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PALEOZOIC SPORES AND POLLEN 18B – MIDDLE AND UPPER DEVONIAN MIOSPORES

M. StreeI & S. Loboziak

INTRODUCTION

By late Early Devonian time, spores had developed most of their Devonian characteristics (Richardson & McGregor 1986, fig. 2). Camerate spores had evolved from two-layered, presumably zonate spores, and almost all kinds of exinal sculpture, including the typical bifurciform ornaments and the bifurcate spines, were present. The average spore size had increased from less than 25 µm (the size of extant bryophyte spores) to 50-150 µm (the size of extant fern spores), occasionally even reaching megaspore size (>200 µm) possibly in relation to incipient heterospory.

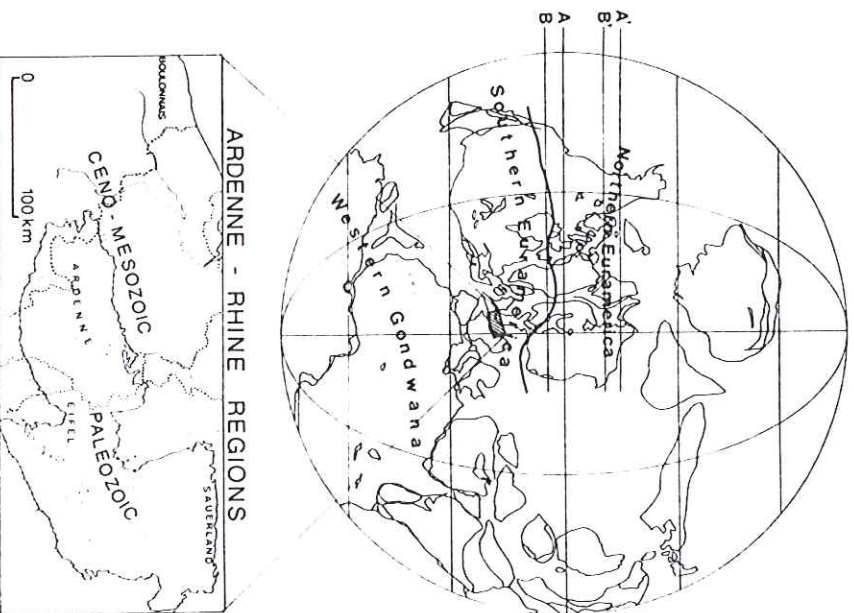
During Middle and Late Devonian time, spore size changed again in two steps:

- 1) a dramatic increase starting just below the Emsian/Eifelian boundary with species, many of them camerate, spanning the 200 µm size limit, again probably related to the development of heterospory;
 - 2) a return to the 50-150 µm size range near the Frasnian/Famennian boundary, which was possibly related to new strategies in plant reproduction such as the differentiation of the seed and prepollen. The first occurrence of endoreticulate miospores near that boundary (Balme 1988; McGregor & Playford 1990), might reflect such a change.
- Consequently, the miospores encountered in the present chapter may correspond not only to isospores, microspores or prepollen but also to possible megaspores spanning the 200µm size limit.

Another implication of the increasing abundance of these large propagules and of the development of heterospory is that the potential for very long distance dispersal of plants had probably become reduced so that miospore assemblages in the sediments represent more than before, regional to local source areas. This is not without consequences for phylogeographic (StreeI *et al.* 1990) and even ecological reconstructions (StreeI & Schaeckler 1990).

The most recent data on Middle and Late Devonian paleogeography, based on paleomagnetism and the distribution of paleoclimatically restricted lithofacies (Scotese & Mckerrow 1990), favor close connections between continents. A Devonian Proto-Tethys Ocean widely separating southern Europe from northern Africa is not acceptable on biogeographical

data. Even a hypothetical Rheic Ocean between southern and northern Europe was in the process of closing during Middle and Late Devonian time (Paris & Robardet 1990). Consequently, at least on a meridian line crossing eastern Euramerica



Text-Figure 1. Middle and Upper Devonian paleogeography, locations and detail of the Ardennes-Rhine regions. Map after Scotese & Mckerrow (1990, fig. 15: Middle Devonian, Givetian). Equator in Givetian (A) and Famennian (B) times after Scotese & Mckerrow (1990, fig. 15, 16). Equator in Middle Devonian (A') and Late Devonian (B') after Witzke (1990, fig. 5, 6). Boundary between northern and southern Euramerica based on the southern limit of *Archaeoperisaccus* after McGregor (1979a) and StreeI (1986). In Ardennes-Rhine regions, dotted lines: geographic boundaries; hatched lines surround area with Paleozoic outcrops.

StreeI, M. & Loboziak, S.

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(the continent resulting from collision between Laurentia and Baltica) and Western Gondwana, dry-land, shallow seas and/or possibly narrow oceans extended from equatorial to polar latitude (Text-Fig. 1) without interruption by a wide ocean.

Local or regional variations in plant distribution were therefore mainly due to climatic differences. In the Upper Devonian, for the first time since the land invasion by plants, climate-dependent phytogeographic reconstructions are possible (Stree1 1986).

At this time, vascular plants invaded new ecological niches, colonised uplands, and for the first time developed peat-forming communities (Scheckler 1986). From then on, as diversification of plant communities increased, paleoecological relationships based on dispersal of their spores were less simple. Transport of spores by water from their source areas to their depositional sites became an important factor to be considered in the reconstruction process. Consequently, species-enriched assemblages deposited preferentially in distal sites reflect a relatively large catchment area containing different plant communities (Stree1 & Richelot 1994).

Middle and Late Devonian time is thus a key period for the development of vegetation on the Earth, with new implications for paleophytogeography, paleoecology and biostratigraphy expressed in the spore record.

BIOSTRATIGRAPHY

Publications on stratigraphic distribution of Middle and Upper Devonian spores effectively started with the classic work of Naumova (1953) on the Russian Platform (northeasternmost Euramerica). Since then, parts of this stratigraphic interval have been zoned by various authors, mainly within the limits of Euramerica (see Richardson & McGregor 1986, fig. 1), but also elsewhere around the world.

