rhinestreet	*hassi*	unzoned 7	ovalis-bulliferus
	Sonyea		Cashaqua	*punctata*	6 5	
			Middlesex	?	unzoned	
	Genesee		West River	*transitans*	4	
			Genundewa	*falsiovalis*	3 2	
			Penn Yan		1 *norrisi*	
Give-tian			Geneseo	*disparilis*		

Fig. 12. Generalized latest Givetian, Frasnian and Early–Middle Famennian chrono-and litho-stratigraphy of western New York State and correlation between two independent conodont zonations after Over (1997, fig. 1 modified. Used with the permission of the author). Conodont zonations: narrow right column after Klapper (1988), other data after Ziegler and Sandberg (1990). Miospore zonation after Richardson and McGregor (1986). The correlation conodont/miospore illustrates the importance of the gap between the *torquata–gracilis* and the *ovalis–bulliferus* assemblage-zones.

Tappan and Loeblich, 1972, p. 206 for genera diversity; Tappan and Loeblich, 1973, p. 215 for species diversity). He claims, as many others (Stanley, 1984, p. 207; Schindler, 1993, p. 117; Klapper et al., 1993, p. 435; Walliser, 1995, p. 234; Schülke, 1998, p. 93), that the phytoplankton was drastically reduced in the Late Frasnian Crisis. Despite these assertions, palynologists (Bouckaert et al., 1972; Vanguestaine, 1986; Martin, 1993; Strother, 1996) have confirmed that the dramatic decline of acritarchs occurs near the end of the Famennian (Fig. 14), not near the FFB.

4.4. Chitinozoans

Following their Silurian acme, the specific diversity of chitinozoans declined progressively from the Lochkovian onwards and ended with the extinction

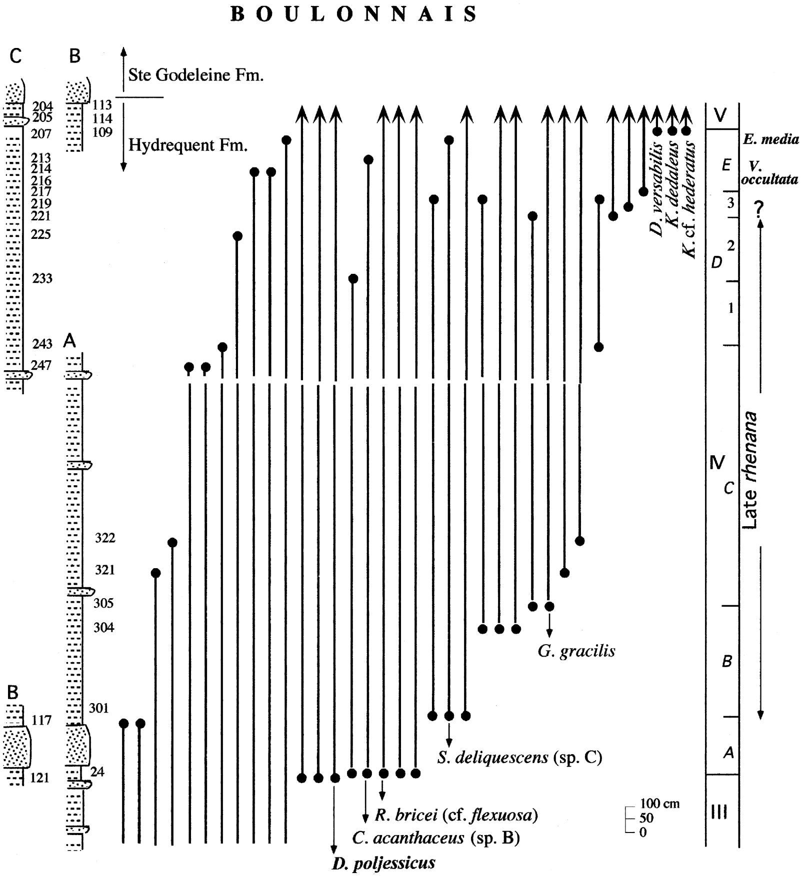


Fig. 13. Distribution of characteristic miospores, acritarchs and miospore zonation from the Hydrequent Formation in the Boulonnais area (northern France), after Loboziak et al. (1983, fig. 1 modified). Conodont correlation after Obukhovskaya et al. (in press). Acritarchs *E. media* and *V. occultata* are known from the transitional Late *rhenana–linguiformis* conodont Zones The FFB is unknown between the base of miospore zone V and the Ste Godeleine Fm. Eighteen species gradually disappear and 25 gradually appear in the interval spanning from Zone "IV" to the beginning of Zone "V". Two species (*Diducites poljessicus* and *Grandispora gracilis*) that mark the base of the *torquata–gracilis* Assemblage Zone of Richardson and McGregor (1986) occur within Zone "IV".

of the group in the Latest Famennian. It is worth noting that the "chitinozoan animals" survived the FF mass extinction, despite the fact that diversity of the group had been declining for a long time (Paris and Nolvak, 1999).

5. The Kellwasser Event

The most devastating diversity loss of Devonian faunas occurs in the *linguiformis* Zone, which may be of 0.3 Ma in duration, and is referred to here as the Kellwasser Event. Among many, mainly pelagic fossil groups that were affected, the conodonts (Sandberg et al., 1988) and ammonoids (House, 1985, 1989) are most often considered. What about land plants and palynomorphs?

First we must realize that, with a time resolution at the Subzonal level, detailed event-stratigraphic investigations become more and more necessary. If rock sequences are subdivided on an extremely fine scale, high resolution correlations between different sections and regions become more accurate and one can realize, for instance, that what had been thought of as a single event may also show a stepwise pattern (Schindler, 1993). The succession of correlation lines might represent time-slices of only some 10,000

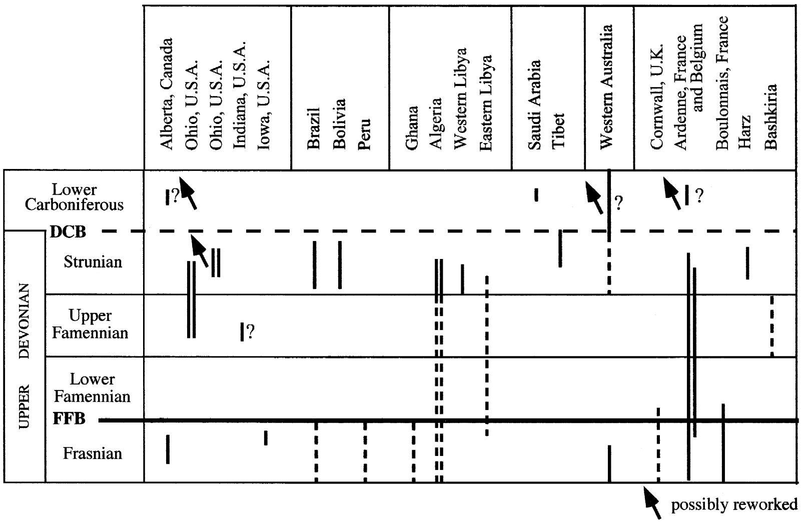


Fig. 14. Approximate stratigraphic distribution of acritarch-bearing sequences in the Upper Devonian and Lower Carboniferous after Vanguestaine (1986, fig. 3 modified). Single line: spot samples, reduced or incompletely studied interval (no proposed zonation); double line: sequence studied in detail (proposed zonation); dashed line or question mark: poorly dated; full line: well dated. The dramatic decline of acritarchs occurs near the DCB, not near the FFB.

years (Schindler, 1993, fig. 7). In many sections, observations concentrate on the Upper Kellwasser Horizon (UKW) and lateral equivalents as well as layers immediately below and above that level. It is represented in the pelagic realm as an intercalation of dark sediments within lighter limestones or shales. A worldwide synchronous character of this lithological unit is often claimed (Walliser, 1995).

The Frasnian/Famennian Global Stratotype Section and Point (GSSP) has been fixed (Cowie et al., 1989) in the Coumiac Section (Montagne Noire, southern France) at a level between the *Palmatolepis linguiformis* and *P. triangularis* Zones of the standard conodont zonation. But here the limits of biostratigraphy are reached. For instance, *P. triangularis* and *P. praetriangularis* (the latter occurring in the *linguiformis* Zone) are sometimes considered as synonymous and even the occurrence of a few specimens of *P. triangularis* is accepted by Klapper et al. (1993, p. 436) in the Frasnian *linguiformis* Zone. Also, the resolution obtained with the evolution of conodont biofacies changes is believed, at the genus level by Girard (1995) and at the species level by Schülke (1998), to be finer than the standard biozonation. So, the FFB at the stratotype of Coumiac has, after Girard (1995, p. 692), to be placed within a ferruginous crust, a few mm thick, or above it, rather than at its base as formerly proposed. Sedimentological and geochemical methods also provide a correlation tool, but they are more important clues to environmental interpretation (Herbosch et al., 1997b; Weis et al., 1998). The UKW is generally admitted to represent a spreading of dysoxic facies coinciding with a rapid transgression followed by a strong regression right at the stage boundary (Sandberg et al., 1988).

Palynomorphs have been obtained from the UKW at Coumiac but are too poorly preserved for precise identification (Klapper et al., 1993, p. 439). Chitinozoans and Prasinophycean green algae (*Maranhites*) were found in the Montagne Noire at La Serre, 30 km from the Coumiac quarry. At La Serre, the FFB falls within interbedded anoxic dark shales and limestones. The almost complete absence of miospores and acritarchs in these beds is probably related to the distal situation of the deposition site (Paris et al., 1996). The major result from this section is the exceptional chitinozoan concentration in the basalmost Famennian bed (Paris et al., 1996, fig. 2, in part reproduced here as Fig. 15).

In order to observe miospores and acritarchs during the Kellwasser Event, we need neritic facies that

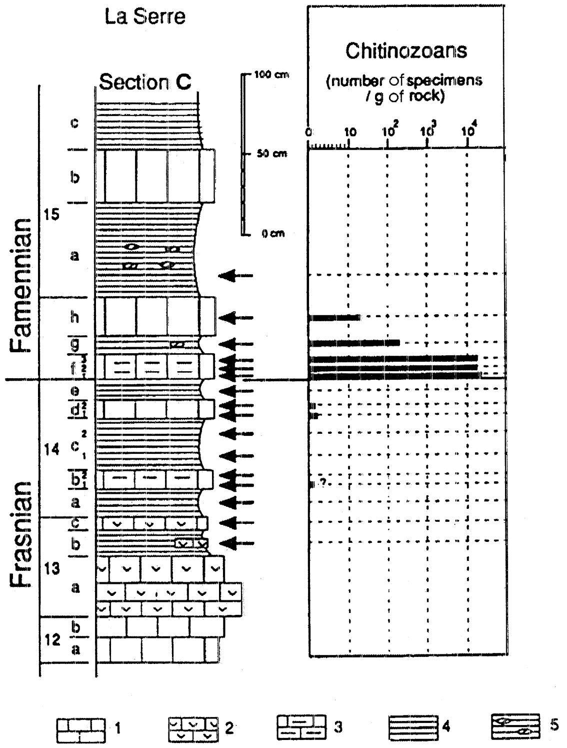


Fig. 15. Chitinozoan distribution and abundance in the Frasnian–Famennian boundary beds in section C at La Serre (Montagne Noire, southern France), reprinted from Paris et al. (1996, fig. 2 modified. Used with permission of the first author). (1) Grey limestone; (2) light grey limestone; (3) black laminated micritic limestone; (4) weathered marly shale; (5) calcareous nodules. The exceptional chitinozoan concentration in the basal-most Famennian beds fits rather well a global cooling hypothesis at that level as cold water seems to have been more favorable for the proliferation of these microfossils.

also yield conodonts to correlate with the GSSP. The former reference section of the base of the Famennian at Senzeilles (southwestern Belgium) contains acritarchs (Martin, 1985) but is poorly dated by conodonts (Bultynck and Martin, 1995). The Hony and Sinsin sections (40 km apart from each other, in southeastern Belgium) have diagnostic conodont faunas (Sandberg et al., 1988) and abundant acritarchs (Vanguestaine et al., 1983; Streel and Vanguestaine, 1989). Miospores, although present and sometimes rather abundant, are poorly preserved and surprisingly not very diverse. One can immediately remark that there first occurs only a few acritarch species in these sections. The UKW influence on these palynomorphs, if any, is only of quantitative character. Important exceptions are the first occurrences of the acritarchs *V.? occultata* and *Ephelopalla media* (Fig. 16) which seem to represent good markers for the transitional Late *rhenana-linguiformis* Zones timespan (Martin, 1993; Bultynck and Martin, 1995) and had been used higher up to date the upper part of the Briquetterie de Beaulieu section in the Boulonnais area. More detailed data on the systematics and quantitative rates of acritarch species across the FFB at Hony and Sinsin is beyond the scope of the present paper. Here we will focus on the concentration (number of specimens, not of species, per gram of sediment) of acritarchs and miospores, as fossil groups, in restricted shaly intervals. Of course, it is not well known how much of the boundary limestone in the GSSP is here represented by shale. Since the palynological analysis published over 10 years ago (Streel and Vanguestaine, 1989), both sections have attracted further investigations which are important for their stratigraphic and sedimentological interpretation. One of the sections (Hony) has also become famous for the discovery of microtektites (Claeys et al., 1992) near the FFB (see later).

5.1. Hony section

The most important acritarch data related to the FFB were published by Vanguestaine et al. (1983, fig. 6, reproduced here as Fig. 17). A major quantitative change is shown near that boundary in the Hony section for nine selected species. The time resolution is, however, too poor to allow evaluation of the Kellwasser Event. Indeed, studied samples around that level are spaced far too apart for allowing detailed analysis. At Hony, 150 cm of shale separate the last Frasnian limestone with conodonts of the *linguiformis* Zone from the first Famennian limestone with conodonts of the Early *triangularis* Zone. Conodont biofacies indicate a regressive trend (abundant *Icriodus*) in both limestones. The shale subdivision is twofold: a grey unit containing coquina layers, 115 cm thick, at the base, and a dark-grey unit, 35 cm thick, at the top (Sandberg et al., 1988). Olive-green shale is present below in the Frasnian and starts again on the top of the Famennian limestone.

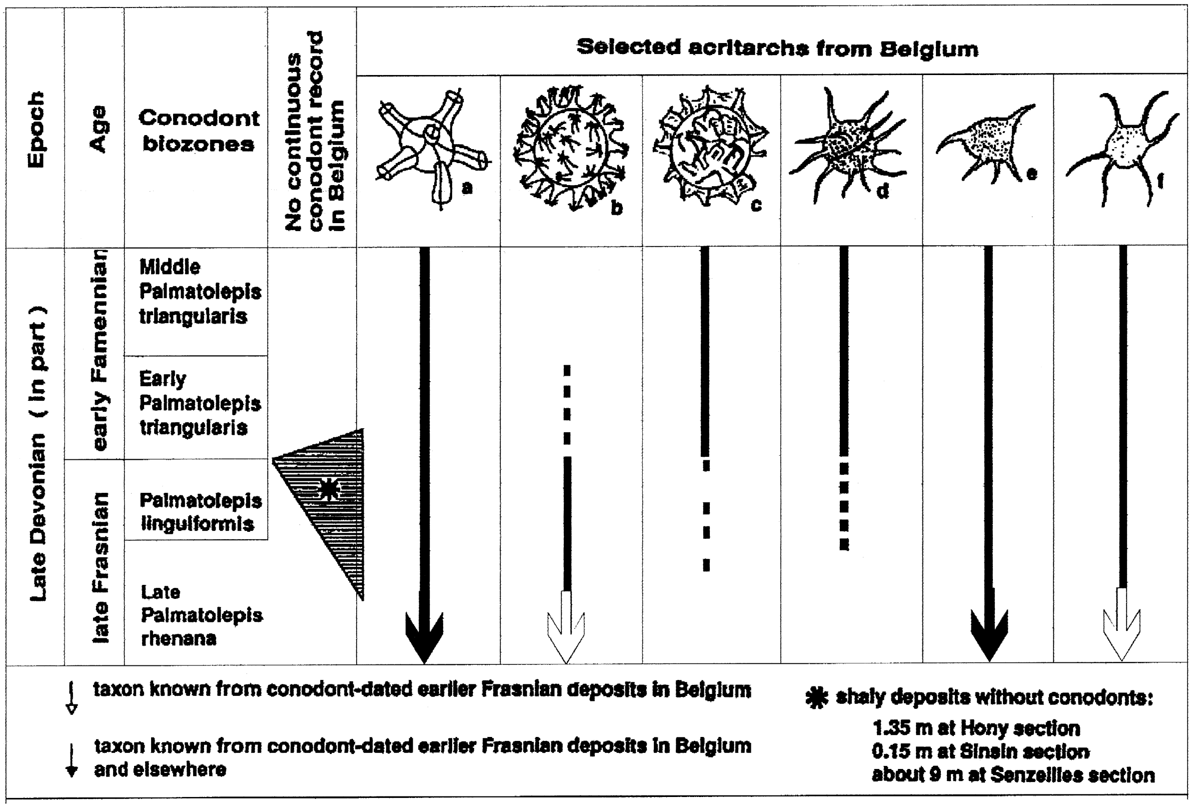


Fig. 16. Selected Frasnian–Famennian acritarchs from Belgium (not to scale), reprinted from Martin (1993, fig. 9. Used with permission of Cambridge University Press). (a) *Daillydium pentaster*; (b) *Visbysphaera? fecunda*; (c) *V.? occultata*; (d) *E. media*; (e) *Villosacapsula ceratioides*; (f) *V. globosa*. (c) and (d) seem to represent good markers for the transitional Late *rhenana–linguiformis* Zones timespan.

Acritarchs (spiny acritarchs) show a continuous decrease from 10,000 sp./gr.sed. at the base of the lower unit to nothing at its top and in the upper unit (Fig. 18). They increase again up to 6000 sp./gr.sed. in the olive-green shale above the top of the Famennian limestone. Miospores oscillate between 600 and 2800 sp./gr.sed. along the lower unit. They almost disappear in most of the upper unit except for the last 10 cm where they increase again and become more abundant in the olive-green shale on the top of the first Famennian limestone. The successive decreasing and increasing upward trends of acritarchs were interpreted by Streel and Vanguestaine (1989) as a progressive regression culminating in the deposition of the dark grey shale (the upper unit) during which a sudden acceleration of the sedimentation rate was believed to have diluted the palynomorphs, followed by a new transgression. They concluded therefore that the palynomorphs originated from that part of the shelf basin where a dominance of acritarchs was progressively replaced landward by a dominance of miospores (hypothesis A of Fig. 19).

Several authors (Claeys, 1993; Claeys et al., 1994, 1996; Herbosch et al., 1996, 1997a) have subsequently proposed that the upper unit probably represents a deepening of the depositional environment. They also demonstrated, through geochemical analyses, that chalcophilous elements show an increase within this upper unit, suggesting an abrupt input of poorly oxygenated waters (Oxygen Minimum Zone or OMZ) into a relatively shallow marine environment. They assume that this level must be equivalent to the UKW. Recently, a new sedimentological analysis based on microfacies study (X. Devleeschouwer, personal communication, June 1999) confirms the deepening interpretation (Fig. 18).

This alternative interpretation has some consequences for the palynomorph quantitative interpreta-

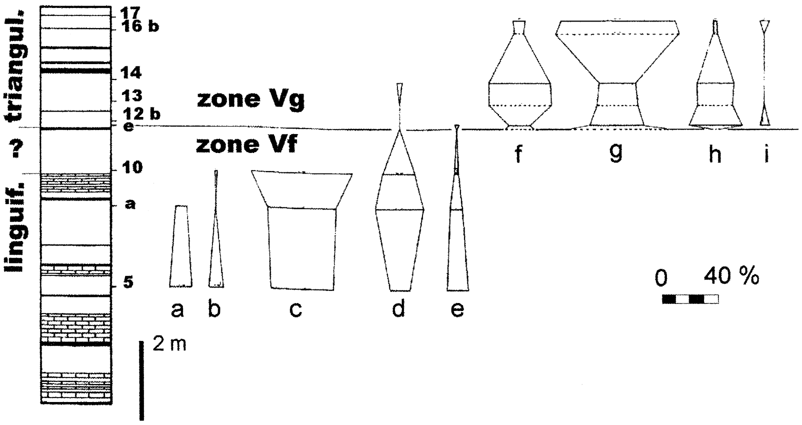


Fig. 17. Relative percentages of nine selected species of acritarchs around the FFB at Hony (Belgium), after Vanguestaine et al. (1983, fig. 6 modified). (a) *Baltisphaeridium* aff. *longispinosum*; (b) *Hercyniana sprucegrovensis*; (c) *Visbisphaera*? *fecunda*; (d) *Baltisphaeridium* cf. *crebum*; (e) *Dilatisphaera*? sp. A; (f) *Diexallophasis remota*; (g) *Villosacapsula globosa*; (h) Herkomorphitae sp. A (= *V*.? *occultata* in Fig. 16); (i) *Baltisphaeridium medium* (= *Ephelopalla media* in Fig. 16). (f) and (g) are known below in Belgium; (h) and (i) are the markers referred to in Fig. 16. Studied samples around the FFB are spaced far too apart for detailed analysis (compare with Fig. 18).

tion. In a second hypothesis (hypothesis B of Fig. 19), one can accept that miospores were transported for long distances offshore by bottom return flows as a consequence of the storm waves, resulting in their poor preservation (many corroded, unidentifiable specimens). It would explain also the presence, known only in these shales, of reticulate specimens formerly assigned to *Corbulispora* sp. (Loboziak and Streel, 1981; Streel et al., 1987), and now interpreted as the mesospore wall layers of freshwater algal Zygnematacea split along their equatorial regions (Grenfell, 1995). According to this hypothesis, the non-marine palynomorphs would have been reworked from continental nearshore sediments and deposited in the distal part of the shelf basin where the abundance of acritarchs is progressively reduced seaward (hypothesis B of Fig. 19).

The Hony section would record, in a small cyclic succession, a regression in the last Frasnian limestone (Sandberg et al., 1988, fig. 9), a transgression in most of the shaly interval, and again a regression which accounts for the uppermost part of these shales, the first Famennian limestone and the lower part of the succeeding olive-green shale.

5.2. Sinsin section

At Sinsin section, about 27 cm only of dark and dark-grey shale separates the last Frasnian limestone bed with conodonts of the *linguiformis* Zone from the first Famennian limestone with conodonts of the Early *triangularis* Zone. Conodont biofacies indicate a regressive trend (abundant *Icriodus*) in both limestones (Sandberg et al., 1988, fig. 10). The shale is subdivided twofold: the lower 12 cm are dark shales containing limy lenses, some of them bearing conodonts of the *linguiformis* Zone; the upper 15 cm are dark-grey shales. Olive-green shale is present below in the Frasnian and starts again on the top of the Famennian limestone. In the lower 12-cm, acritarchs and miospores are poorly represented except in one sample. In the upper 15 cm, acritarch abundance (spiny acritarchs) shows a continuous upward decrease from 10,000 sp./gr.sed. at the base of the dark-grey shales to 3000 sp./gr.sed., 10 cm higher. It increases again from 8000 sp./gr.sed. to very high values of 50,000 sp./gr.sed. in the upper 5 cm of these shales. Miospore abundance oscillates between 1800 and 3800 sp. gr.sed. in the lower 10 cm of the dark-grey shales and increases again up to 8000 sp./gr.sed. in the upper 5 cm of these shales (Fig. 20).

As explained for Hony, Streel and Vanguestaine (1989) interpreted the successive decreasing and increasing upward trends of the acritarchs as a progressive regression followed by a transgression. They also remarked that the miospore/acritarch ratio evolved in a similar fashion in both sections. They

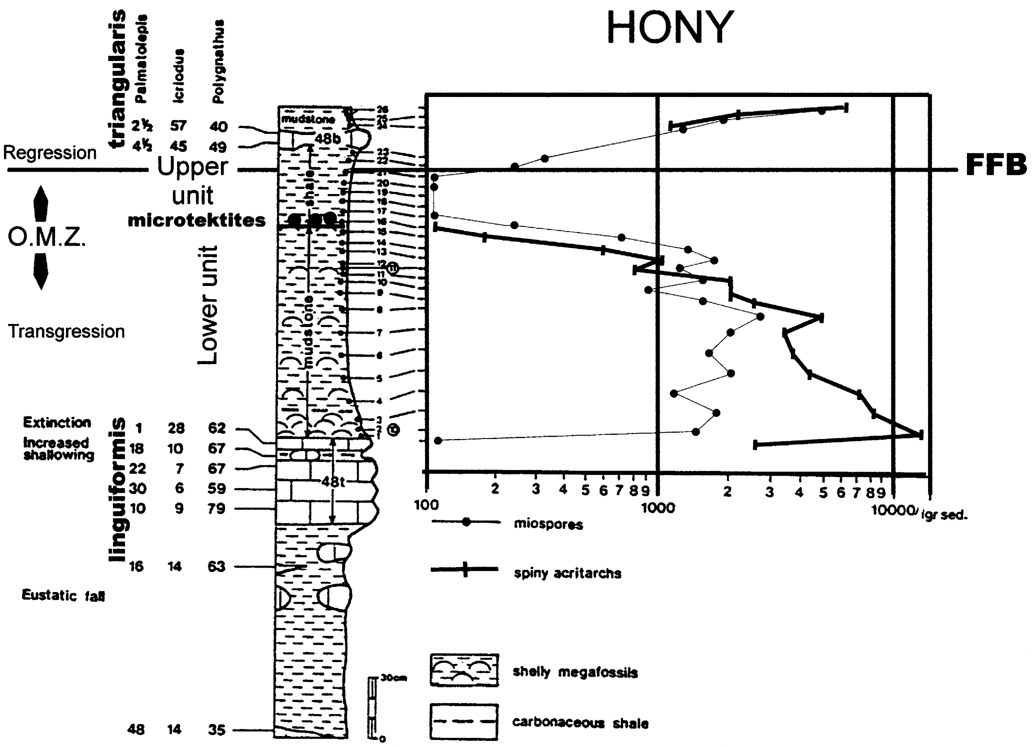


Fig. 18. Palynomorph stratigraphic distribution near the FFB at Hony, after Streel and Vanguestaine (1989, fig. 2 modified). Lithology and conodont Zones and Biofacies after Sandberg et al. (1988, fig. 9 redrawn). Oxygen Minimum Zone (OMZ) after Claeys et al. (1996, fig. 7). Sedimentological analysis based on microfacies study (X. Devleeschouwer, personal communication, June 1999) indicates the existence of two relatively different shallow marine domains: (1) in the lower part of the lower unit, a zone where the sea floor was affected by storm waves but not by fair-weather waves and where sediments show evidence of frequent storm reworking; (2) in the remaining part of the lower unit and the major part of the upper unit, a zone where sediments were deposited below the storm wave base. Allochthonous faunal and floral elements were transported from nearshore environments to deeper environments. In the uppermost dark-grey shale, microfacies indicate a brief return to shallower conditions where sparse and distal tempestite deposition may occur. Acritarchs (spiny acritarchs) show a continuous decrease from 10,000 sp./gr.sed. at the base of the lower unit to nothing at its top and in the upper unit (this figure). They increase again up to 6,000 sp./gr.sed. in the olive-green shale above the top of the Famennian limestone. Miospores oscillate between 600 and 2800 sp./gr.sed. along the lower unit. They almost disappear in most of the upper unit except for the last 10 cm where they increase again and become more abundant in the olive-green shale on the top of the first Famennian limestone.

hesitated to conclude that similarity implies contemporaneity, although noting that the dark-grey shales present at Hony might be missing at Sinsin. Subsequently, Casier and Devleeschouwer (1995) discovered a very rich and well preserved ostracod fauna in the upper 5 cm of the dark-grey shales. This assemblage is indicative of a brackish-water environment with strong marine influence and clearly corresponds to a regression in that part of the shales which Streel and Vanguestaine (1989) had attributed to a transgression.

We propose therefore that, at Sinsin, palynomorphs originated from that part of the shelf basin where the abundance of acritarchs is progressively reduced seaward (hypothesis B of Fig. 19). We propose also that the similarity in the concentration curves of miospores and acritarchs in both Hony and Sinsin sections is indicative of their contemporaneity, also with the significant difference that a major part of the dark-grey shale at Hony is missing at Sinsin (Fig. 20).

In both sections, we observe successively a regression in the last Frasnian limestones or shales containing limy lenses (Sandberg et al., 1988), a transgression in most of the shaly interval culminating at Hony in the development of oxygen-poor

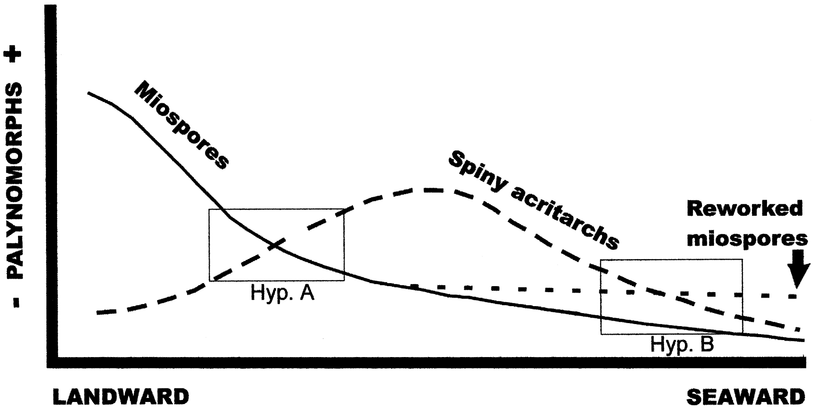


Fig. 19. Hypothetical distribution of palynomorphs in sea basin. After Jekhowsky (1963), modified. According to hypothesis B, the non-marine palynomorphs would have been reworked from continental nearshore sediments and deposited in the distal part of the shelf basin where the abundance of acritarchs is progressively reduced seaward.

bottom waters and again a regression in the uppermost part of these shales, with a possible sedimentary gap at Sinsin (Casier and Devleeschouwer, 1995). We must remember now that the Kellwasser Event is generally admitted, in the Rhenish regions at least, to represent a spread of dysoxic facies coinciding with a rapid transgression and that the transgression reversed subsequently into a strong regression right at the stage boundary. We suggest therefore that the FFB at Hony and Sinsin should be placed near the base of the regression within the upper part of the dark-grey shales.

It is evident that the Kellwasser Event did not affect significantly the phytoplankton more than it did with the chitinozoans. The almost complete absence of acritarchs at the FFB may be explained by the sedimentary conditions, not necessarily by a genuine extinction. But what about the miospores?

To answer this question we have to move again (see the Late Frasnian Crisis, above) to the (30 m thick) Briquetterie de Beaulieu section, of the Hydrequent Formation (Boulonnais, northern France), where shales with abundant and well preserved miospores and less numerous acritarchs are present (Loboziak et al., 1983; Streel and Loboziak, 1994, fig. 1). No conodonts were recorded in this section which is known to cover more or less the Late *rhenana-linguiformis* Zones in a more nearshore facies than the Hony and Sinsin sections. There is no lithological equivalent of the UKW in this facies, but this stratigraphic interval can be assumed to correspond to the topmost 2.5 m of the section containing in succession the acritarchs *V.? occultata* and *E. media* (Fig. 13). We do not know, however, the exact location of the FFB in this section. The sharp contact between the marine Hydrequent Shales and the overlying, palynomorph barren, Sainte Godeleine Sandstones might even represent it. Therefore, we cannot confirm any changes, even of a quantitative nature, in the miospore distribution at the FFB in the Boulonnais area. The successive reduction and increasing of miospore abundance at Sinsin and Hony might well be, as noticed for the acritarchs, of sedimentological nature, not necessarily a consequence of a sudden but ephemeral change of the vegetation on Earth. However, it should be realized that, for the time being, no continuous miospore succession is known for certain across the FFB.