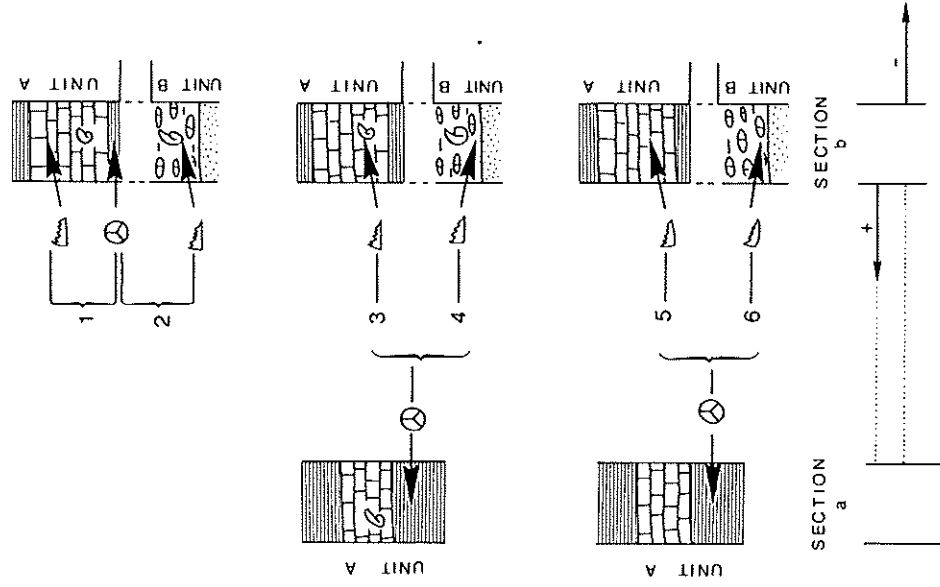
Two major works provide the reader with reviews and references (McGregor 1979a; Richardson & McGregor 1986), and also contain detailed stratigraphic syntheses, while illustrating most of the characteristic spores. There is no need to duplicate them here.

The zonal concept used in Richardson & McGregor (1986) is the Assemblage Zone, defined, in part, and correlated by assemblages of characteristic taxa. This concept was proposed as the only one that would allow correlation on a global scale. It has been applied to the Old Red Sandstone (ORS) Continent and adjacent regions, i.e. to regions obviously belonging to different major phytogeographic provinces (Richardson & McGregor 1986, fig. 6). Indeed, to accommodate a maximum of the available data, it was necessary to apply such a loose concept of zonation (see also McGregor & Playford 1992).

Another zonal concept, the Interval Zone, was introduced for the spores of the whole Devonian by Stree1 *et al.* (1987). First or last occurrences of single species (First Occurrence Biohorizon or FOB, or Last Occurrence Biohorizon or LOB) are searched for in continuous marine spore-bearing sequences, preferably in uniform lithologies.

The advantage of this Interval Zone concept is that it allows unequivocal correlations with Interval Zones based on other fossils. The quality of these correlations depends on the distance in time and space between the spore data on one hand and the nearest faunal data on the other hand, but as well on the kind of stratigraphy (litho- versus bio-) used for correlation (see CQI in Text-Fig. 2).

C.Q.I.



Text-Figure 2. Quality Index in correlation (CQI) between reference faunal (here conodont) and spore zones: 1 to 6 = best to worst. 1. Reference fauna in same section and same lithological unit as reference point of spore zone. 2. Reference fauna in same section but in other lithological units than reference point of spore zone. 3. Reference fauna in another section (3+ at short distance, 3- at long distance) but in same lithological unit, and with other fauna or flora also known in reference section of spore zone. 4. Reference fauna in another section (4+ at short distance, 4- at long distance) in other lithological units, but with other fauna or flora also known in reference section of spore zone. 5. Reference fauna in another section (5+ at short distance, 5- at long distance) in same lithological unit, but without fauna or flora in common with reference section of spore zone. 6. Reference fauna in another section (6+ at short distance, 6- at long distance) in other lithological units, and without fauna or flora in common with reference section of spore zone.

This concept is applied here within the limits of a single major phytogeographic province. Later in the text we compare both zonal concepts, and their proposed correlations between two adjacent major phytogeographic provinces and even beyond their immediate realms.

Western Gondwana – southern Euramerica, a single major phytogeographic province in Middle and Late Devonian time

From analyses of the stratigraphic distribution of miospores in North Africa and South America (Loboziak *et al.* 1988; Streef *et al.* 1988; Loboziak & Streef 1989), it has been shown that, since the Emsian at least, the miospore zonation developed in the Ardennes-Rhine regions (Streef *et al.* 1987) can be applied to Devonian strata of all areas in this single major phytogeographic province (Text-Fig. 1). This province can be extended to include most of southern Euramerica using, for instance, data summarized by McGregor (1979b).

We have selected twenty key species based on the following criteria: 1) unambiguous morphology, 2) common presence in significant sections studied throughout the province, 3) the same sequence of first occurrences in these sections, 4) no, or little, restriction in known lateral distribution. These species are presented and discussed below, starting with the oldest.

Selection of biohorizons in the Ardennes–Rhine regions and the faunal control of their age

In the discussion of the key species and the biohorizons defined by them, and also in Text-Figure 3, the values of the CQI refer to the correlation index of the acceptable position of the miospore biohorizon in terms of the conodont scale. If only a single value is given, it means that the biohorizon has to be found within the range of one single conodont zone. If two values of the CQI separated by a “/” are given, they refer to the correlation index of respectively the lowermost and uppermost acceptable position of the biohorizon within the range of two or more conodont zones.

1. 2. *Acinosporites apiculatus*, *Grandispora protea* potential First Occurrence Biohorizons.

Plate 1, Figures 9, 27, reproduced from Loboziak & Streef (1989, pl. 1, fig. 3, and pl. 6, fig. 5; respectively from samples at 1700 m and 1874 m in Borehole A1-69, Hammadah Basin, western Libya).

Bio-stratotype: Uppermost Wetteldorf Formation at Plain Quarry, Salmerswald Syncline, Eifel region (Richardson & McGregor 1986, p. 14). Data on the distribution of miospores at this locality have not been published. However, Riegel (1982, fig. 1) indicated that *A. apiculatus* and *G. protea* occur in similar succession.

Fauna: Conodont data are not published from this locality but lithological correlations suggest that these biohorizons correspond to the conodont *costatus parvulus* Zone (CQI 5 in Text-Fig. 2). Pending a new examination of the distribution of miospores and fauna at or near this locality, these biohorizons remain tentative.

3. *Grandispora velata* First Occurrence Biohorizon.

Plate 1, Figure 28, reproduced from Loboziak & Streef (1980, pl. 3, fig. 4; from sample 01 in unit H of the Blacourt Formation, Boulonnais region).