6. The causes of the Late Frasnian Crisis and the Kellwasser event

Following the suggestion by McLaren (1970) that the Late Devonian mass extinction might have been triggered by the impact of an asteroid, the search for evidence of such impact(s) in the geological record rapidly emerged. Also, the finding of an iridium anomaly at the Cretaceous-Tertiary boundary by Alvarez et al. (1980) suggested a new approach for the

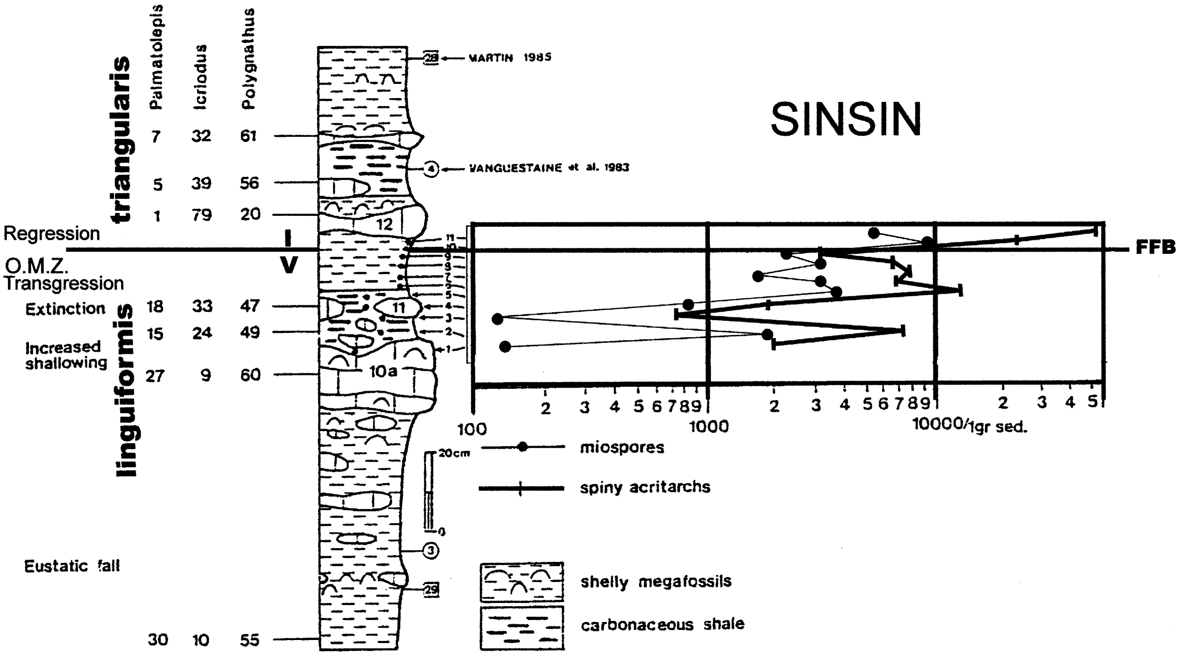


Fig. 20. Palynomorph stratigraphic distribution near the FFB at Sinsin, after Streel and Vanguestaine (1989, fig. 3 modified). Lithology and conodont Zones and Biofacies, after Sandberg et al. (1988, fig. 10 redrawn and modified). Oxygen Minimum Zone (OMZ) and ostracod assemblages, after Casier and Devleeschouwer (1995). I: very rich ostracod fauna but poorly diversified characteristic of semi-restricted conditions; V: Myodocopid (*Entomozoacea* and *Cypridinacea*) ostracods characteristic of dysoxic conditions. In the upper 15 cm of the transitional shale unit, acritarch abundance (spiny acritarchs) shows a continuous upward decrease from 10,000 sp./gr.sed. at the base of the dark-grey shales to 3000 sp./gr.sed., 10 cm higher. It increases again from 8000 sp./gr.sed. to very high values of 50,000 sp./gr.sed. in the upper 5 cm of these shales. Miospore abundance oscillates between 1800 and 3800 sp./gr.sed. in the lower 10 cm of the dark-grey shales and increases again up to 8000 sp./gr.sed. in the upper 5 cm of these shales.

"impact theory". But there are no anomalous concentrations of iridium so far in the sampled sections of Belgium (Claeys et al., 1994; McGhee, 1996) and nothing unequivocal, right at the FFB, around the world.

Microtektites have been reported from two localities of Belgium: at Senzeilles (Claeys et al., 1992), near the uppermost part of the Early *triangularis* Zone (Bultynck and Martin, 1995) and at Hony (Claeys et al., 1994), at the base of the dark-grey shales, i.e., immediately below the here suggested FFB. The absence of microtektites at Sinsin can be explained by the sedimentary gap occurring at that level. The record at Senzeilles is doubtful because the glasses closely resemble the chemical composition of reflective beads used for road marking (Marini and Casier, 1997). It is not the case for the Hony microtektites, which might well represent the best evidence of an impact of extraterrestrial body on Earth corresponding to the UKW, although as Walliser (1995, p. 236) notes "microtektites are found in various quantities in Paleozoic conodont samples from many layers lacking any indication of an unusual geological or biological change".

The effect of an extraterrestrial body crash on global climate has often been discussed. "Large amounts of debris from the vaporized bolide and impact site would be injected into the atmosphere. Such a global dust cloud could result in the total blockage of sunlight from the Earth's surface" (McGhee, 1996, p. 163) and initiate a global cooling on Earth resulting in a short glaciation. "Equally, the impact of a large extra-terrestrial body into the ocean might also promote higher temperatures through the vaporization of large amounts of water. The increased cloud cover which would result from this would also insulate the Earth, preventing heat loss and thereby causing global warming" (Bennett and Glasser, 1999, p. 11). Ozone depletion caused by the impact can result in elevated UV-B radiation on the surface of the Earth acting as a kill mechanism (Cockell, 1999). Each of these mechanisms might result in the death of both the phytoplankton of oceans and plant life on land, but we know now that it was not the case near the FFB.

The exceptional chitinozoan concentration in the basal-most Famennian bed in La Serre (Paris et al., 1996, fig. 2, partially reproduced here as Fig. 15) fits rather well the global cooling hypothesis as cold water seems to have been more favorable for the proliferation of these microfossils (Paris et al., 1996, p. 143). A (very) short glaciation would explain the sudden and short, major eustatic fall shown at the end of the T-R cycle IId (Fig. 21) of Johnson et al. (1985). Short-term glacial phases during a "warm mode" period are known in the Paleozoic and in the Mesozoic. Brenchley et al. (1994) demonstrate bathymetric and isotopic evidence for a short-lived (0.5–1 Ma) Late Ordovician glaciation in a "warm mode" period. Even in the Late Cretaceous, which is often presented as a good example of an ice-free world, isotopic and sequence stratigraphic evidence for an early Maastrichtian, very rapid (much less than 1 Ma) growth of an ice sheet and attendant glacio-eustatic lowering has been recently presented by Miller et al. (1999). The sudden growth and decay of an Earliest Famennian ice sheet might have been the result of the reduction and later, increase in greenhouse capacity of the atmosphere as the consequence of sudden changes in the mode of ocean-atmosphere operation (Broecker and Denton, 1989).

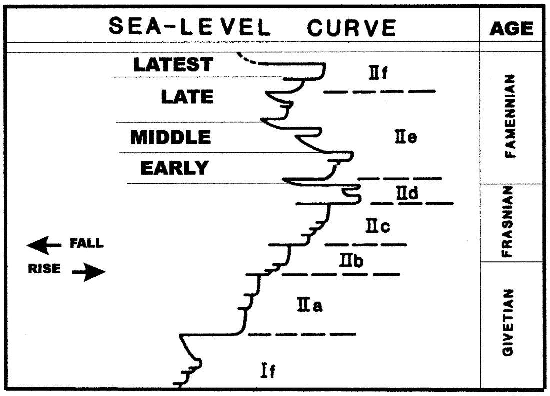


Fig. 21. The Devonian sea-level curve of Johnson et al. (1985) from Hallam (1992, modified. Used with the permission of the author). Sub-stages of the Famennian after Fig. 6. A major eustatic fall is shown at the end of the T-R cycle IId. A dominantly transgressive curve characterizes the lower half of T-R cycle IIe. A dominantly regressive curve characterizes the upper half of T-R cycle IIe. A widespread transgression culminates within the T-R cycle IIf while the important glacio-eustatic fall at the end of the Famennian is only suggested.

Kegel (1953) was the first to demonstrate the glacial origin of diamictite beds with faceted and striated clasts in the Upper Devonian of the Parnaíba Basin, northern Brazil. Malzahn (1957) described striated pavements on sandstones then attributed to the Pimenteira Formation in the southeastern sector of the same basin in the Piaui State. "There is, therefore, unequivocal evidence for widespread continental glaciation in one area belonging to the eastern half of the Parnaíba Basin" (Boucot, 1988, p. 222) but the latter author added that the timing of this event was rather imprecise. Indeed, according to Rocha-Campos (1981), the diamictites and associated rocks of alleged glacial origin in the Parnaíba Basin, which were partly maintained in the Pimenteira Formation by Andrade and Daemon (1974), were placed in the overlying Cabeças Formation by Carozzi et al. (1975). This became an important distinction since Loboziak et al. (1992, fig. 4) have suggested (Fig. 22), based on new palynological evidence, that most of the Famennian might be missing between the Latest Frasnian–Earliest Famennian strata of the upper Pimenteira Formation and the Latest Famennian Cabeças Formation. Later, in 1996, one of us (J.H.G.M.) has been in the same area studied by Malzahn (1957) and could verify that the striated pavements are covered with tillites, and these latter covered by transgressive marine siltstones and sandstones belonging to the Longá Formation, thus confirming, on the basis of lithological arguments, that the tillites do belong to the topmost Cabeças Formation (see also Caputo, 1985). Therefore, the glaciation evidence from the southeastern Parnaíba Basin is probably not of the Latest Frasnian–Earliest Famennian age.

The recent discovery of dropstones in the Colpacuchu Formation of the Peru–Bolivia (Altiplano) Basin assumed by Isaacson et al. (1999, p. 241) to belong to "late Frasnian and early Famennian" after

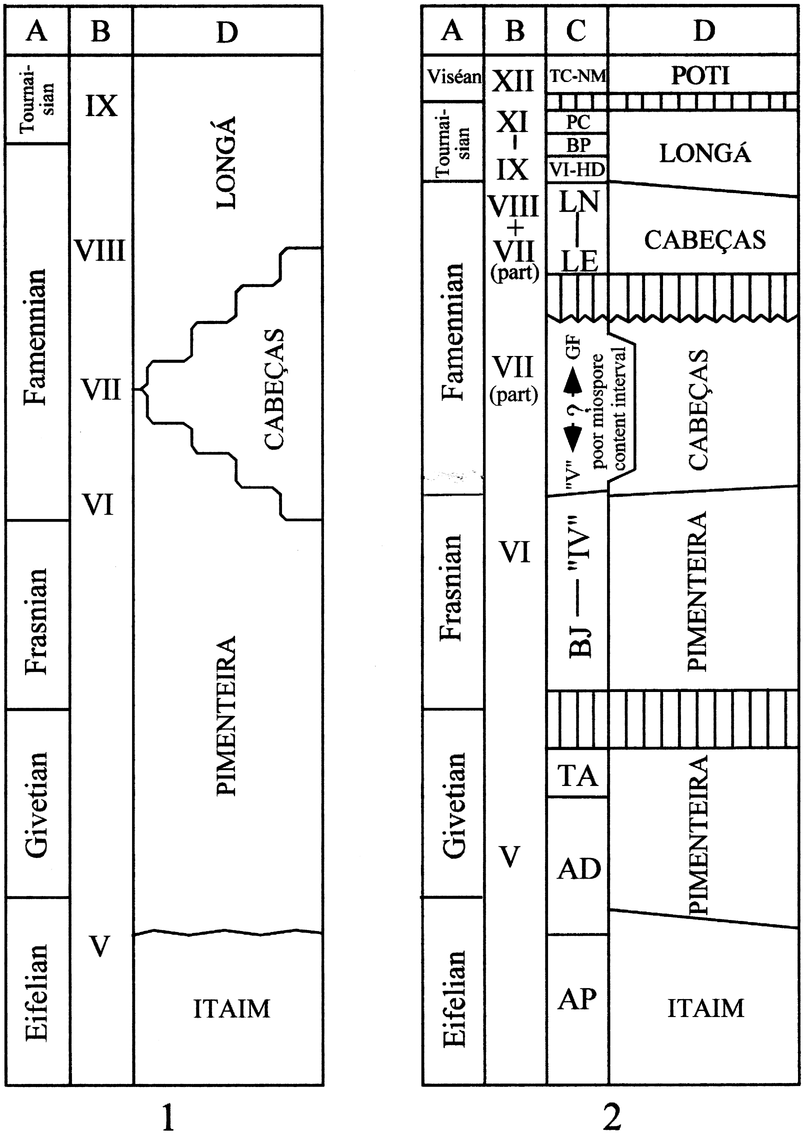


Fig. 22. Comparison of Parnaíba Basin former stratigraphic scheme (1), after Caputo (1985), with new results (2), from the central-western parts of the Parnaíba Basin, Brazil, after Loboziak et al. (1992, fig. 4 modified). (A) chronostratigraphy; (B) biostratigraphy after Daemon (1974); (C) biostratigraphy after Loboziak et al. (1992) and unpublished data from S. Loboziak and J.H.G. Melo; (D) lithostratigraphy. Most of the Famennian might be missing between the Latest Frasnian–Earliest Famennian strata of the upper Pimenteira Formation and the Latest Famennian Cabeças Formation.

Racheboeuf et al. (1993) is not correctly dated. Indeed, this formation is said by the latter authors to correspond to the late Frasnian "at least", on the base of an acritarch species (*Maranhites insulatus*) found in one sample from the Colpacuchu Formation and known from the Frasnian to the Tournaisian in Brazil (Racheboeuf et al., 1993, p. 801).

However, despite the fact that there is no palynological evidence for a glaciation of the Latest Frasnian–Earliest Famennian age, one can wonder whether a very short glaciation period, as suggested by the very short eustatic fall duration, had any chances to be recorded by characteristic marine sediments, because glacial deposition is commonly initiated by a recession of the ice at the end of the glaciation (Crowell, 1999; Crowell and Frakes, 1972; Visser, 1990, 1991), and such deposits might well have been soon redistributed by the succeeding transgression. The development of mountain (alpine type) glaciers, not recorded at sea level, is another possibility.

As noticed by Narkiewicz and Hoffman (1989, p. 23), the rate of eustatic sea-level change was so rapid immediately after the FFB that it cannot be accounted alone for by a mechanism referring to slow down in spreading rates of oceanic ridge systems.

A glaciation would explain the abundance of chitinozoans at the basal-most Famennian of La Serre section and why "the hexactinellids (glass sponges) migrate from deeper-water regions into the shallows and undergo a burst of diversification in species number" across the FFB (McGhee, 1996, p. 121). Modern glass sponges are indeed considered to be better adapted to cold waters than most other invertebrate species. It would also explain why the Earliest Famennian low-latitude faunas were drastically reduced and the diversity loss less severe in high-latitude regions. High-latitude faunas were less affected as many species could simply have migrated to lower latitudes and so maintain their tolerable temperature ranges (Copper, 1977, 1986, 1998; McGhee, 1996, p. 130). Earliest Famennian global warming, suggested by others (Brand, 1989; Thompson and Newton, 1988) would not explain the observed faunal latitudinal zonations.

The diversity loss in pelagic fossil groups like conodonts and ammonoids might well be the result of the rapidity of the climatic change itself that, after Fisher and Arthur (1977) and also Crowley and North (1988), may be the major trigger mechanism of global ecosystem collapse. Such rapid climatic change is well known in more recent time. For instance, several rapid temperature oscillations are recorded in the Middle Miocene of Pacific Ocean prior to the major onset of the Antarctic glaciation. The character of the Middle Miocene isotopic record suggests that the Earth's climatic system became extremely unstable and for perhaps 1 Ma oscillated back and forth between glacial and interglacial modes (Woodruff et al., 1981, fig. 1). Unfortunately, there exists so far no well-documented quantitative data on miospore successions across the FFB which would allow testing the rapid climatic change hypothesis on such an accurate scale.

In order to explain the Late Frasnian diversity crisis, spanning at least 2.0 Ma, McGhee (1996) and Racki (1999) call upon a "multiple impact theory". Several impacts would have affected, from time to time, the marine ecosystem by very short, rapid climatic oscillations (not reaching the glacial level). However, the stability of land floras as deduced from the miospore analysis (see above) does not confirm strong climatic oscillations during that entire interval of time. Instead, we must even admit a stable Late Frasnian climate with the equatorial climatic belts having reached a maximum width.

Would the Late Frasnian diversity loss in miospores be rather the result of a warming trend of the climate? Here comes back the volcanic hypothesis (Racki, 1998b). Example of volcanogenic rocks near the FFB may be found, for instance, in the east of the Pripyat Depression (Belarus) in the upper part of Evlanov Horizon and in Liven and Domanovichi Horizons, dated by miospores (Obukhovskaya et al., in press). The role of wildfire on land, initiated by terrestrial volcanic activities, was important in carbon cycling since the Late Devonian (Jones, 1999). Large amounts of CO_2 from violent submarine volcanism might have caused long-term atmospheric warming, sea transgression and anoxia during the Late Frasnian. The anoxia may have been caused by the intrusion of the OMZ on epicontinental and shelf basins of the world during sea transgressive pulses (Greenhouse effect, see also Caputo, 1994, 1995). To the thermal stress on land can be added the adverse effects of volcanic poisons such as arsenic, fluorine and particularly chlorine (Keith, 1982, p. 2632). The proposed volcanic warming might have also slowed down the deep circulation of aerated polar waters and developed stagnant ocean conditions incrementing the periodic development of anoxic conditions as suggested by Wignall and Twitchett (1996, p. 1157) for the end-Permian mass extinction.

Such changes should be recorded by positive excursion of the $\delta^{13}C$ curve followed by negative excursion in marine sediments at the FFB. Unfortunately, carbon isotope measurements in the related timespan have given so far discordant results (McGhee, 1996, p. 224), but the inconsistency of published data might well be caused by imperfect biostratigraphic definitions of the FFB (Buggisch, 1991). Indeed, sedimentologic and isotopic carbon studies carried out on stratigraphically well documented Late Frasnian and Early Famennian strata in Austria, France and Germany (Joachimski and Buggisch, 1993) support the idea that an increasing positive excursion of the $\delta^{13}C$, reflecting an increasing biomass burial, corresponds to the UKW level (up to +2.8‰ over a Frasnian background value of +1‰). The same authors explain that the enhanced burial of organic carbon may have a significant effect on the CO_2 and O_2 concentrations in the oceans and atmosphere at the end of Frasnian time. "A lowering of the atmospheric CO_2 concentration causes global climatic cooling and may result in a worldwide regression, if the icehouse effect is strong enough to initiate the buildup of polar ice caps" (Joachimski and Buggisch, 1993, p. 677). This negative $\delta^{13}C$ anomaly is associated with an increase in $\delta^{18}O$ values. The very fast shift toward positive $\delta^{18}O$ values with an amplitude of about 2‰ indicates a short-lived decrease in temperature of about 10°C below the Latest Frasnian temperature in the Luoxiu section, South China (Zheng et al., 1993), assuming that a 0.2‰ increase in $\delta^{18}O$ values represent a 1°C drop. This record supports the existence of polar ice in the Earliest Famennian. $\delta^{18}O$ values are driven primarily by a combination of glacio-eustatic sea level and temperature. Therefore, the $\delta^{18}O$ signal is a parameter available for estimating the magnitude and rate of change in sea level independently of other geological records (Williams, 1988). The stable oxygen isotope values can add a new dimension concerning timing, magnitude, and rates of sea-level changes. The best estimate for this effect in the Pleistocene is a 0.11‰ change for every 10 m of seawater removed. The change in $\delta^{18}O$ through the FFB is +2‰ in South China. This signal predicts a drop in sea level through the FFB of about 180 m. Part of this $\delta^{18}O$ record must be due to temperature and climatic deterioration, but this estimate compares with Issacson et al. (1999) estimates of 100–140 m drop in sea level during the Earliest Famennian. A major event of increased positive $\delta^{34}S$ isotope values in sulfates, named the Soures event (Holser, 1977), indicates a prolonged anoxic interval with $\delta^{34}S$ + 30‰ values in Late Frasnian time. The $\delta^{34}S$ values sharply decreased to +20‰ at the Early Famennian suggesting abrupt water turnover that might have been caused by dense oxygenated polar water currents.

Buggisch's (1991) model maintains that the Late Devonian climate oscillated frequently between warm and cold (glacial) phases and was, in fact, similar to the variable climates of the Cenozoic. Such model cannot be entirely applied during the Late Frasnian because supposed glacial phases are not matched by regression trends in the Late Frasnian T-R cycles. It would apply, however, to the Earliest Famennian and later to the Late and Latest Famennian.. Also, the oceanic overturn model of Wilde and Berry (1984, 1986) suggesting a hypothetical sudden injection of deep anoxic bottom waters into the normally aerated waters of the shallow marine platform might explain some loss of diversity in neritic species. However, the phenomenon does not seem to have poisoned the upper part of water column since we know now that the plankton was not annihilated. It would not have either any impact on the land floras.

In conclusion, we suggest that atmospheric increase of CO_2 from violent volcanism might have caused long-term warming during the Late Frasnian and was succeeded by a very short-term glacial phase in the Earliest Famennian. Each episode of the crisis (Late Frasnian to Earliest Famennian) might indeed have been triggered by different factors (Bennett and Glasser, 1999). Whether they were, at least partially, controlled by bolide impact(s), volcanic paroxysm or (and) changes in CO_2 and O_2 concentrations in the oceans and the atmosphere, short cooling and glaciation seem the best reasonable explanation for the major eustatic fall following the Kellwasser Event. How much time did the changeover take from the dysoxic conditions of the UKW to the oxic and regressive phase of the Earliest Famennian? Bratton et al. (1999) suggest that anoxia pre-dated the FFB by about 0.1 Ma, a timespan which, according to Sandberg et al. (1988, p. 297) might have been much shorter.

7. The Early and Middle Famennian vegetation crisis

In northwestern Canada, the Early Famennian and the Earliest Middle Famennian are characterized by six miospore zones (Fig. 9) and 10 first occurrences of taxa (Braman and Hills, 1992, text-fig. 5). In Early and Middle Famennian strata from eastern Europe, seven miospore zones (Fig. 10) are present, characterized by 29 first occurrences (Avkhimovitch et al., 1993, fig. 3). A very characteristic Middle Famennian miospore assemblage, the *Cornispora varicornata* Zone, is present all over Northern Euramerica, dated by conodonts of the *rhomboidea* and *marginifera* Zones. According to Streel (1986), the latitudinal distribution of this zone (Fig. 23) matches the latitudinal distribution of *Archaeoperisaccus* in the Frasnian (Fig. 1).

By contrast, in the Early and Middle Famennian of southern Euramerica, only four, sometimes poorly defined, miospore zones characterized by six first occurrences are known in western Europe (Streel et al., 1987), and only two miospore Zones characterized by five first occurrences occur in eastern North America (Richardson and Ahmed, 1988). In western Gondwana, i.e., in northern Africa (Paris et al., 1985) and in Brazil (Loboziak et al., 1992, and Fig. 22), Early and Middle Famennian miospores are almost unknown and only a few miospore species, but none of the miospore zones cited above, have been recognized. The diversity loss of miospores, observed in the Late Frasnian, is obvious also in the Early and Middle Famennian but becomes more and more severe from the paleo-tropical to the paleo-subpolar regions. A strong climatic gradient from a warm equator to a cool pole was apparently operating during the Early and Middle Famennian (Streel, 1992).

Global cooling, except probably in the equatorial belt, forced land plants to migrate from high latitudes to lower latitudes but the available data do not record this migration process. We must also keep in mind that the equatorial belt might well have kept its moderate thermoperiodism, that is, the comparatively low level of environmental fluctuations, so that land plants which were not able to adapt to the moderate thermoperiodism had no other alternative than to collapse. The post-extinction Famennian recovery phase of marine faunas, “which looks less like a

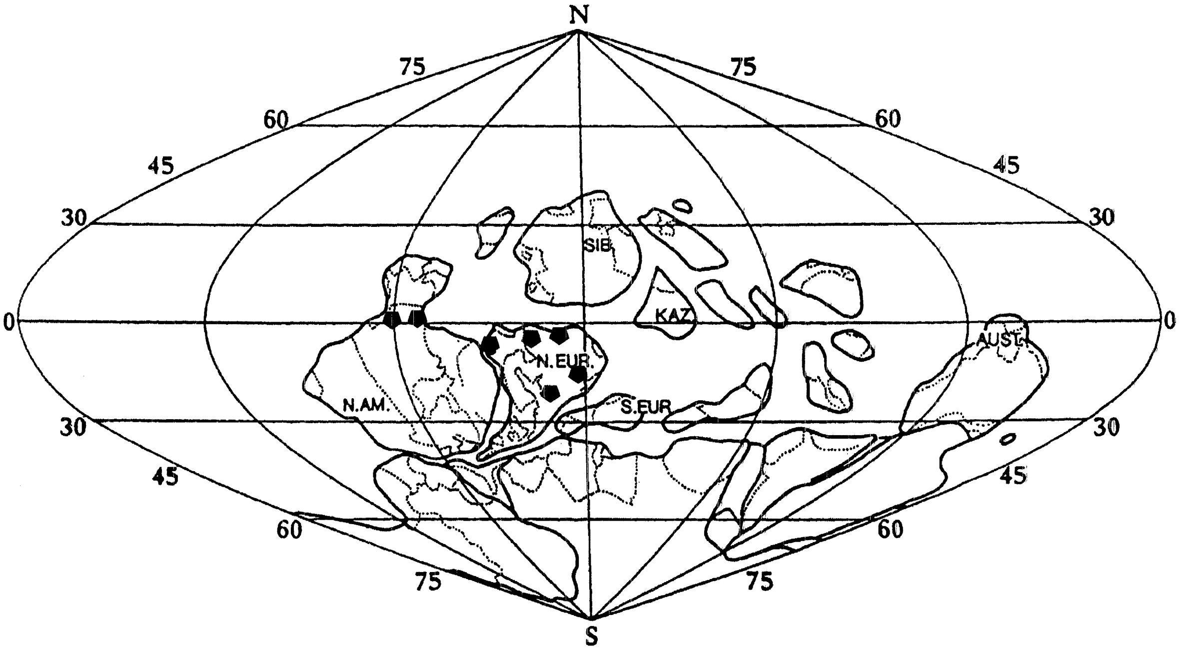


Fig. 23. Paleophytogeographic distribution of the equatorial Middle Famennian miospore *Cornispora varicornata* Zone, after Streel (1986, fig. 5), based on the Middle Devonian map of Heckel and Witzke (1979). The latitudinal distribution of this zone matches more or less the latitudinal distribution of *Archaeoperissacus* (Fig. 1), but data are scarce during the Middle Famennian and are even absents in Alaska and Siberia.

phase of explosive radiation but more like a long-term recovery of 4–5 Ma featuring expansion of climatically more tolerant/resistant organisms" (Copper, 1998, p. 139) is matched by an equally long-term period of poor development of land plants from (sub)tropical (non-equatorial) to subpolar regions.

This Early and Middle Famennian vegetation crisis is underlined by an unexpected phenomenon affecting the mean size of miospores that are significantly smaller in the Famennian than in the Frasnian. This was demonstrated by Naumova (1953) in the transitional Frasnian–Famennian beds of the Central Russian Platform, and also described by Becker et al. (1974, enclosure II, fig. 3) for a widespread Late Devonian species closely related to the *Archaeopteris* miospore *G. lemurata*, namely *Aneurospora greggsii*. The reduction of size is also mentioned by Richardson and McGregor (1986, p. 21). The phenomenon is contemporaneous to the progressive development in size of the megaspore, its reduction in number within the megasporangium and, later, the initialization of the first seeds. It is of a different nature than the reduction in size of the conodont *Palmatolepis* observed by Renaud and Girard (1999) across the FFB and the small phenotypes of brachiopods occurring in the post-Kellwasser Event (Balinski, 1996). These are ephemeral phenomena of organisms living in physiologically highly stressed environments (the "Liliput effect" of Urbanek, 1993) and seem to be a result of high juvenile mortality and possibly stunting (Kammer, 1986).

The suggested Early and Middle Famennian almost global cooling, which would explain the vegetation crisis, is not matched by a major regression of the sea level. Instead, Johnson et al. (1985) show (Fig. 21) a dominantly transgressive curve in the lower half of their T-R cycle IIe. Except for the noticeable regression at the base, only minor (if any) glacial phases are required for that part of the Famennian. Indeed, cooling does not mean glaciation which requires, first of all, heavy snow fall. Now Orminston and Klapper (1992) and Ormiston and Oglesby (1995) maintain that there was no perennial snow cover even in the high latitudes of Gondwana during the Late Devonian, in spite of projected winter land temperatures as low as −40°C. This was due (according to their model) to the lack of sufficient polar transport of moisture to form extensive snow cover, because there was less midlatitude cyclonic activity during the Late Devonian than in the modern world (McGhee, 1996, p. 134). The same phenomenon is locally matched today in the Barren Grounds in the Canadian NW Territories where the climate is cold and dry with no ice and almost no vegetation cover. A glaciation may even require the interaction of warm ocean currents, moisture-laden warm air and cold winds generated by the glacial ice itself (Brooks, 1949; Meyerhoff et al., 1996, p. 48).

8. The Late Famennian

The Late Famennian starts with a major regression marking the end of carbonate-platform sedimentation in many countries and the onset of continent-wide erosion (Johnson et al., 1986; Thorez and Dreesen, 1997). It corresponds to the start of the upper half of T-R cycle IIe of Johnson et al. (1985). It is tempting to relate the major marine regressions of the upper half of the T-R cycle IIe (Fig. 21) with ice volume buildup on Gondwana despite the absence of recorded glacigenic sediments at that time. Probably, mountain (alpine type) glaciers were then developing which are not recorded at sea level (Sablock, 1993). Crowell and Frakes (1970, fig. 7) have very well explained the many factors that interplay to bring about ice ages.

From the start of the Late Famennian, miospore diversity increases again (Raymond and Metz, 1995, fig. 3) (Fig. 8). The climatic gradient was probably less marked because the same miospore zones are recorded again (like in the Frasnian) from paleo-tropical to paleo-subpolar regions, in the Peru–Bolivian (Subandean) Basin (Perez-Leyton, 1991) and in the Amazon Basin (Loboziak et al., 1993; Melo et al., 1996 and Fig. 24), as in western Europe (Maziane et al., 1999). Additionally, the paleo-tropical miospore zones have greater affinities than before with the paleo-equatorial miospore zones (e.g., all regions show the development of the *Diducites* assemblages, Avkhimovitch et al., 1993, p. 90).

In the paleo-tropical Late Famennian of Virginia and West Virginia (USA), on the western side of the Acadian Mountains, a peat-forming vascular plant community occurs for the first time (Scheckler, 1986; Retallack et al., 1996). Quantitative palynology of

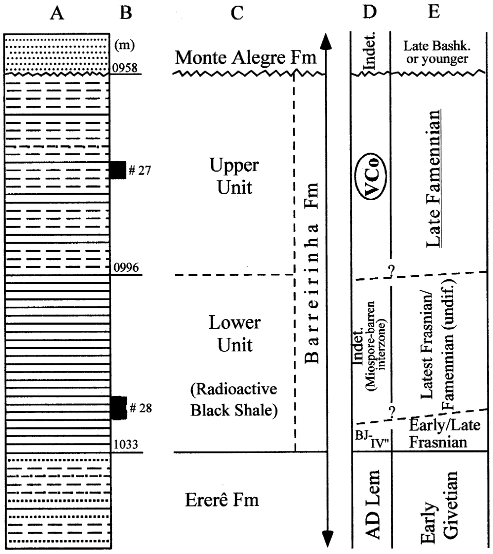


Fig. 24. Occurrence of the Late Famennian miospore *versabilis–cornuta* Zone (VCo) in the Barreirinha Formation of the borehole 2-MN-1-AM, Amazon Basin, Brazil, after Melo et al. (1996, fig. 1 redrawn). (A) Lithologic log; (B) cores and depth of lithostratigraphic boundaries; (C) lithostratigraphic units; (D) biostratigraphy; (E) inferred age.

autochthonous sediments is now possible. It allows to recognize there (Fig. 25) different swamp and near-swamp characteristic. Downstream (coastal lowland) “coal” swamp and swamp margin environments are characterized, respectively, by *Diducites* (*D. plicabilis*) and *Vallatisporites* (*V. hystricosus*) miospores (Streel and Scheckler, 1990). They are directly controlled by the short-term sea-level changes: any high sea-level phase will induce a high fresh-water table in those environments and therefore increase their importance by means of a higher proportion of their miospores in neighboring seas. Poumot (1989) demonstrates palynocycles in the tropical Neogene of the Gulf of Guinea and in Southeast Asia where the variation of the littoral flora indicates eustatic events, highstands of sea level corresponding to the extension of the coastal lowland swamps.

The upstream (upland) “coal” swamp is also characterized by *D. plicabilis* but upstream swamp margin environments are characterized by other taxa (i.e., *Grandispora gracilis* and *Apiculiretusispora coniferus*). They are not directly affected by the sea-level fluctuation. Their regression or expansion are first controlled by dry versus wet climates. Wet climates produce flooding episodes that, in turn, carry more upland miospores into the sea basin. Streel and Scheckler (1990) conducted detailed analyses on the eastern side of the Acadian Mountains in a shallow epicontinental sea bordering the southern part of the Old Red Continent (in the Ourthe Valley in southeast Belgium). They suggest that recurrence of high sea levels, on one hand, and wet climates, on another hand, (Fig. 26) are independent sixth-order cycles, i.e., about 30–40 ka in duration (Streel,

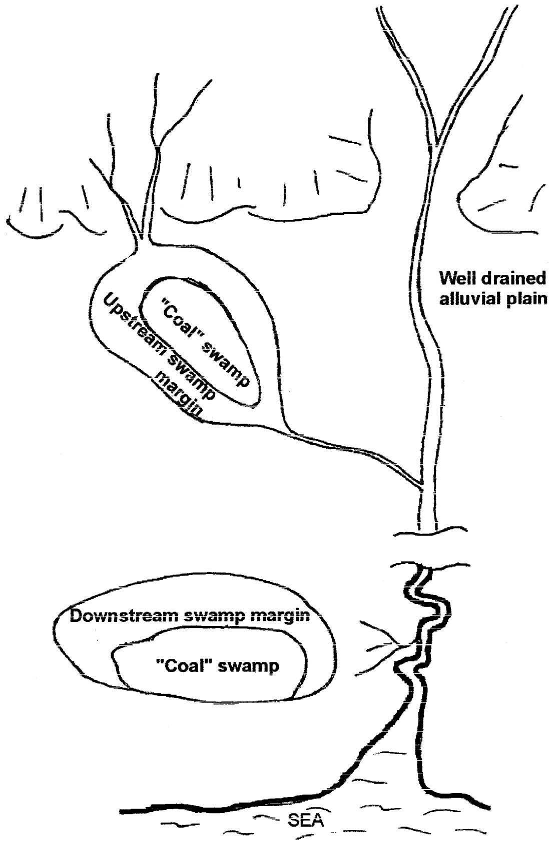


Fig. 25. Late and Latest Famennian specific continental environments, after Streel (1999). Miospore characteristics after Streel and Scheckler (1990), Jarvis (1992), Dreesen et al. (1993). Well-drained alluvial plains: *Aneurospora greggsii* (probably *Archaeopteris* microspore). Upstream and downstream “Coal” swamps: *Diducites plicabilis–Auroraspora varia* Complex (*Rhacophyton* isospore). Upstream swamp margins: *Grandispora gracilis, Apiculiretusispora coniferus*. Downstream swamp margins: *Vallatisporites hystricosus, Auroraspora asperella, Retispora lepidophyta.*