Bio-stratotype: At the level of sample 507 in the Lauch Formation in the “Wetteldorf Richtschmitt”, Pflim Syncline, Eifel region (Riegel 1982, fig. 1). Ten samples without *G. velata* have been analysed within a few meters below this biohorizon.

Fauna: Sample 507 belongs to a sequence of sediments containing the conodont *costatus parvulus* Zone (CQI 1 in Text-Fig. 2). This locality is also the reference section for the base of the Eifelian Stage, which has been fixed a few meters below this biohorizon, at the base of the conodont *costatus parvulus* Zone.

4. 5. *Acinosporites acanthomammillatus*, *A. macrospinosus* potential First Occurrence Biohorizons.

Plate 1, Figures 10, 8, reproduced from Loboziak & Streef (1989, pl. 1, fig. 4; from sample at 1483 m in Borehole A1-69, Hammadah Basin, western Libya) and from Paris *et al.* (1985, pl. 29, fig. 15; from sample at 2995 m in Borehole A1-37, northeastern Libya).

Bio-stratotype: Nohn Formation at Lierberg section, Sörsenich Syncline, Eifel region (Richardson & McGregor 1986, p. 15). Data on the distribution of miospores at this locality have not been published; however, these same authors (fig. 3) indicated that *A. acanthomammillatus* and *A. macrospinosus* occur in succession.

Fauna: Conodont data have not been published from this locality but lithological correlation suggests that these biohorizons correspond to the conodont *costatus costatus* Zone (CQI 5 in Text-Fig. 2). Pending a new examination of the distribution of miospores and fauna in this region, these biohorizons remain tentative.

6. *Chelinospora timanica* potential First Occurrence Biohorizon.

Plate 1, Figures 4, 5, respectively from sample 16, 1 m above sample 15 (see below; not previously published), and reproduced from Loboziak & Streef (1989, pl. 2, fig. 9; from sample at 650 m in Borehole A1-69, Hammadah Basin, western Libya).

Bio-stratotype: At the level of sample 15, between 29.1 and 29.4 m in the Giesdorf Member of the Junkerberg Formation in the exploratory trench of Bohmert Flür, Hillesheim Syncline, Eifel region.

Fauna: This sample belongs to a sequence of sediments with the conodont *ensensis-obliquimarginatus* Subzone sensu Weddige (1984; CQI 1 in Text-Fig. 2). The first occurrence of *C. timanica* is near the important gap recorded by Struve (1982) in the lowermost part of the overlying Freilingen Formation. Although the gap seems to be of less importance in the Hillesheim Syncline than elsewhere, we prefer to wait for the examination of more samples below this *C. timanica* occurrence before defining the biohorizon.

7. *Geminospira lemurata* First Occurrence Biohorizon.

Plate 1, Figures 19, 20, reproduced from Loboziak *et al.* (1991, pl. 1, figs. 6, 7; from sample 22, see below).

Bio-stratotype: Sample 22 in Ahbach Formation, at Müllerichen Quarry, Hillesheim Syncline, Eifel region (Loboziak *et al.* 1991, fig. 2, 3). Sixteen samples taken from a 23 m interval below sample 22 (and many more in the older formations of other nearby sections) contained miospores but lacked *G. lemurata*.

Fauna: Sample 22 belongs to a sequence of sediments with the conodont *ensensis-obliquimarginatus* Subzone sensu Weddige (1984; CQI 1 in Text-Fig. 2).

8. *Samarisporites triangulatus* First Occurrence Biohorizon.

Plate 1, Figures 17, 18, reproduced respectively from Loboziak *et al.* (1991, pl. 2, fig. 11; sample 44 in the Kerpen Formation, see below) and Loboziak & Streeel (1980, pl. 2, fig. 12; from sample 27 in the Blacourt Formation, see below).

Bio-stratotype: At the level of sample 44 in the lower part of the Kerpen Formation at Kerpen, Hillesheim Syncline, Eifel region (Loboziak *et al.* 1991, fig. 5). Six samples from the underlying Cürten Formation, 108 to 162 m, did not contain *S. triangulatus*.

Fauna: The Kerpen Formation at Kerpen (as well as the Cürten Formation) is correlated with the conodont *ensis-sis-bipennatus* Subzone (Weddige 1984; 1988, p. 150; CQI 1 in Text-Fig. 2).

The typical radial extensions of the zona of *S. triangulatus* in the Kerpen Formation are very short, possibly marking an early stage in the development of this species. In the Blacourt Formation (Boulonnais region), containing the conodont Late *varcus* Zone, the typical radial extensions are better developed and more conspicuous (Pl. 1, Fig. 17).

9. *Chelinospora concinna* First Occurrence Biohorizon.

Plate 1, Figures 6, 7, reproduced from Loboziak & Streeel (1980, pl. 2, fig. 16; from sample 01, see below) and from Loboziak & Streeel (1981, pl. 1, fig. 18; from sample 53 in level Q of the Beaulieu Formation, Boulonnais region).

Bio-stratotype: At the level of sample 01, unit H of the Blacourt Formation, at the Ferques railroad trench, Namur Synclinorium, Boulonnais region (Loboziak & Streeel 1980, fig. 1). Two samples from a 3 m interval below sample 01 did not contain *C. concinna*, but these samples immediately overlie a reef, 190 m thick, that lacks palynomorphs.

Fauna: Sample 01 is taken within a sequence containing conodont faunas ranging from the Middle to the Late *varcus* Zone (Loboziak & Streeel 1988, fig. 2; CQI 1/1 in Text-Fig. 2).

10. *Verrucosiporites bulliferus* First Occurrence Biohorizon.

Plate 1, Figure 2, reproduced from Loboziak & Streeel (1981, pl. 1, fig. 10; from sample 05, see below).

Bio-stratotype: At the level of sample 05 in unit O of the Beaulieu Formation, at Ferques railroad trench, Namur

Synclinorium, Boulonnais region (Loboziak & Streeel 1981, fig. 1). Five samples have been studied below the biohorizon in a 45 m interval above the base of the Beaulieu Formation, and *V. bulliferus* was absent in these.

Fauna: Sample 05 was taken between two limestone beds. The limestone bed above sample 05 contains *Arcyrodiella gigas* and is correlated with the conodont *punctata* Zone; the limestone bed below sample 05 is correlated with the conodont *transitans* Zone. Therefore, the *V. bulliferus* FOB belongs either to the conodont *transitans* Zone or to the conodont *punctata* Zone (CQI 1/1 in Text-Fig. 2).

11. *Rugospora bricei* First Occurrence Biohorizon.