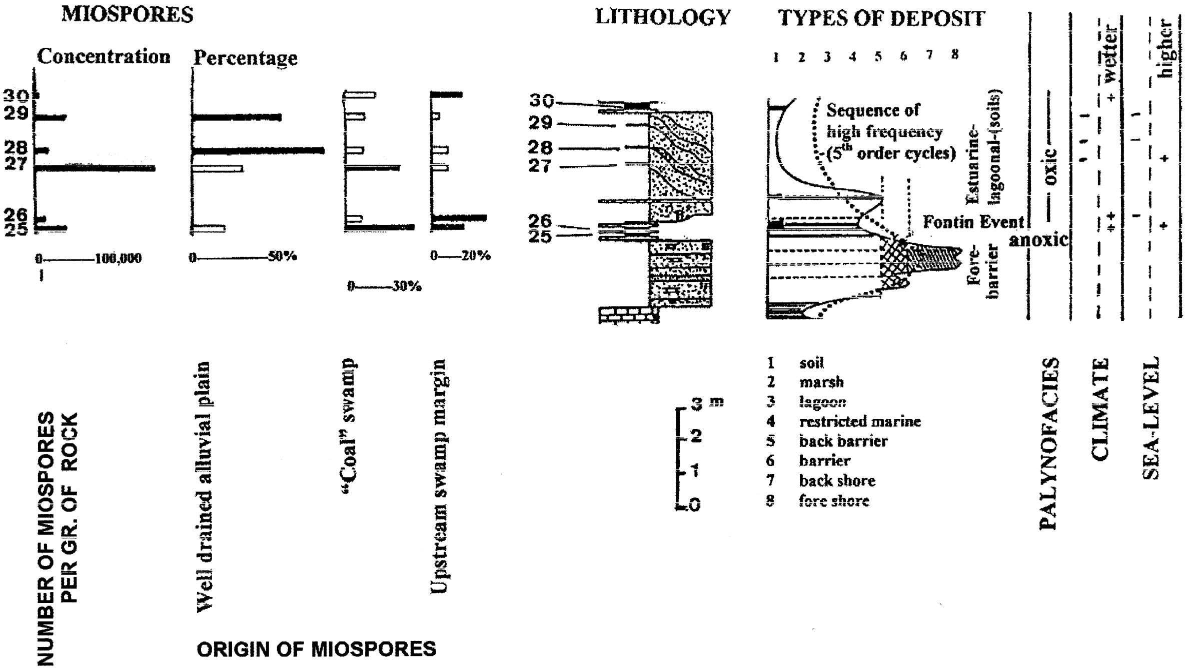


Fig. 26. Quantitative palynology in the upper part of the Esneux-railway section (Late Famennian, Evieux Formation, Ourthe Valley, Belgium), after Streel (1999, fig. 3. Used with permission of the Geologische Bundesanstalt of Austria). Lithology and types of deposits after Lafleur (1991). The analysis of types of deposit illustrates a sequence of high frequency (fifth order cycle) of about 0.1 Ma (Lafleur, 1991). Recurrence of high sea-levels, on one hand, and wet climates, on another hand (both inferred from quantitative analysis of characteristic miospores) are believed to correspond to independent sixth-order cycles, i.e., about 30–40 ka in duration.

1999). They demonstrate also that this shallow epicontinental sea received major floods from local rivers.

In the high latitudes, the Late Famennian climate was probably less cold than before but probably wetter, allowing snowfall on the mountains and vegetation in the lowlands. *Vallatisporites* (*V. hystricosus*, *V.* sp. cf. *V. anthoideus*) are characteristic species of these lowland vegetations in regressive marine strata of the Late Famennian Upper Barreirinha and Lower Curiri Formations of the Amazon Basin in Brazil (Loboziak et al., 1997a). Therefore, they might well derive from coastal lowland swamp margin environments bordering the marine basin. In low latitudes, paleovertisols in Fa2c of the paleo-tropical Catskill Formation indicate a seasonally wet-and-dry climate (Bambach et al., 1999). Potential monsoonal circulation pattern makes the climate in the deep tropics more savannah-like than everwet tropical. However, the development in the low latitudes of the *Diducites* assemblages might well reflect also the expansion of downstream (coastal lowland) swamps and explain the growing affinities between paleo-tropical and paleo-equatorial floras.

Seed plants appear in the Late Famennian (Fairon-Demaret and Scheckler, 1987). The differentiation of the seed was a key innovation in early land plant evolution, facilitating exploitation of a range of environments and ecological strategies (Sims, 1999). After a first occurrence in Frasnian time and a long gap of record comprising most of the Famennian (McGhee, 1996, p. 87), tetrapods "reinvaded" the land. They are dated by miospores as "Fa2b" in Greenland (Marshall et al., 1999), and "Fa2c" in Pennsylvania (Cressler and Daeschler, 1999).

If the major marine regressions of the upper half of T-R cycle IIe are related with ice volume buildup on Gondwana, then the Buggisch's (1991) model, with warm phases alternating with glacial phases, can now be applied. A cyclic operation process might have developed with the following succession: transgression — high organic production — deposition and high preservation of organic carbon — lowering of CO_2 in the atmosphere and ocean — icehouse effect — polar (alpine type) glaciation — regression — erosion and low preservation of organic carbon and resupply of CO_2 to the ocean and atmosphere — greenhouse effect — deglaciation — transgression.

9. The Latest Famennian (Strunian)

The early Latest Famennian starts with a widespread transgression (Fig. 21) which could correspond to the melting phases of the hypothetical Late Famennian mountain glaciers. The miospore zones are characterized by the incoming of *Retispora lepidophyta* which belongs, together with *Vallatisporites hystricosus,* to the coastal lowland swamp margin environments (Streel, 1999) and is directly controlled by sea-level changes. The coastal lowland miospore assemblage containing *R. lepidophyta* (the *R. lepidophyta–K. literatus* or LL Zone) dominates both the paleo-equatorial and the paleo-tropical regions. The miospore zone and most of the species are now the same in both regions (Avkhimovitch et al., 1988a,b), but these assemblages are missing in sub-polar western Gondwana. In the Amazon Basin (Fig. 27), for instance, there is a miospore gap (sediment palynologically barren) between the Late Famennian upper Barreirinha and lowest Cururi beds and the late Latest Famennian upper Cururi with glacio-marine sediments (Loboziak et al., 1996, p. 211 and 1997b, p. 39; Melo et al., 1996, fig. 1). It might be the result of a new but short-term, cold and dry phase in sub-polar region where the absence of snowfall does not allow mountain glaciers to develop. With the transgression, major changes occur in several fossil groups like the Rugosa, which radiates again after their decline during the Late Frasnian (Poty, 1999).

The late Latest Famennian starts with the first occurrence of an almost cosmopolitan, but not abundant miospore species, *Indotriradites explanatus* (the *R. lepidophyta–I. explanatus* or LE Zone), succeeded by *Verrucosiporites nitidus* (the *R. lepidophyta–V. nitidus* or LN Zone) accompanied by a *Vallatisporites* species (*V. vallatus*) probably evolved from the former *V. hystricosus* (Streel and Traverse, 1978). Now, the coastal lowland vegetation that produces *R. lepidophyta* has a worldwide distribution (Byvsheva et al., 1984) from sub-polar to equatorial regions (Fig. 28). The climate had become less cold in high latitudes but wetter than before probably because the midlatitude cyclonic activity allowed sufficient polar transportation of moisture to form large snow cover. Extensive coastal glaciers (Caputo, 1985, 1994; Caputo and Crowell, 1985; Diaz et al., 1999) developed in different Bolivian and Brazilian Basins, well dated by miospores (Perez-Leyton, 1991; Loboziak et al., 1992, 1993, 1997b and Fig. 29; Diaz et al., 1993a,b, Vavrdová et al., 1991, 1993, 1996). Bär and Riegel (1974) have also pointed the exact lithofacies similarity between the Longá Formation in the Parnaíba Basin of Brazil and the Ghanean Takoradi Shales of probable glacial origin, in western Africa. The late Latest Famennian age and the correlation between Brazil and Ghana has been confirmed by Maziane (1997) who demonstrated that even the important reworked part of the miospore assemblages were almost identical in both regions.

One of us (M.V.C.) has studied samples from the Tahara Formation in the A.1-NC 58 wildcat well at the central Murzuq Basin (Libya), near the Algerian and Nigerian borders. Study results indicate that the Tahara Formation, at that locality, contains diamictite, conglomerate, sandstone and shale interbeds. The glacial nature of the diamictites was inferred from their rock textures. The occurrence of *R. lepidophyta* in the Tahara Formation (Coquel and Moreau-Benoit, 1986) dates the diamictite suggesting that the Latest Famennian glaciation might have reached southern Libya.

There are no other, biostratigraphically controlled, Late Devonian glacial deposits in Africa. The Niger tillites mentioned by Scotese et al. (1999, p. 110) is only known as “older than Viséan” (Lang et al., 1991) and the so-called Devonian–Carboniferous Mambéré Formation from central Africa (cited by Isaacson et al., 1999, p. 241) is only indirectly dated by paleomagnetic observations according to which the pole “is close to Middle Devonian–Lower Carboniferous poles” (Censier et al., 1995, p. 24).

Available evidence of glaciation includes diamictites with striated, faceted and polished pebbles; rhythmites with dropstones; erratic boulders, striated pavements, and glacially deformed sedimentary rocks

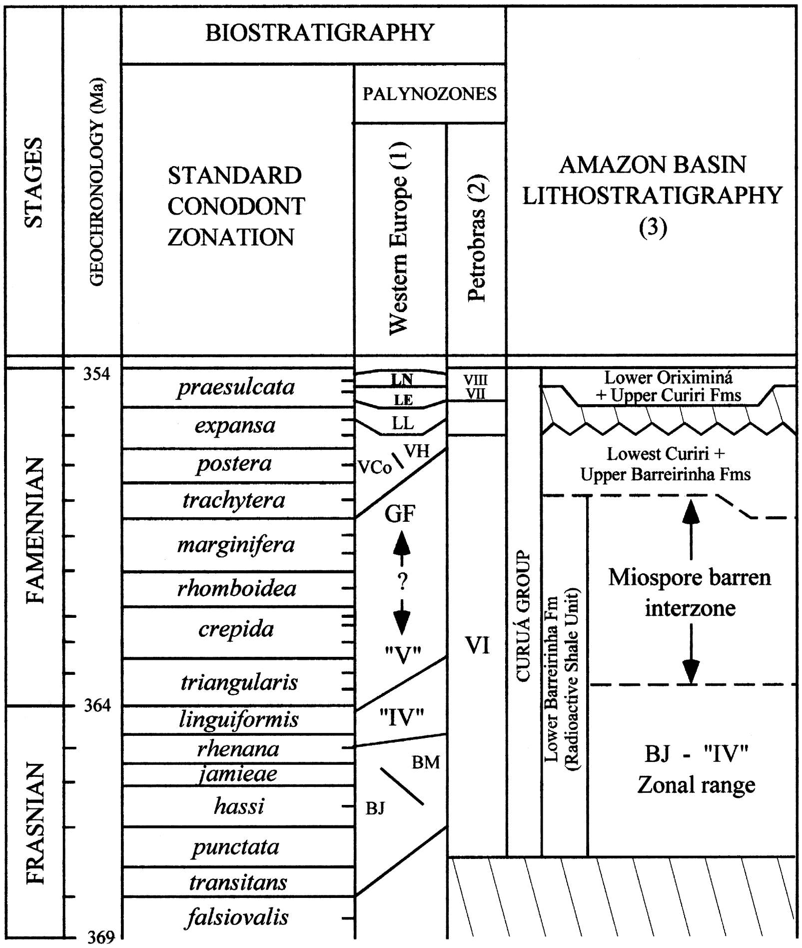


Fig. 27. Gap in the Latest Famennian succession of the Amazon Basin, Brazil, after Loboziak et al. (1996, fig. 1 modified) and Loboziak et al. (1997b). Palynozones: (1) after Streel et al., 1987, Streel and Loboziak, 1996, Maziane et al., 1999; (2) modified from Daemon and Contreiras (1971) and Daemon (1974, 1976). Lithostratigraphy (3) modified from Caputo (1985). In the Amazon Basin, the miospore gap (sediment palynologically barren) occurs between the Late Famennian upper Barreirinha and lowest Cururi beds and the late Latest Famennian upper Cururi with glacimarine sediments (Loboziak et al., 1996, p. 211 and 1997b, p. 39; Melo et al., 1996, fig. 1). It might be the result of a new but short-term, cold and dry phase in sub-polar region where the absence of snowfall does not allow mountain glaciers to develop.

(sandstone and lodgment tillites). These diamictites usually contain a large amount (often, over 50% of the total assemblage) of reworked miospores from Givetian and Frasnian assemblages. This reworked material, which is very well preserved, is recognizable only by its stratigraphic range known elsewhere. The most recent reworked miospores belong to the Late Frasnian Zone "IV". No reworked miospores from Early to Late Famennian can be demonstrated which confirms that sparse vegetation was present during this timespan in the hinterland of the Latest Famennian high latitudes. Some rhythmites (see Caputo, 1985, fig. 13 or Caputo and Crowell, 1985, fig. 11) proved to be real varves (Streel et al., in press). They contain species belonging to a high stratigraphic position within the Latest Famennian (the LN Zone), but presenting a different quantitative composition in alternating sandy and silty laminites. Sandy layers were probably first settled after the local seasonal melting of the ice cover and the rush

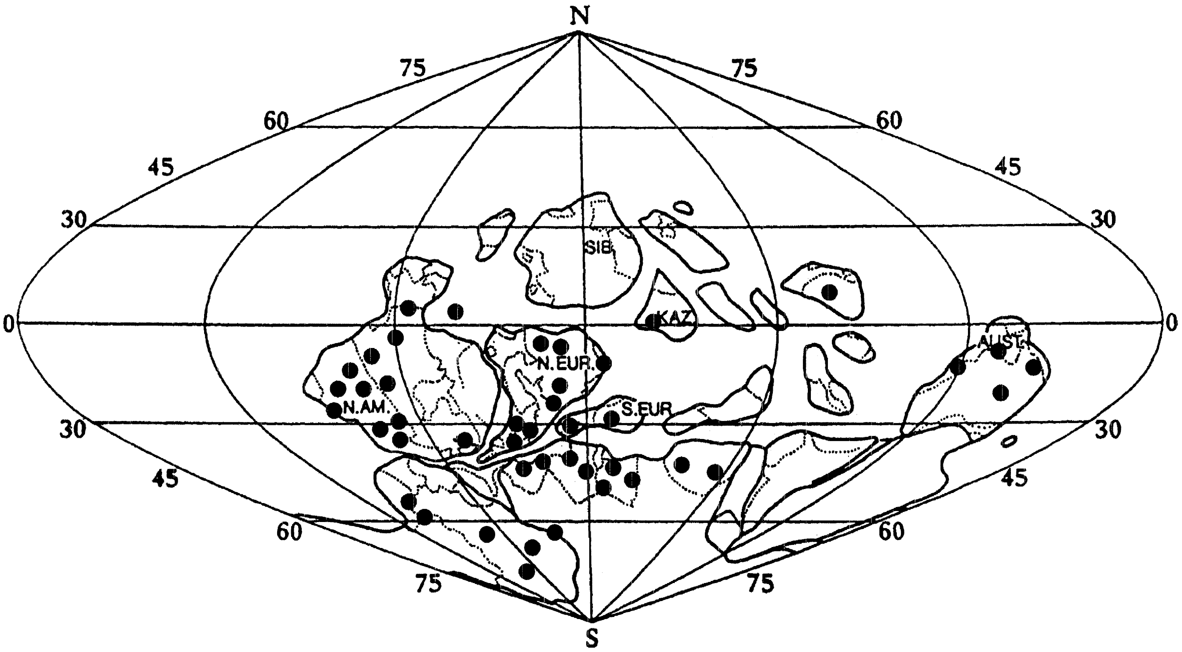


Fig. 28. Paleophytogeographic distribution of the Latest Famennian miospore *R. lepidophyta*, after Streel (1986, fig. 6), based on the Middle Devonian map of Heckel and Witzke (1979). The worldwide distribution of *R. lepidophyta* is obvious (no data available from Siberia for that period of time). This species is produced near the deposition site explaining its exceptional abundance in most localities. The vegetation represented by these assemblages is believed to be cosmopolitan coastal lowland vegetation which depends more on a local moisture and equable climate than on the maybe adverse climates of distant hinterland areas.

of fresh water supply, the silty layers being deposited when the spring water run-off decreases.

During the Latest Famennian, the climate was, thus, cold in the high latitudes but probably warmer

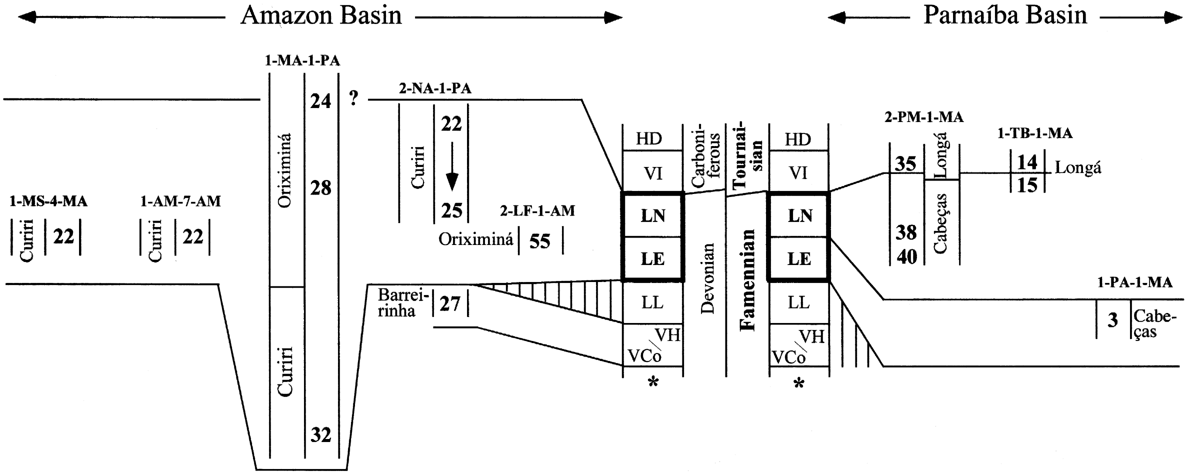


Fig. 29. Age assignment (Late Famennian to Tournaisian) and biostratigraphic correlation between Amazon and Parnaíba Basins, Brazil, after Loboziak et al. (1993, fig. 5 modified with unpublished data from S. Loboziak and J.H.G. Melo). * Miospore Zonation after Streel et al. (1987), Higgs et al. (1988) and Maziane et al. (1999). The undifferentiated *lepidophyta–explanatus?* and *lepidophyta–nitidus* (LE?–LN) Zones are known with diamictites from many boreholes of the Amazon and Parnaíba Basins.

than before in the intertropical regions. Valentine (1984, fig. 1) gave broad-scale paleotemperature estimates for low latitudes and high latitudes during the Cenozoic which clearly show that oceans in the late Neogene (during the onset of the Antarctic glaciation) were significantly cool in high latitudes but warmer than before in low latitudes. Similarly, Raymond et al. (1989) suggested that high latitude cooling and equatorial warming between the Namurian A and B may have been caused by the onset of glaciation in the Southern Hemisphere. Data given by Brand (1993, fig. 3), based on isotopic studies of brachiopod shell material, indicate that temperatures in the Latest Famennian ranged from 32–38°C in the equatorial belt to 17–18°C only in the subtropical belt (Fig. 30). Even accepting adjustments (Brand, 1989, p. 321) to bring such values into "realistic environmental and biological conditions" would not change much the picture that the latitudinal gradient of temperatures was important during the Latest Famennian. It seems that the development of polar glaciers and the simultaneous extension of the arid tropical belt might have confined the intertropical convergence zone (the belt of low level of environmental fluctuations) to a narrow latitudinal, and perhaps discontinuous, range surrounding the equator, a situation comparable to what happened during the Pleistocene Late Glacial Maximum. But it was probably not a permanent situation because we know that rapid climatic changes also characterize the onset of glaciation. The cyclic nature of climate allowed even intertropical marine faunas to reach occasionally the subpolar areas during climatic temperate phases, as indicated for instance by the occurrence, in South America, of the Latest Famennian cephalopod *Wocklumeria* (Becker, 1993; House, 1996).

Wide latitudinal gradient of temperatures and quick cyclic climatic changes might well be considered unsuitable conditions for the cosmopolitan character of the end-Famennian vegetation. One must remember, however, that this vegetation is only known through the filter of transport processes carry-

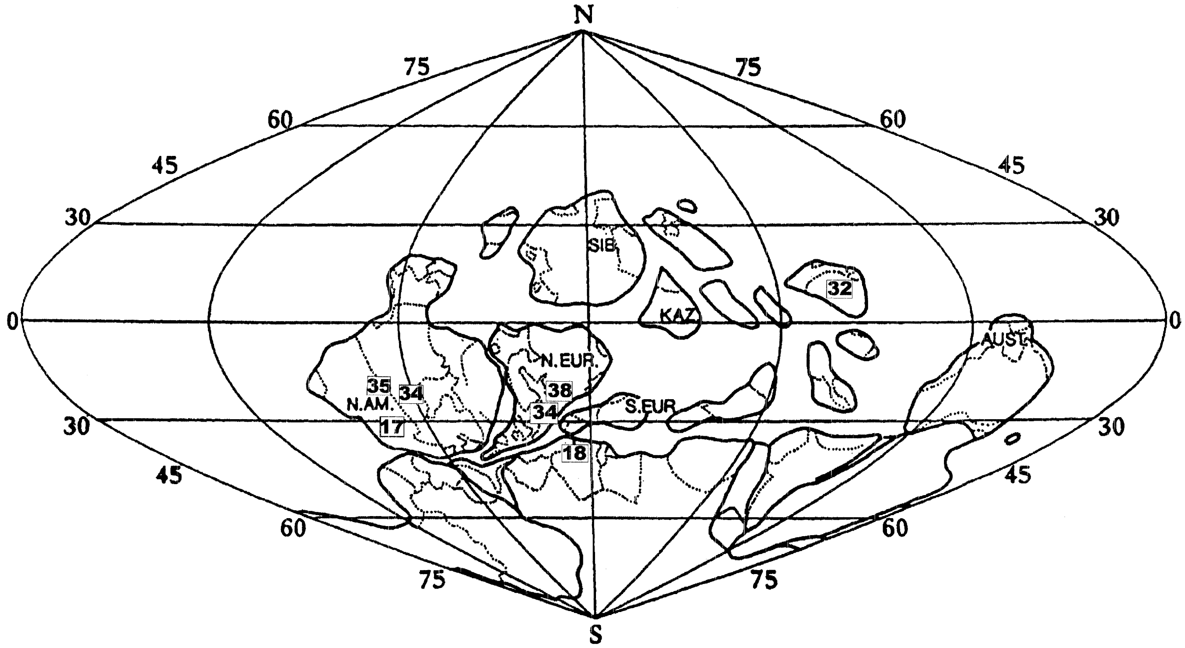


Fig. 30. Model of water temperatures of "global" Famennian seawater based on calculations of oxygen isotope data after isotopic studies of brachiopod shell material made by Brand (1993). Base map: Middle Devonian map of Heckel and Witzke (1979). Data indicate that temperatures in the Latest Famennian ranged from 32–38°C in the equatorial belt to 17–18°C only in the subtropical belt. Even accepting adjustments (Brand, 1989, p. 321) to bring such values into "realistic environmental and biological conditions" would not change much the picture that a qualitative latitudinal gradient of temperatures was important during the Latest Famennian.

ing miospores from their source area to the sea basin. Now the Latest Famennian miospore assemblages have an unusual characteristic: the almost invariable dominance of one single species (*R. lepidophyta*), which often constitutes more than 50% of all miospores present. This means that this species is produced near the deposition site and that the vegetation represented by these assemblages is cosmopolitan coastal lowland vegetation that depends more on a local moisture and equable climate than on the probably adverse climates of distant hinterland areas. The high proportion of coastal lowland vegetation miospores in the assemblages might be also a result of the poor miospore production by a scarce vegetation cover in these hinterland areas.

10. The end-Famennian Crisis and the Hangenberg Event

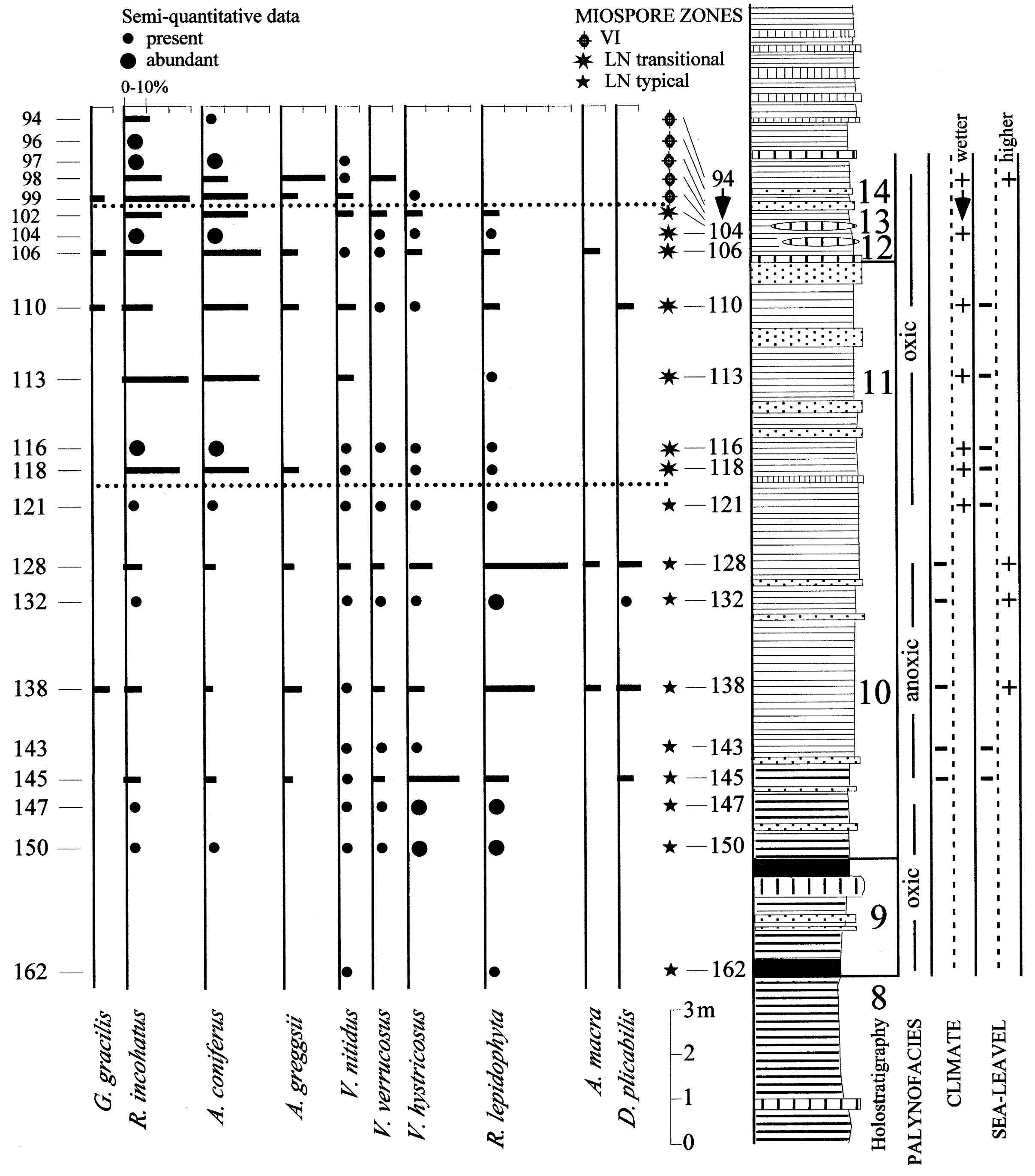
By comparison with the first chapters of this paper, concerned with the Late Frasnian to Early Famennian 3 Ma timespan, it is unnecessary to discuss the end-Famennian events in separated chapters because it seems that they all occurred in a rather short interval of time, perhaps only 0.1 Ma (Sandberg and Ziegler, 1996). The end-Famennian crisis is linked by most authors to the Hangenberg Event (Walliser, 1984), defined at the base of the Hangenberg Black Shale (HBS), in the Sauerland, Germany, on the top of the Wocklum Limestone, the uppermost part of which bears the poorly characterized Middle *praesulcata* conodont Zone and the LE miospore Zone. When the Late *praesulcata* conodont Zone occurs in the Stockum Limestone, immediately beneath the DCB, the extinction crisis is over.

Although in the literature the Hangenberg Event is not included in the “big 5” bio-events (like the Late Frasnian Crisis), it is one of the most severe bio-events in the Phanerozoic. Drastic mass extinction took place at that level, e.g., involving the clymenid ammonoids and the hemipelagic and pelagic ostracodes (Walliser, 1995). As many as 21% of the marine genera and 16% of the marine families (Sepkoski, 1996) became extinct. Simakov (1993) even estimates about 20% extinction during the Hangenberg Event, at the family level. Land plants (Fairon-Demaret, 1986), miospores (Streel, 1986) and acritarchs (Vanguestaine, 1986) show obvious important changes near the end of the Devonian. However, these changes occur clearly above the Hangenberg Event (above the HBS), i.e., closer to the DCB. Indeed the base of the HBS corresponds to the base of the *R. lepidophyta–V. nitidus* or LN miospore Zone (Higgs and Streel, 1994), which, except for a few added species, is very similar to the former LL and LE Zones. Moreover, the occurrence of Devonian trees like *Archaeopteris* in Ireland (Jarvis, 1992) and rich acritarch assemblages in the Riescheid section in Sauerland (Weldon, 1997) are coeval with the LN miospore Zone. Obviously, the major terrestrial event does not exactly coincide with the marine one (in contradiction with the opinion of Hallam and Wignall, 1997, p. 74).

The Devonian/Carboniferous Global Stratotype Section and Point (GSSP) has been fixed (Paproth et al., 1991) in the La Serre Section (Montagne Noire, southern France) at a level between the *Siphonodella praesulcata* and *S. sulcata* Zones of the standard conodont zonation. It is far from being an ideal GSSP (for instance it yields no palynomorphs) and therefore Auxiliary Stratotypes Sections (ASS) have been designated in the Sauerland (Germany) and Nambiancun (China) areas. The Stockum section, near the ASS of the Sauerland, displays a well-documented transition across the DCB. T-R cycles (Bless et al., 1993, fig. 4) or holostratigraphic intervals (Becker, 1996, table 2) and miospore quantitative analyses of the Stockum section (Fig. 31) allow subdividing, with detail, the rather short timespan between the Hangenberg Event and the DC Boundary.

10.1. The Stockum section

In the HBS (sample 162, Fig. 31), the miospores are scarce but black homogeneous palynodebris are abundant, corresponding to oxic conditions of the palynofacies (see below). In the overlying lower part of the Hangenberg Shales, miospores are abundant and rather well preserved, palynodebris being more heterogeneous and translucent than in the HBS. Probably, the deposition of the Hangenberg Shales was very rapid, preventing oxidation of the palynodebris. Here the coastal lowland swamp margin miospores (*V. hystricosus*, *R. lepidophyta*) are abundant. In the upper part of the Hangenberg Shales and Sandstones and in the overlying Stockum Limestone, sandstones are progressively more abundant and the



palynofacies return to oxic conditions. Coarser sediments and oxic conditions result probably from river run-off after a wetter climatic development. Indeed, upstream swamp margin miospores (*A. coniferus*) become abundant and take over the *R. lepidophyta* dominance. The strong regression of the coastal lowland swamp margin miospores and the almost complete extinction of the "coal" swamp miospore, *D. plicabilis*, suggest that this new, wet climatic condition matched the lowest sea-level condition. These probably adverse climatic and edaphic environmental changes strongly reduced the Latest Famennian coastal lowland swamp margin and "coal" swamp vegetation. These plant communities completely disappear immediately below the Stockum Limestone (i.e., very near but below the DCB), being replaced by a new, poorly defined miospore Zone, the *V. vallatus–Retusotriletes incohatus* or VI Zone where *A. coniferus* is abundant.

At the level of sample 94, immediately above the last sandstone horizon, very abundant acritarchs suddenly occur, making 70% of the total palynomorphs (miospores + acritarchs). Surprisingly, the assemblage is composed of one single "species" of *Micrhystridium*, representing a first opportunistic bloom of one taxon after the "Latest Devonian extinction". At Stockum, it seems to coincide with the basal Carboniferous eustatic rise.

10.2. The Sauerland area

The cyclicity observed in quantitative palynology above the Hangenberg Event in the Sauerland is obviously of the same nature as the two kinds of cycles (change of sea level and of climate) described in the Late Famennian of the Ourthe valley, in Belgium (Fig. 26). Therefore, they probably correspond to sixth-order cycles, adding some support to Sandberg and Ziegler's (1996) opinion of a short time-range (0.1 Ma) for the Middle *praesulcata* Zone. Consequently, the rate of sedimentation operating during the LN miospore Zone in the Sauerland was high compared to the rate observed during the VCo Zone in the Ourthe valley. In low latitudes, higher sedimentation rate and sandy input should correspond to wetter climate phases and increased river supply during the Latest Famennian compared to the Late Famennian.