Plate 1, Figures 11-13, reproduced respectively from Loboziak & Streeel (1989, pl. 3, fig. 2, 1; from sample at 650 m in Borehole A1-69, Hammadah Basin, western Libya), and from Loboziak & Streeel (1981, pl. 1, fig. 11; from sample 117, on top of the "banc dolomitique", see below).

Bio-stratotype: At the level of sample 24, immediately below the "banc dolomitique" in the upper Hydrequent Formation at Briqueterie de Beaulieu, Namur Synclinorium, Boulonnais region (Loboziak *et al.* 1983, fig. 1). Two poor samples, without *R. bricei*, occur within the 2 m below the biohorizon, and another one 25 m below.

Fauna: Conodonts have not been found in this section; however, in the La Parisienne Quarry, 500 m north of the Briqueterie de Beaulieu, and about 85 m stratigraphically below the *R. bricei* FOB, *Arcyrognathus triangularis euglypheus* is present, indicating the conodont Late *hassi* or *jamiene* Zone (CQI 6+ in Text-Fig. 2).

In the uppermost part of the Hydrequent Formation, about 23 m above the *R. bricei* FOB, acritarchs characteristic of the conodont *linguiformis* Zone have been identified (Loboziak *et al.* 1983, fig. 2; CQI 4- in Text-Fig. 2). According to these correlations, the *R. bricei* FOB is therefore in the Late *hassi*, the *jamiene*, or the *linguiformis* Zone.

12. *Grandispora gracilis* First Occurrence Biohorizon.

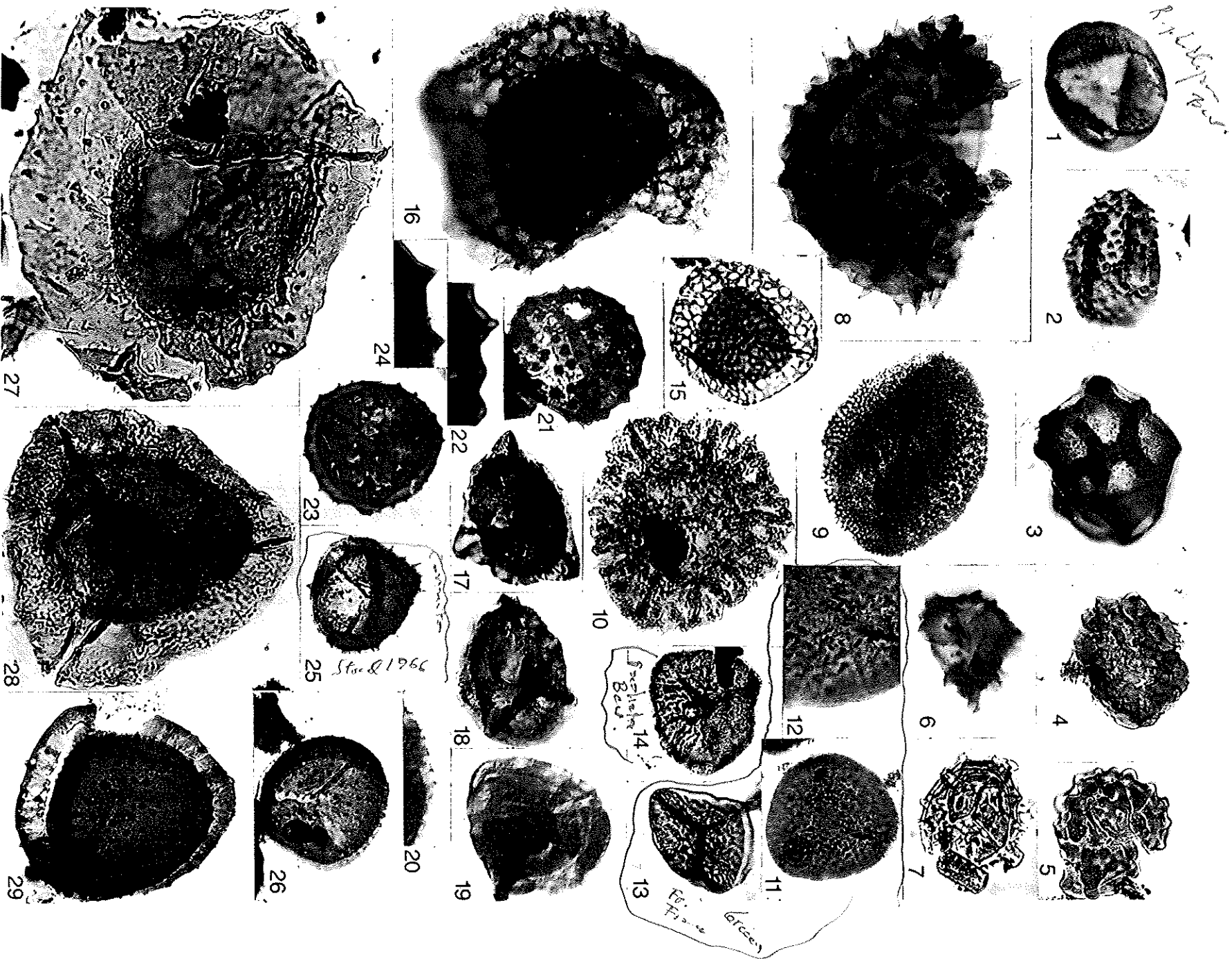
Plate 1, Figure 26, reproduced from Loboziak & Streeel (1981, pl. 2, fig. 13; from sample 109 in the Hydrequent Formation, see below).

PLATE 1

All figures 500x and in transmitted light unless otherwise stated.

1	<i>Retusotriletes phillipsii</i> ; Famennian, Belgium.	16	<i>Retispora macroreticulata</i> ; Famennian, Belgium.
2	<i>Verrucosiporites bulliferus</i> ; Frasnian, France.	17, 18	<i>Samarisporites triangulatus</i> ; 17: Givetian, France; 18: Givetian, Germany.
3	<i>Knoxisporites delatatus</i> ; Famennian, France.	19, 20	<i>Geminispora lemurata</i> ; Givetian, Germany (20, 1800x).
4, 5	<i>Chelinospora imannica</i> ; 4: Givetian, Germany; 5: Givetian, Libya.	21, 22	<i>Grandispora famenensis</i> var. <i>famenensis</i> ; Famennian, Belgium (22, 1800x).
6, 7	<i>Chelinospora concinna</i> ; Givetian, France.	23, 24	<i>Grandispora famenensis</i> var. <i>minuta</i> ; Famennian, Belgium (24, 1800x).
8	<i>Acinosporites macrospinosus</i> ; Eifelian, Libya.	25	<i>Grandispora cornuta</i> ; Famennian, Belgium.
9	<i>Acinosporites apiculatus</i> ; Eifelian, Libya.	26	<i>Grandispora gracilis</i> ; Frasnian, France.
10	<i>Acinosporites acanthomammillatus</i> ; Eifelian, Libya.	27	<i>Grandispora protea</i> ; Eifelian, Libya.
11, 12, 13	<i>Rugospora bricei</i> ; 11, 12: Frasnian, Libya (12, 1800x), 13: Frasnian, France.	28	<i>Grandispora velata</i> ; Givetian, France.
14	<i>Rugospora radiata</i> ; Famennian, Belgium.	29	<i>Indotriradites explanatus</i> ; Famennian, Germany.