Evidence of wetter climate may have started in the upper part of the Wocklum Limestone, i.e., in the Drewer Sandstone (Fig. 32). This would explain the genesis of the overlying HBS in the Sauerland. After Van Steenwinkel (1993, p. 678), the HBS is a condensed unit created by sediment starvation and corresponds to a worldwide event characterized, in the Sauerland area, by basinal condensation during a maximum rate of eustatic sea-level rise. After Van Steenwinkel (1993), it represents the condensed Latest Devonian Transgressive and Highstand System Tracts (TST + HST) of the previous sequence, whereas the Wocklum Limestone (including the Drewer Sandstone) corresponds to the underlying Lowstand System Tract (LST). During the deposition of the upper part of the Wocklum Limestone, erosion of organic soils and vegetation cover probably started on the continent. Rivers discharged a large amount of sand, mud and organic matter into the sea. Except in some nearshore areas, like in the neighboring Riescheid locality where pre-LN shaly sediments are rather thick, this erosional material was then transported by marine currents far offshore, the sand being deposited first, as on the shoal of the Drewer area (Bless et al., 1993, fig. 3), the mud and organic matter bypassing the shoals to be deposited farther into the basin in the form of lowstand submarine fans. Subsequently, during the next sea-level rise,

Fig. 31. Quantitative palynology in the Latest Famennian and Tournaisian Stockum trench II section (Sauerland, Germany), after Streel (1999, fig. 4. Used with the permission of the Geologische Bundesanstalt of Austria). Miospore Zonation and lithology after Higgs et al. (1993, fig. 1 modified); holostratigraphy after Becker (1996). DCB is between samples 97 and 99 or between holostratigraphic intervals 13 and 14. Recurrence of high sea-levels and wet climates (both inferred from quantitative analysis of characteristic miospores) are believed to correspond to sixth-order cycles, i.e., about 30–40 ka in duration, by comparison with data from the Late Famennian of Belgium (Fig. 26), adding some support to Sandberg and Ziegler's (1996) opinion of a short time-range (0.1 Ma) for the Middle *praesulcata* Zone (see also Fig. 32).

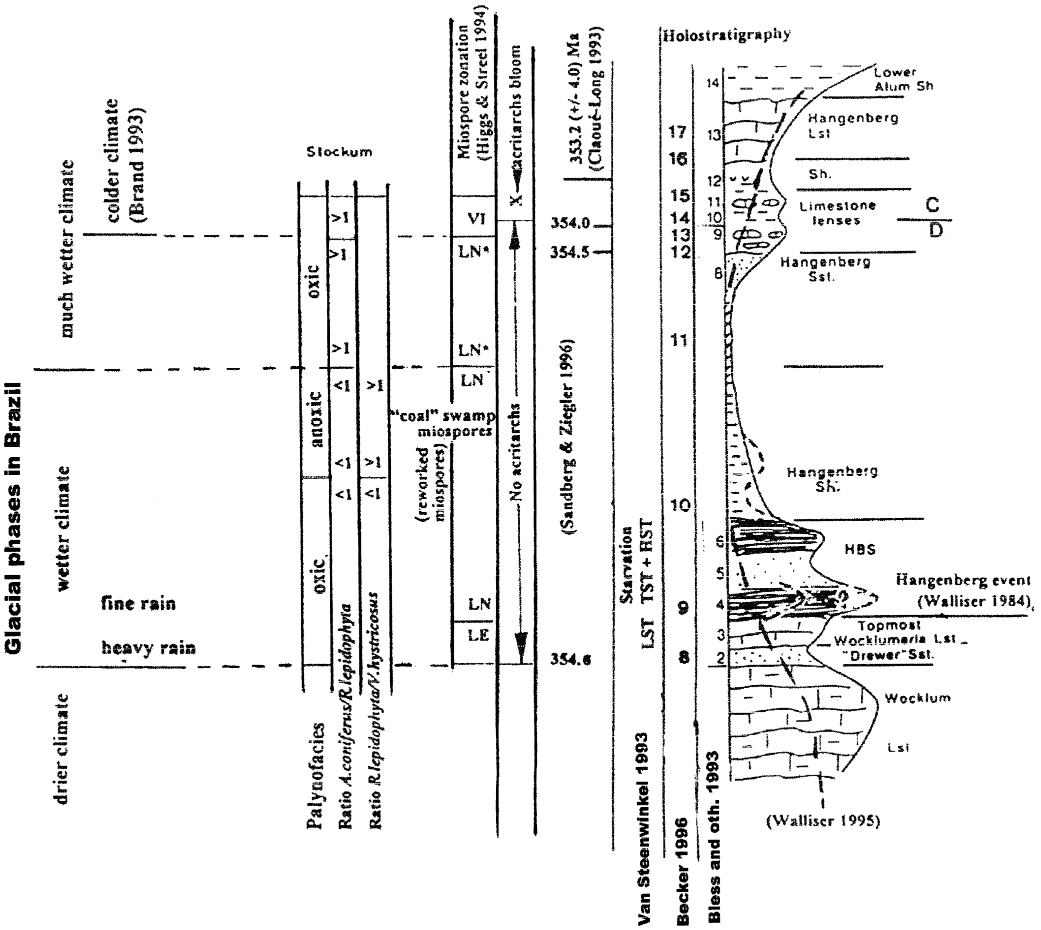


Fig. 32. Synthesis of quantitative palynology and comparison with sedimentology and climatology in the Latest Famennian and Tournaisian sections of Sauerland (Germany) after Streel (1999, fig. 5. Used with the permission of the Geologische Bundesanstalt of Austria). Lithology has no scale. Holostratigraphic levels (Becker, 1996) allow comparing with the detailed lithology of section Stockum in Fig. 31. C/D: Devonian/Carboniferous Boundary or DCB. Glacial phases in Western Gondwana (Brazil), dated by LE?–LN Zones, immediately preceded a very wet and, soon, colder climate in the southern tropical belt (Sauerland).

together with the rise of the anoxic zone, upwelling or overturn (Girard, 1994) could have spread the black mud almost all over the basin, except on the nearshore (Riescheid) area. Much as Pedersen and Calvert (1990, p. 463), we believe that the proportion of organic matter of terrestrial vs. marine origin in black shales varies widely between locations, indicating in many cases the dominance of local or regional factors rather than ocean-wide phenomena. The perfect synchroneity of the HBS around the world is far from being demonstrated because few regions present marine guide fossils and miospores closely associated, and thus correlations are often too imprecise (for instance the incorrect association of the LN Zone and Late *praesulcata* in Caplan and Bustin, 1999, figs. 2 and 3).

But the almost complete absence of acritarchs demonstrates that the HBS in the Sauerland was never deposited nearshore before being deposited farther into the basin and then redistributed by upwelling or overturn. Even leiospheres, which demonstrate a capability for surviving widespread extinctions of acritarchs at that stratigraphic level (Olempska, 1997), are almost, absent in the HBS. Moreover, the impoverished miospore content and the destruction of the thinner, more or less translucent, heterogeneous debris of the palynofacies point out to extensive transportation into the sea prior to deposition in the anoxic zone.

Climatic changes across the DCB have been investigated on the basis of brachiopod shell geochemistry (Brand, 1989, 1993; Brand and Legrand-Blain, 1993). These authors note that it was not until the latest part of the Latest Famennian that temperatures started to decline in the low latitudes. Detailed conclusions, however, are hampered by the poor biostratigraphic resolution of studied horizons. Indeed, no samples were tested which fit, without doubt, the HBS and Hangenberg Shales and Sandstones interval (because they normally lack brachiopods). The Wocklum Limestone is older. The Louisiana Limestone, in eastern Missouri (USA) and the "Middle siliciclastic calcarenite" in the "Griotte Formation" at La Serre might be slightly younger than the sequence under consideration as they are assumed of Late *praesulcata* "age" (but see Girard, 1994). Only the basal, shaly part of the "lower oolite" in the Griotte Formation of La Serre might be an equivalent of the Hangenberg Shales (Bless et al., 1993; Girard, 1994). It is thus of some significance that temperature fall is only recorded higher than this oolite, i.e., in the upper part of the "middle siliciclastic calcarenite" at La Serre, corresponding to the same level where, in the Sauerland, the LN Zone definitively ended.

The sea-level lowstand documented by, possibly, the topmost Wocklum Limestone and certainly the Hangenberg Sandstone corresponds to the development of coastal glaciers in high latitudes because western Gondwanan glacio-marine sediments are demonstrated to contain perhaps the LE Zone but certainly the LN Zone (According to Melo et al., 1999, supposed occurrences of the LE Zone in Brazil might well correspond to an impoverished LN Zone). Miospore analyses in the tropical region, corresponding to the peak of the regression, point out to a wetter climate which has strongly modified the contemporary "upland" and "coastal lowland" plant communities. The "coastal lowland" community (the *lepidophytus* complex) did not recover after that peak, probably as a consequence of an Earliest Tournaisian (Fig. 32) colder climate (Brand, 1989, 1993), which could have extended even into low latitudes.

What are the ultimate causes of the end-Famennian glaciation? Was it, at least partly caused, by a bolide impact, a volcanic paroxysm and/or a change in CO_2 and O_2 concentrations in the oceans and atmosphere also postulated for the hypothetical lowermost Famennian glaciation? To our knowledge, no microtektites have been reported from near the DCB. Iridium peaks are known in Austria, Canada, France and China at the HBS or equivalent level (Wang et al., 1993), but they are interpreted as resulting from a sudden change in paleo-redox conditions during deposition and/or diagenesis. Woodrow et al. (1990) show evidence of an impact-event in the Appalachian Basin (USA), near the DCB. The Spechty Kopf "polymictic diamictite" would have been deposited rapidly and all at once over 400 km and dated by the presence of the miospore *R. lepidophyta* (McGhee, 1996, p. 187). Unfortunately, it seems that the miospore assemblage, recovered in these sediments, did not allow using the very precise correlation data existing between miospore and conodont zonations (Streel et al., 1987). Therefore, if any correlation really exists between the "polymictic diamictite" and an impact-event, it can only be assigned, in terms of conodont stratigraphy, to within the Late *expansa*–Late *praesulcata* interval. Evidence for highly explosive volcanism is found in the occurrence of the "Bombenschalstein" in the basal Wocklum Stufe of the Rhenish Massif. Also containing a *R. lepidophyta* miospore assemblage (Somers and Streel, 1978), these sediments were, however, regarded as a Late *expansa* or Early *praesulcata* equivalent (Dreesen, 1986, p. 35), i.e., rather older than the Hangenberg Event. A major, sudden negative excursion of the $\delta^{13}C$ curve, reflecting a decreasing biomass in the Muhua section in China (Xu et al., 1986), is referred to the DCB event by Rampino and Haggerty (1996, p. 20) but occurs much higher, i.e., at the base of the Tournaisian *S. crenulata* conodont Zone. Thus there is no evidence of any bolide impact or volcanic paroxysm firmly related to the Hangenberg Event. Buggisch's (1991) model (see the end of Section 8), with warmer phases (the equivalent of most of the Wocklum Limestone and the HBS) alternating with glacial phases (the equivalent of the Drewer Sandstone and the Hangenberg Shale and Sandstone) can probably be applied. However, it is true that, if the stratigraphy of the DCB has been intensively studied during the two last decades, geochemical and sedimentological data, on the contrary, are still rather scarce at that level compared with what is known for the FFB.

11. Comparison of the Kellwasser and Hangenberg Events with immediate post-events

Both the Kellwasser and the Hangenberg events are generally admitted to represent dysoxic facies coinciding with a rapid transgression which reversed subsequently (the post-events) into a major regression. Whether or not this eustatic fall might correspond to a short glacial phase in the high latitudes after the Kellwasser Event is still unknown, but it certainly does after the Hangenberg Event. Altogether events and subsequent post-events might have lasted about 0.1 Ma or even less. Changes in CO_2 and O_2 concentrations in the oceans and the atmosphere were probably the first cause of the rapid change of climate. At the Paleocene/Eocene transition large perturbations in the global carbon cycle have recently been demonstrated to last about the same short time range (Norris and Röhl, 1999). Possible coincidence of bolide impact and/or volcanic paroxysm with the icehouse climate might have contributed to induce a short glacial phase in the high latitudes immediately after the rather warm period of the Latest Frasnian. At the end of the Famennian, however, the high latitudes were already cold when the climatic changeover allowed the glacial phase to reach the sea level. The hypothesis of an extraterrestrial or volcanic contribution is then not necessary and, anyway, it is not supported by facts. The climatic contrast from the event to the post-event was obviously greater in the first case than in the second one. In both cases, however, it has not particularly affected the land flora and the phytoplankton, the end-Famennian vegetation crisis occurring later, immediately below the Late *praesulcata* conodont Zone, i.e., beneath the DCB.

It is tempting to remark that the former (1983) definition accepted for the FFB, the Middle *triangularis* conodont Zone, had the advantage to be at some distance higher than the major crisis interval, which is often characterized by condensation or physical breaks in sedimentation (Ziegler and Klapper, 1985, p. 108). The same point was taken into account when defining the DCB at the base of the *sulcata* conodont Zone (Paproth and Streel, 1985) rather than at the HBS level as recommended by Walliser (1984). The subsequent change in favor of a FFB fixed at the base of the Early *triangularis* Zone (Cowie et al., 1989) is rather unfortunate because it places that boundary between the event and the post-event, i.e., at a critical level, whereas the DCB remains fixed after the post-event.

12. Discussion

The history of the Late Frasnian–Famennian climates based on palynomorph analyses is built on three postulates: (1) Euramerica at slightly lower latitudes than generally accepted by most paleomagnetic reconstructions; (2) a conodont time-scale accepted as the most used available subdivision of time; and (3) Late Devonian sea-level fluctuations mainly governed by glacio-eustasy. The two first postulates have been discussed in Sections 2 and 3 and there is no need to reopen the discussion here. On the contrary, even the reality of some sea-level fluctuations was challenged recently, i.e., by Hallam and Wignall (1999) who minimize the existence of a major eustatic fall following the Kellwasser Event. They base their argumentation on the failure to detect regressive intervals in the FFB of Poland and Morocco. However, many other independent evidences support a worldwide drop in relative sea level (see for instance Muchez et al., 1996). The registrated imprint of eustatic movements in the sediment does not depend only on their vertical range but depend also on their duration, a very short one in the case of the FFB. Also, breaks which exist, close to the FFB, in the involved Moroccan sequences (Schindler, 1990), may be alternatively interpreted to be of local importance only (Wendt and Belka, 1991, p. 72) where the relative movements are also controlled by block faulting (see Wendt, 1985, p. 817). Finely, if Narkiewicz and Hoffman (1989) found indeed no evidence for any major sea-level changes in the late Frasnian record of the carbonate platform of southern Poland, on the contrary, Devleeschouwer (1999, p. 218), using a sedimentologic approach and magnetic susceptibility curves on the same sections as above, conclude that the sequence stratigraphy model he has developed in Germany and in the Montagne Noire (Southern France) can be applied also in southern Poland and shows a sequence boundary at the FFB. We believe therefore that the model illustrated by Hallam and Wignall (1999, fig. 11) showing Kellwasser crisis and post-crisis entirely enclosed in a transgressive phase is, to say the least, far too selective.

The Famennian global cooling is part of a long-term event (Berner, 1990) with a sharp falloff in CO_2 values occurring in the interval of time from the Middle Devonian into the Early Carboniferous (Algeo et al., 1995). Algeo and Scheckler (1998) and Berner (1999) show that it is the result of a massive increase of land plant biomass which occurs in just 15 to 20 Ma in the Middle and Late Devonian. Another very important contributing factor for the Famennian global cooling may have been the transference of CO_2 from the atmosphere and sea water to organic sediments during the Devonian time, when large amounts of anoxic shales were deposited in Gondwana and Euramerica intracratonic and shelf basins due to the expansion of the oxygen-minimum zone. The decrease in the CO_2 atmospheric content was caused by significant transgressive phases that increased the rate of organic matter burial. Brazilian Frasnian and Famennian anoxic shales have a moderate-to-high (1–15%) content of organic matter in the Amazon, Solimões, Parnaíba and Paraná intracratonic basins. In the United States and Canada, there are extensive occurrences of Middle Devonian to Mississippian shales, partly euxinic, represented by the Chattanooga Shale and its equivalents (Conant and Swanson, 1961; Geldsetzer et al., 1985). In Belgium, France and Germany, the Matagne Shale and its correlatives were deposited with thin layers of Kellwasser Limestone, under anoxic conditions during Frasnian time. The Timan-Pechora, Volga-Ural and Peri-Caspian Paleozoic basins in the former Soviet Union have high oil and gas production from widespread rich organic shale beds of Frasnian and Famennian ages (Ulmishek, 1982; Peterson and Clarke, 1983). According to Kalvoda (1986), a large-scale anoxic environment was also present in the Latest Famennian time (lower *praesulcata* Zone) in Moravia. Morocco (North Africa) also has Frasnian and Famennian organic-rich shales (Joachimski and Buggisch, 1993). The Karoo Basin in South Africa contains thick dark shale beds in the upper Devonian and lower Carboniferous section of the Witterberg Group (Streel and Theron, 1999). The Frasnian basinal shales of the Canning Basin in Australia are also rich in organic matter (Playford et al., 1989). This deposition of worldwide anoxic shales that sequestered a large amount of CO_2 from the atmosphere and sea water may have provoked anti-greenhouse effects and cooling events in Famennian and Tournaisian times (Caputo, 1995).

Berner (1993) concluded that the massive burial of sedimentary organic matter (lignin) during the Carboniferous and Permian periods evidenced by the abundance of coal of this age, amplified the large drop in CO_2 concentration in that time. This hypothesis is worth for the mid-Carboniferous onward, but it does not explain the more than 10 million years icesheet-free at sea level in Gondwana from the Earliest Famennian to the mid-late Tournaisian times, Devonian and Tournaisian coal reserves being far less important than later. It also does not explain older glaciation events when true forests did not exist. An alternative cause to explain the decreasing CO_2 atmospheric content may be found in major transgressive cycles that increase the rate of organic matter burial. Continental phytomass production today is three times as large as the oceanic production (Walter, 1984) but the comparison was probably in favor of the oceanic production at the end of the Devonian. Marine organic matter preservation during major transgressive anoxic events may have surpassed continental phytomass preservation. For example, the Cretaceous marine organic muds contain an order of magnitude more carbon than that in all known reserves of coal and petroleum (Keith, 1982). The burial of high amounts of organic matter may have caused climatic cooling (Arthur et al., 1988) or glaciation (Jeans et al., 1991) at the Cenomanian/Turonian boundary. The preservation of large amount of organic matter in sedimentary rocks provokes global climatic cooling and may result in a significant worldwide regression, if the icehouse effect is strong enough to initiate the buildup of continental glaciers (the Buggisch's model) as happened occasionally in late Devonian and early Carboniferous time. However, in most transgressive cycles, glacial events are not developed because the volume of organic shale deposition is not large enough to deplete atmospheric CO_2 and trigger glaciation. From mid-Carboniferous time onward, the spread of forests and related organic soils to lowlands generated by low sea level due to the worldwide regression may have delayed recoveries in atmospheric CO_2 content, leading to longer lasting glacial ages.

13. Conclusions

13.1. The Latest Givetian–Frasnian

The comparison based on conodont correlations, between Givetian and most of the Frasnian miospore assemblages from, respectively, northern and southern Euramerica demonstrates a high taxonomic diversity in the equatorial belt and much difference between equatorial and (sub) tropical vegetation (Fig. 33). On the contrary, a similar vegetation pattern and therefore probably compatible climatic conditions are present from tropical to subpolar areas. This vegetation seems to have extended its range into high latitudes from the Givetian to the Frasnian. Indeed characteristic miospores of medium to high latitudes of western Gondwana almost disappear at the end of the Givetian Stage. This probably corresponds to the persistency of rather hot climates during the Frasnian, culminating in the Latest Frasnian when it is noted that the equatorial climatic belt reaches its maximum width. Atmospheric increase of CO_2 derived from submarine and continental violent volcanism and high sea-level stands might have caused the long-term warming during the Late Frasnian. To the thermal stress on land can be added the adverse effects of diverse volcanic poisons. It would explain the minimum diversity of miospores occurring progressively in the Late Frasnian. The warming episode might have also slowed down the deep circulation of aerated polar waters and developed stagnant ocean conditions incrementing the periodic development of anoxic conditions, e.g., the Latest Frasnian Kellwasser Horizon (UKW).

13.2. The Earliest Famennian

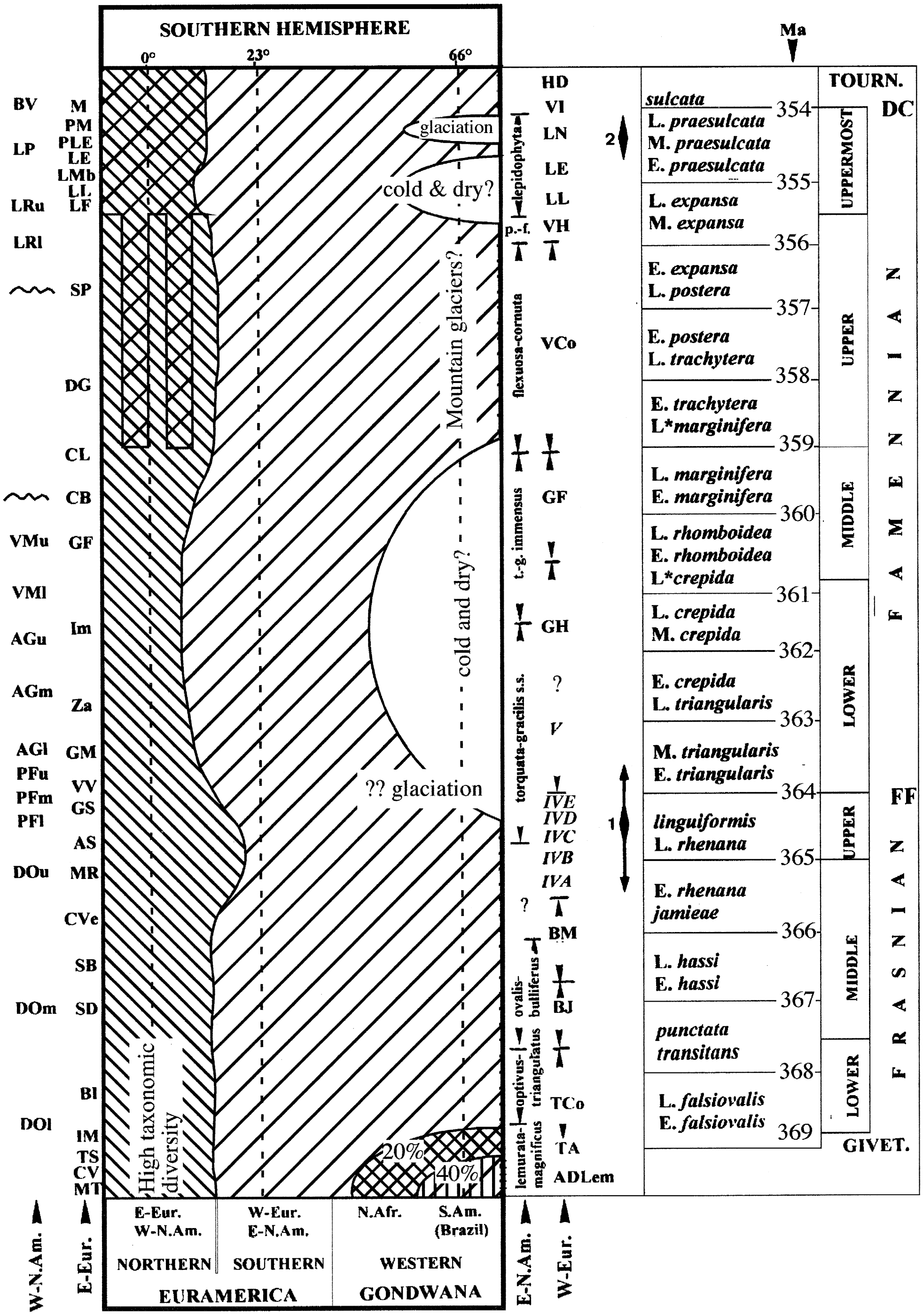
Even if glacial evidences are not known at that time, a short (0.1 Ma?) glaciation seems the best reasonable explanation of the major eustatic fall following the Kellwasser Event. The sudden growth and decay of a hypothetical Earliest Famennian ice sheet can be explained by the reduction and, later increase in greenhouse capacity of the atmosphere. These changes in the atmospheric CO_2 might have provoked changes in the mode of ocean-atmosphere operation. It may also be partly controlled by a volcanic paroxysm and/or bolide impacts. Indeed, the Hony microtektites represent the best-known evidence of the impact of extraterrestrial bodies on Earth corresponding to the UKW, and they are immediately followed by a regression, suggested by the quantitative analysis of acritarch assemblages. The almost complete absence of acritarchs right at the FFB is explained by the sedimentary conditions, not necessarily by a real extinction. Unfortunately, for the time being, no accurate miospore succession is known for certain across the FFB.

13.3. The Early–Middle Famennian

The diversity loss of miospores, observed in the Late Frasnian, is obvious also in the Early and

Fig. 33. Synthesis of quantitative palynology and comparison with climate from the Latest Givetian to the Latest Famennian in the Southern Hemisphere. Conodont Zone and chronology after Sandberg et al. (1997, Fig. 2). Frasnian and Famennian: — narrow hatch pattern for equatorial vegetation; — wide hatch pattern for tropical to subpolar vegetation. Givetian vegetation: see Fig. 5. Euramerican miospore Zonations: after Braman and Hills (1992) for westnorthern America (W-N. Am.); after Avkhimovitch et al. (1993) for eastern Europe (E-Eur.); after Richardson and McGregor (1986) and Richardson and Ahmed (1988) for eastnorthern America (E-N.Am.); after Streel et al. (1987) and Maziane et al. (1999) for western Europe (W-Eur.). (1) Late Frasnian Crisis and Kellwasser Event; (2) Hangenberg Event. The chart is organized to display the changes of the vegetation pattern over the south hemisphere against conodont and miospore biozonations so that each event can be situated in time and space. Climate in highest latitudes is superposed to the vegetation data. Most often, only the symbols of the miospore zones are provided. Four miospore biozonations are given, all from Euramerica. The two biozonations from northern Euramerica seem very different, but this actually reflects two different schools of palynology (western world versus former USSR), rather than deep biotic divergence. The two biozonations from southern Euramerica are rather similar, one being more detailed than the other. In this paper, the most detailed one is used for the Gondwanan vegetation.

Middle Famennian but it becomes more and more severe from the paleo-tropical to the paleo-subpolar regions. A strong climatic gradient from a warm equator to a cool pole seems to be operating during



the Early and Middle Famennian. Cooling does not mean glaciation which needs, first of all, heavy snow fall. As the sea level remains rather high during this timespan, the climate was probably cold but dry. Global cooling, except probably in the equatorial belt, forced land plants to migrate from high latitudes to lower latitudes but the available data do not record this migration process. The equatorial belt might well have kept its moderate thermoperiodism, i.e., the comparatively low level of environmental fluctuations, so that land plants which were not able to adapt to the moderate thermoperiodism had no other alternative than to collapse.

13.4. The Late Famennian

It is tempting to relate the major marine regressions starting in the Late Famennian with ice volume buildup on Gondwana despite the absence of recorded glacigenic sediments at that time. Perhaps mountain (alpine type) glaciers were then developing which are not recorded. From the start of the Late Famennian, the diversity of miospores increased again. The strong climatic gradient of the Early–Middle Famennian become less marked because the same miospore zones are recorded again (like in the Frasnian) from paleo-tropical to paleo-subpolar regions. Additionally, these miospore zones have greater affinities than before with the paleo-equatorial miospore zones. In the paleo-tropical Late Famennian, a peat-forming vascular plant community occurs for the first time and makes possible quantitative palynology of autochthonous sediments allowing the recognition of different swamp and near-swamp characteristic miospores. In the high latitudes, the Late Famennian climate was probably less cold than before but probably wetter, causing snowfall on the mountains and vegetation growth in the lowlands. The conspicuous latitudinal gradient of vegetation seems to attenuate but it might be above all the result of the development in the low latitudes of coastal lowland vegetations (coastal lowland swamps) dependent on moist and equable local microclimates. Buggisch's (1991) model, with warm phases alternating with glacial phases, is probably applicable for this interval.

13.5. The Latest Famennian

The early Latest Famennian starts with a widespread transgression, which could correspond to the melting phases of the hypothetical Late Famennian mountain glaciers. It might be the result of a new but short-term, cold and dry phase in sub-polar region where the absence of snowfall does not allow the mountain glaciers to develop. The miospore zones are dependent of the coastal lowland swamp margin

Fig. 34. Latest Famennian glacially striated pavement from the Cabeças Formation of the Parnaíba Basin (Northern Brazil). Located close to the Calembe village at about 11 km southward from the town of Canto do Buriti on the road (Br 324) to the town of Raimundo Nonato.

environments and are directly controlled by the changes in sea level. During the end-Famennian, the coastal lowland vegetation has a worldwide distribution from sub-polar to equatorial regions. The climate has become less cold in high latitudes but wetter than before probably because the midlatitude cyclonic activity allows sufficient polar transportation of moisture to form large snow cover. Extensive coastal glaciers (Fig. 34) developed in different Bolivian and Brazilian basins, well dated by miospores. During the Latest Famennian, the climate is, thus, cold in the high latitudes but probably warmer than before in the intertropical regions. It seems that the development of polar glaciers might have confined the intertropical convergence zone (the belt of low level of environmental fluctuations) to a narrow latitudinal, and perhaps discontinuous, range surrounding the equator. But rapid climatic changes also characterize the onset of glaciation. The cyclic nature of climate allowed even intertropical marine faunas to reach occasionally the subpolar regions. The coastal lowland vegetation dominates the miospore assemblages and it depends more on a local moisture and equable climate than on the climate from distant inner areas. Buggisch's (1991) model, with warmer phases (the equivalent of most of the Wocklum Limestone and the HBS) alternating with glacial phases (the equivalent of the Drewer Sandstone and the Hangenberg Shale and Sandstone), probably remained applicable. For the plant kingdom, the crisis, which follows the Hangenberg Event was more severe than the Late Frasnian Crisis.

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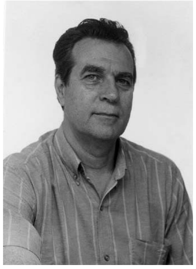
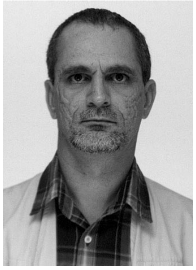
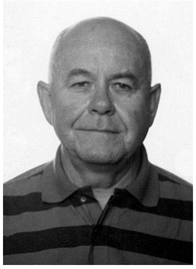


Mario Vicente Caputo graduated in Geology at the Federal University of Rio Grande do Sul in 1961, and in 1962 he joined Petrobras (the Brazilian state-owned oil company). He began his career as a field geologist working in several basins of Northern Brazil, then carried out technical and management activities at the Stratigraphy and Sedimentology Lab and the Division of Interpretation of Petrobras' northern district in Belém. He obtained his Ph.D. degree in 1984 at the University of California, USA, specializing on Stratigraphy and Paleoclimatology with studies on the Devonian glaciation in South America. He is a voting member of the International Subcommission on the Silurian System, and the only Latin American representative in that commission. In 1992, he joined the Federal University of Pará as a visiting professor, lecturing on Stratigraphy, Brazilian Geology and Energy Resources. Ever since he has carried out paleoclimatological research in addition to teaching activities.



José Henrique G. Melo holds a B.Sc. in geology from the Rio de Janeiro Federal University (1978), and an M.Sc. from the same university (1985). Since 1984 he has worked at Petrobras Research Centre (CENPES) as a stratigrapher, paleontologist and palynologist. His main research interests are in Silurian–Devonian palynology, stratigraphy and paleogeography of Brazilian Paleozoic basins. He has also carried out palynological investigations in Ordovician through Carboniferous strata of other South American countries as well as Ordovician rocks of NE Libya. Jointly with Dr. Stanislas Loboziak, he is currently leading a research project at CENPES. This involves a re-evaluation and an update of the Devonian–Mississippian miospore biostratigraphy in the Amazon and Solimões basins of northern Brazil.



Stanislas Loboziak graduated as a geologist from the Lille University, France. His Ph.D. (1969) was a contribution to the study of mio- and megaspores of the Westphalian of northern France. Since then he works at the same university as researcher at the French National Centre of Scientific Research. His work deals mainly with the palynology of Paleozoic dispersed miospores and its applications, especially in the field of biostratigraphy. He has contributed to the development of reference scales for the Devonian and Carboniferous of Western Europe and to their implementation in comparative studies, particularly with Central Europe, North Africa, Western Asia and North and South America. He is a consultant palynologist to Elf E.P. and Petrobras, and has participated for a few years, in an updating of the biochronostratigraphy of the Devonian and Lower Carboniferous of Paleozoic basins of northern Brazil.

Maurice Streel graduated (1957) as a botanist from Liège University, Belgium. His Ph.D. (1961) was a contribution to the phytogeography of Central African Savannahs. Later on he was Assistant, and then Professor, at the Paleobotany Department of the same university, teaching Paleobotany and Stratigraphy to students in Botany, Geology and Applied Geology. He introduced palynology lectures and researches. His main research interest was in the miospore stratigraphy of the Devonian Ardenne-Rhine regions. He was Secretary of the IUGS Working Group on the Devonian–Carboniferous Boundary and a voting member, and now corresponding member, of the International Subcommission on the Devonian System. He retired from the University in 1995 but is still active as a palynologist working particularly on the Quaternary and the quantitative approach of Late Devonian assemblages in relation to sedimentology and climatology.