MIDDLE AND UPPER DEVONIAN MIOSPORES



Bio-stratotype: At the level of sample 305 in the upper Hydrequant Formation, at Briqueterie de Beaulieu, Namur Synclinorium, Boulonnais region (Loboziak *et al.* 1983, fig. 1). Six samples in a 4.5 m interval below sample 305 did not contain *G. gracilis*.

Fauna: Conodonts have not been found in this section, but see fauna in Biohorizon 11. The *G. gracilis* FOB is also in the Late *hassi*, the *jamieae*, or the *linguiiformis* Zone. (CQI 6+ / 4- in Text-Fig. 2.)

13. *Knoxisporites dedaleus* First Occurrence Biohorizon.

Plate 1, Figure 3, reproduced from Loboziak & Streel (1981, pl. 3, fig. 11; from sample 109, see below).

Bio-stratotype: At the level of sample 109 in the uppermost Hydrequant Formation, at Briqueterie de Beaulieu, Namur Synclinorium, Boulonnais region (Loboziak & Streel 1981, fig. 1; Loboziak *et al.* 1983, fig. 1). Sixteen samples rich in miospores but lacking *K. dedaleus* have been studied in the 6 m of sediments immediately below sample 109.

Fauna: There are no conodont data available in the Hydrequant Formation at this locality. Acritarchs allow, however, an accurate correlation between the upper part of the Hydrequant Formation and similar sections in the Ardennes region where conodonts are well documented. For instance, a comparison between the Boulonnais locality and the sections at Hony and Sinsin (Dinant Synclinorium) in the Ardennes (Streel & Vanguetaine 1989) shows that sample 109 is about 1.5 m higher than the equivalent of the Frasnian/Famennian limit (base of the conodont Early *triangularis* Zone; CQI 4- in Text-Fig. 2). No independent data allow dating of the miospores from sample 109 upwards in the Hydrequant Formation. Consequently, the *K. dedaleus* FOB is within the *triangularis* Zones or even higher in the Famennian (CQI?).

14. *Grandispora famenensis* First Occurrence Biohorizon.

Plate 1, Figures 21-24, reproduced from Loboziak *et al.* (1995, pl. 2, fig. 10, 12, 16, 17; from samples 13 and 9, in the Esneux Formation at the Esneux locality, see below).

Bio-stratotype: *G. famenensis* var. *minuta*, a variety with reduced ornamentation, occurs at the level of sample 4 in the Esneux Formation at the Esneux locality, Dinant Synclinorium, Ardennes Region (Loboziak *et al.* 1995). *G. famenensis* var. *famenensis* occurs only in sample 13, 11 m higher.

Fauna: Lithological correlation suggests that the equivalent of the conodont Early *marginifera* Zone also occurs in the upper part of the Esneux Formation, in a section studied at Modave-Pont de Bonne, 25 km to the west (F. Bode, pers. comm. 1991). However, a correlation with the conodont Late *rhomboidea* Zone is also possible (Loboziak *et al.* 1995; CQI 5- in Text-Fig. 2).

Conodonts of the Early *marginifera* Zone are known from another lithological unit in the same section about 23 m above sample 4 (CQI 2 in Text-Fig. 2).

15. *Retispora macroreticulata* potential First Occurrence Biohorizon.

Plate 1, Figure 16, from sample J in the Evieux Formation of the Esneux railway section near Esneux (Dreesen *et al.* 1993).

Bio-stratotype: At the level of sample 19 in the Montfort Formation in the Comblain-au-Pont/Bon Mariage section,

Dinant Synclinorium, Ardennes region (Bouckaert *et al.* 1968). One sample, 9 m below sample 19, is known to lack *R. macroreticulata*.

Fauna: Sample 19 was taken from a succession of sediments containing conodonts of the Latest *marginifera* Zone (CQI 1 in Text-Fig. 2). The scarcity of studied miospores in the Montfort Formation does not allow an accurate definition of this biohorizon.

16, 17, 18. *Grandispora cornuta*, *Rugospora radiata*, and *Retusotriletes phillipsii* potential First Occurrence Biohorizons.

Plate 1, respectively Figure 25 (*G. cornuta*, reproduced from Streel 1966, pl. 2, fig. 27) from the Chanxhe section, Figure 14 (*R. radiata*, not previously published), and Figure 1 (*R. phillipsii*, from Becker *et al.* 1974, pl. 15, fig. 12). The latter two are from the Comblain-au-Pont/Beverire section, where miospores are better preserved than in the La Gombe/Montfort section.

Bio-stratotype: The best, but now almost inaccessible locality is in the lower part of the Evieux Formation in the Gombe/Montfort section (sample 36), Dinant Synclinorium, Ardennes region (Bouckaert *et al.* 1971, fig. 6; Bouckaert & Streel 1974; Thorez *et al.* 1977, p. 18). Ten samples from an interval between 50 and 180 m below sample 36 contained miospores, but lacked these three key species.

Fauna: *Scaphignathus velifer velifer* (first occurrence in the conodont Latest *marginifera* Zone) is known 162 m below sample 36 in the same section (CQI 2 in Text-Fig. 2). *Spathognathodus bohlerianus*, recorded from Haversin, 40 km to the southwest (Dreesen & Duser 1975) in the Ciney Formation, a supposed lateral equivalent of the Montfort Formation (Thorez *et al.* 1977, hors-texte 1), is no longer believed to be a useful tool for subdividing the old conodont *velifer* Zone (Duser & Dreesen 1985, p. 32). Therefore the existence of the conodont *trachytera* Zone below the miospores here discussed can no longer be demonstrated at the Haversin locality. The conodont Middle *expansa* Zone is known in the upper part of the Evieux Formation (see 19, below) in the nearby Esneux railway section, 2 km from the La Gombe/Montfort section (CQI 6+ in Text-Fig. 2). Consequently, the *G. cornuta*, *R. radiata* and *R. phillipsii* First Occurrence Biohorizons are between confirmed Latest *marginifera* and Middle *expa.* Zones.

First occurrences of these three species have been recorded in New York State U.S.A., at close but slightly different stratigraphic levels (Clendening *et al.* 1980; Richardson & Ahmed 1989, fig. 3). A comparison between New York State and Belgium, and evaluation of their respective controls by faunas, is given in Streel & Loboziak (1994). Because the stratigraphic distance between samples with and without these species in the La Gombe/Montfort section is important, and because the section is now almost inaccessible, we prefer to wait for the results from other nearby localities now being investigated before defining these biohorizons formally.

19. *Retispora lepidophyta* First Occurrence Biohorizon.

Plate 1, Figure 15 (see below under 21, *Retispora lepidophyta* LOB).

Bio-stratotype: Bed 94, at the level of sample 4 in the uppermost Evieux Formation, in the Chanxhe section, Dinant Synclinorium, Ardennes region (Streel *et al.* 1974, p. 29, pl. 1, fig. 7).

Fauna: The conodont Middle *expansa* Zone has been found (Dreesen *et al.* 1993) in the underlying Evieux Formation of the Esneux railway section, 3 km from Chanxhe (COI 2 in Text-Fig. 2). The conodont Late *expansa* Zone is known (Dreesen *et al.* 1993) from the same section and formation, about 5.5 m higher than sample 4 (COI 1 in Text-Fig. 2). Consequently, the *R. lepidophyta* FOB is in the Middle or Late *expansa* Zone.

20. *Indotriadites explanatus* First Occurrence Biohorizon.

Plate 1, Figure 29, reproduced from Higgs & Streel (1984, pl. 4, fig. 15; from sample Rh10, see below).

Bio-stratotype: The greenish silty shales (Hangenberg Schiefer equivalent) in the Riescheid section, Remscheid-Altena Anticline, Sauerland region, at the level of sample Rh10 (Higgs & Streel 1984, fig. 3). Three samples in the underlying 2.5 m interval lacked *I. explanatus* (Higgs & Streel 1994).

Fauna: The conodont *costatus* Zone, after Lane & Ziegler (in Paproth & Streel 1982), was found in almost the same bed (equivalent to the conodont Early or Middle *praesulcata* Zone).

Other, better dated, locality for the interval zone: 50 cm below the top of the Wocklum Kalk, at Hasselbachtal (28 km east of Riescheid), same anticline, single sample (Hb1) in the conodont Early *praesulcata* Zone (COI 1 in Text-Fig. 2). No samples with miospores are known below this single sample (Becker *et al.* 1984).

21. *Retispora lepidophyta* Last Occurrence Biohorizon.

Plate 1, Figure 15, reproduced from Higgs & Streel (1984, pl. 4, fig. 3; from sample Hb18-19, see below).

Bio-stratotype: At the level of sample Hb 18-19 in the Hangenberg-Schiefer in the Hasselbachtal section, Remscheid-Altena Anticline, Sauerland region (Higgs & Streel 1984, fig. 4). Six samples in the overlying 14 cm did not yield *R. lepidophyta* but were dominated by simple laevigate taxa.

Fauna: The *sulcata* conodont zone (its lower part corresponding to the trilobite *Archegonus abruptrachis* Zone) occurs 14 cm higher than LOB 21. The Early *praesulcata* Zone is about 6 m below (see FOB 20; Becker *et al.* 1984).

Other, better dated, localities are in (unfortunately only temporary) trenches at Stockum and Seiler. At Stockum new trench II (Higgs *et al.* 1993), assemblages from six samples in the 4.5 m interval immediately below the Stockum Limestone are transitional in composition to those of the overlying miospore zone. This is because *R. lepidophyta* is a rare but consistent element in these assemblages, characteristically forming less than 1% of the total spore content. In this trench II, the Stockum Limestone carries the conodont Late *praesulcata* Zone. Sample Str.A5, with *R. lepidophyta*, was obtained from the Hangenberg-Schiefer in the Seiler 1979 trench, Remscheid-Altena Anticline, 15 km east of the Hasselbach section, same region (Paproth & Streel 1982, p. 58, fig. 34). It was collected above samples A2/A3 that contain the Late *praesulcata* Zone. Combining the data from all localities, *R. lepidophyta* LOB is within the conodont Late *praesulcata* Zone (COI 1 in Text-Fig. 2).

The correlation between the miospore biohorizons and the standard conodont zones is shown in Text-Figure 3. All these data originate from the Ardenne-Rhine regions but other regions may contribute to refinement of the results. For instance, we have indicated in the legend of Text-Figure 3

additional correlation data from Bohemia (a) and New York State (b). Evaluating the quality of the correlation inevitably focusses attention on those parts of the biostratigraphic scheme that need further research.

Refinement of the miospore-based stratigraphy through intra-generic or intra-specific variations

Observing subtle morphological differences between species, like the random radial folding in the morphon *Rugospora bricei*-*R. radiata*, or the size of the typical radial extensions of the zona of *Samarisporites triangulatus*, one can be attracted by the possibility of demonstrating lineages and using them to refine stratigraphy.

Such attempts have been made with the genera *Ancyrospora* (Richardson 1962), *Rhabdosporites* (Richardson 1965), *Valaisporites* (Streel & Traverse 1978), and more recently by using the morphon concept, e.g. with *Cyrtospora cristifera* (van der Zwan 1979) and *Diducites* (van Veen 1981).

Such methods require the examination of large numbers of specimens to be statistically reliable. Unfortunately most of these taxa commonly display some restriction in lateral distribution (see below) which can reduce their potential for correlation.

Taxa with restricted lateral distribution

Even if the biostratigraphic scheme described above can be applied in the whole of the Western Gondwana-Southern Euramerica phytogeographic province, it does not mean that the flora was homogeneous over such a huge area. Two kinds of climatic restrictions appear to have disturbed such homogeneity: (1) macroclimatic, probably latitudinal, differences determining subprovinces and (2) microclimatic, mainly altitudinal, variations affecting plant communities in local areas.

Macroclimatic, probably latitudinal subprovinces

Differences between polar and tropical regions were especially pronounced during the Givetian and persisted in the Frasnian. A few endemic species might even represent a significant part of the miospore assemblages, particularly when the percentages, computed for each sample, are based on the number of specimens rather than on the number of species (Loboziak *et al.* 1989; Streel *et al.* 1990, fig. 2). For instance, the five paleo-polar (South American) to paleo-subtropical (North African) species *Canarozonotriletes?*, *conarous*, *Craspedispora shadamsensis*, *Grandispora gabesensis*, *Gilbyensis* and *G. riegelei* may together represent as much as 38% of the whole assemblage in South America, and 18% in North Africa. These differences seem to decrease significantly from the upper Givetian upwards (Streel *et al.* 1990).

A few Frasnian species are apparently restricted to the paleo-polar (e.g. South American) subprovinces, e.g. *Acinisporites eumammiliatus* and *Grandispora demonii*.

Paleo-tropical (Western European) assemblages, in which these species are lacking, might instead contain a few species that are often abundant in the nearby Northern Euramerica phytogeographic province, such as *Cristatisporites deliquescens* (as *Samarisporites* sp. C in Loboziak *et al.* 1983; see Avkhimovich *et al.* 1989, p. 563), and members of the *Cyrtospora cristifera* Morphon. The latter is commonly present in the uppermost Famennian of Ireland (van der Zwan 1980), and may occur in the lowermost Famennian in the Boulonnais region (Loboziak

& Streel 1981) and the paleo-subtropical subprovince of northeastern Libya (Paris *et al.* 1985).

Microclimatic, mainly altitudinal areas

The existence of both distinct upland and "marginal" or coastal miospore assemblages in the Middle Devonian and Frasnian has been recognized and/or discussed by Streel (1964, 1967), Richardson (1965), Becker *et al.* (1974, p. 22), and Allen & Marshall (1981). The variety in local abundance of species belonging to *Rhadospories* and the *Hystriospores* (mainly *Arcyrospora* and *Hystriospories*) was emphasized.

A more recent approach has taken into account the sedimentological environment of deposits. Species such as *Teichospora torquata*, or species of the *Diductes* morphon like *Diductes commutatus* (see van der Zwan & van Veen 1978), or species of the *Vallatisporites* complex, like *V. hystricosus* (see Streel & Schaeckler 1990), are locally abundant in different facies of alluvial and coastal plains, and may represent plants that preferred these environments.

Northern Euramerica, a single major phytogeographic province in Middle and Late Devonian time

McGregor (1979a) and Streel (1980, 1986) have plotted, on different paleogeographic maps, the distribution of *Archaeopertisaccus* versus other Frasnian miospore assemblages containing *Geminospora lemurlata*. The distribution of *Archaeopertisaccus* is believed to characterize a single major phytogeographic province: Northern Euramerica. The southern limit of its distribution is shown here (Text-Fig. 1) on one of the most recent Middle Devonian paleogeographic reconstructions (Scotese & Mckerrow 1990, fig. 15), just south of the Givetian paleo-equator, where it almost coincides with the Famennian paleo-equator. Alternative positions of the paleo-equator, as suggested by Witzke (1990) on the supposition that the Devonian paleomagnetic poles of the earth did not coincide with the rotational poles, indicate that Northern Euramerica might well have been equatorial, a supposition that is accepted here as the most rational hypothesis (Streel *et al.* 1990, p. 295).

Richardson & McGregor (1986, fig. 6) checked the first occurrence of ten zonally significant species of their own zonation in a number of Givetian and Frasnian spore and conodont bearing strata from the western (Canada) and the eastern (former U.S.S.R.) parts of Northern Euramerica. Five species (our biohorizons 6 to 10) have stratigraphic distributions compatible with Southern Euramerica and therefore allow north-south correlation. But despite these observations indicate that at least the Frasnian miospore assemblages of the Northern Euramerica province differ to some extent from those described in the Southern Euramerica-Western Gondwana province. Loboziak & Streel (1981), for instance, found it difficult to correlate conodont-dated Frasnian miospore zonations from the Russian Platform and Timan-Rechra, in the Commonwealth of Independent States, with the Boulonnais region in northern France. McGregor (1981) remarked that many Givetian and Frasnian species of the C.I.S., regarded as stratigraphically important by local workers, have not been recognized in other regions.

To illustrate these differences between the two major provinces more clearly, in Text-Figure 4 we compare, as did Avkhimovitch *et al.* (1989), the zonation recently published

for Byelorussia with that proposed for the Ardenne-Rhine regions by Streel *et al.* (1987), indicating also the biohorizons mentioned in this chapter. A comparison (after Streel *et al.* 1987) with the Old Red Sandstone Continent zonation shows, for instance, that no less than 15 Byelorussian palynozones correspond to just three latest Givetian to early-middle Famennian assemblage zones of Richardson & McGregor (1986). Even the more subdivided zonation of the Ardenne-Rhine regions does not match the detail of the Byelorussian zonation (a comparison tempered by the recognition of the Acme-Zone character of the latter). Also, despite the nomenclatural problems that are still important between the two provinces, the palynofloras of Byelorussia and, more generally, of the Russian Platform and of Arctic Canada (see also Branan & Hills 1992), probably contain many more species than those from Southern Euramerica-Western Gondwana, within the latest Givetian to early-middle Famennian timespan.

Eastern Gondwana (mainly Australia), a single phytogeographic province in Middle and Late Devonian time?

As stated by McGregor & Playford (1992), enough similarities exist between Euramerican and Australian Middle and Upper Devonian spore assemblages to sustain long distance biostratigraphic correlation using a modified version of the assemblage-zones of Richardson & McGregor (1986). Although these authors did not separate Northern and Southern Euramerican provinces in their range-charts (ie. fig. 7 in McGregor & Playford 1992), it is apparent that Australia shares more Givetian-Frasnian taxa with Southern Euramerica-Western Gondwana than with Northern Euramerica. The many similarities between Australian and Euramerican miospores imply, as already stated in the introduction of this chapter, sufficiently close proximity of Gondwana and the Old Red Sandstone Continent to allow considerable floristic interchange.

On the other hand, several hundred of the Euramerican taxa have not been observed in Australian palynofloras, including for instance typical cingulizone spores (McGregor & Playford 1992). About 150 Australian species are apparently unrepresented in Euramerican assemblages. Compared to the latitudinal subprovinces discernible, mainly on a quantitative basis, within the Western Gondwana-Southern Euramerica Province, Australia might well correspond to a single phytogeographic entity.

Cosmopolitan late Famennian miospore assemblages

Early to middle Famennian time (*crepida-trachlytera* time) is palynologically poorly documented all over Gondwana despite many sections studied from Bolivia in the west to Australia in the east. How far this is due to incomplete study of available rocks, to palynologically unfavourable types of sediments, or to a scarce vegetation cover in these areas at the time, is still unknown. The latter explanation seems compatible with the strong gradient of climate suspected from comparison of northern and southern Euramerican miospore assemblages of this age.

Late Famennian miospore assemblages contrast with earlier assemblages by their cosmopolitanism, culminating in the latest Famennian *Retispora leptodiphyta*. This species began

and developed during Middle *expans-praesulcata* time and collapsed at the Devonian-Carboniferous (*praesulcata/sulcata*) boundary, allowing accurate correlations throughout the world. This was a period of quickly changing climates, emphasized by glacial and interglacial alternations in South America (Loboziak *et al.* 1993).

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List of taxa

- Actinosporites acanthomammillatus* Richardson 1965
Actinosporites apiculatus (Stree) Stree 1967
Actinosporites eumammillatus Loboziak, Stree & Burjack 1988
Actinosporites macrospinosus Richardson 1965
Ancrospora Richardson 1960
Archaeopersaccus Naumova 1953, emend. McGregor 1969
Camerozonotrites? concavus Loboziak & Stree 1989
Chelinospora concinna Allen 1965
Chelinospora limnica (Naumova) Loboziak & Stree 1989
Cornispora varicornata Staplin & Jansonius in Staplin 1961
Craspidispora glandamsensis Loboziak & Stree 1989
Cristatisporites deliquescens (Naumova) Arklangel'skaia 1987
Cyrtospora cristifera (Lieber) van der Zwan 1979
Didictes van Veen 1981
Didictes commutatus (Naumova) Avchimovitch, in Avchimovitch *et al.* 1988
Geminospora lenurata Balme 1962, emend. Playford 1983
Grandispora cornuta Higgs 1975
Grandispora daemontii Loboziak, Stree & Burjack 1988
Grandispora famenensis (Naumova) Stree in Becker *et al.* 1974
Grandispora famenensis var. *famenensis*
Grandispora famenensis var. *minuta* Nektrata 1974
Grandispora gabesensis Loboziak & Stree 1989
Grandispora gracilis (Kedo) Stree in Becker *et al.* 1974
Grandispora ligyensis Moreau-Benoit 1980
Grandispora protea (Naumova) Moreau-Benoit 1980
Grandispora riegeii Loboziak & Stree 1989
Grandispora velata (Eisenack) Playford 1971
Hysticosporites McGregor 1960
Indotritoides explanatus (Lieber) Playford 1991
Knottisporites dedalatus (Naumova) Stree 1977
Retispora lepidophylla (Kedo) Playford 1976
Retispora macroreticulata (Kedo) Byvsheva 1985
Retisporites philippsii Clendening, Eames & Wood 1980
Rhabdosporites Richardson 1960
Rugospora brizei Loboziak & Stree 1989
Rugospora radiata (Lushko) Byvsheva 1985
Samarisporites triangulatus Allen 1965
Teichertospora torquata (Higgs) McGregor & Playford 1990
Vallatisporites Haquebard 1957
Vallatisporites hystericus (Winslow) Byvsheva 1985
Verrucosisporites bulliferus Richardson & McGregor 1986
- AVCHIMOVITCH, V. I., BYVSHEVA, T. V., HIGGS, K., STREEL, M. & UMNNOVA, V. T.
 1988 Miopore systematics and stratigraphic correlation of Devonian-Carboniferous boundary deposits in the European part of the USSR and Western Europe. *Courier Forschungsanstalt Senckenberg*, 100: 169-191, pl. 1-5.
- AVKHMIVITCH, V. I. - also see AVCHIMOVITCH, AVKHMIVITCH.
- AVKHMIVITCH, V. I.
 1986 Zonal differentiation of Devonian/Carboniferous boundary deposits of Byelorussia (Pripiat Depression) and spore correlation with the reference sections of the Franco-Belgian Basin. in: *Paleontology and its role in the study of geological structure of Byelorussia*; Minsk, Nauka i Tekhnika, p. 145-165. (In Russian.)
- AVKHMIVITCH, V. I., NEKRYATA, N. S. & OBUHOVSKAYA, T. G.
 1989 Devonian palynostratigraphy of the Pripyat Depression, Byelorussia; in: MCWILLIAN, N. J., EMBRY, A. F. & GLASS, D. J. (ed.), *Devonian of the World*, 3, Paleontology, paleoecology and biostratigraphy; *Canadian Society of Petroleum Geologists, Memoir*, 14: 559-566 [Imprinted 1988.]
- BALME, B. E.
 1988 *Teichertospora* n. gen., an endoreticulate miospore from the Late Devonian of Western Australia; *Senckenbergiana Lethaea*, 69: 159-169, pl. 1.
- BECKER, G., BLESS, M. J. M., STREEL, M. & THOREZ, J.
 1974 Palynology and ostracode distribution in the Upper Devonian and basal Dinanthen of Belgium and their dependence on sedimentary facies; *Mitteilungen Rijks Geologische Dienst*, n. serie, 25(2): 9-99, pl. 1-30.
- BECKER, T., BLESS, M. J. M., BRAUCKMANN, C., FRIMAN, C., HIGGS, K., KEUPP, H., KORIN, D., LANGER, W., PAPROTH, E., RACHEBOEUF, P., STOPPEL, D., STREEL, M. & ZAKOWA, H.
 1984 Hasselbachthal, the section best displaying the Devonian-Carboniferous boundary beds in the Rhensish Massif (Rheinisches Schiefergebirge); *Courier Forschungsanstalt Senckenberg*, 67: 181-191, pl. 1.
- BOUCKAERT, J. & STREEL, M.
 1974 General information; in: BOUCKAERT, J. & STREEL, M. (ed.), *International Symposium on Belgian Micropalaeontological Limits, Namur 1974, Guidebook*; Brussels, Geological Survey of Belgium, 19 p.
- BOUCKAERT, J., STREEL, M. & THOREZ, J.
 1968 Schéma biostratigraphique et coupes de référence du Famennien belge. Note préliminaire; *Annales de la Société géologique de Belgique*, 91: 317-336.
- 1971 Le Famennien et les couches de transition Devonien-Carbonifère dans la vallée de l'Ourthe (sud de Liège, synclinorium de Dinant); *Congrès et Colloques de l'Université de Liège*, 55: 25-46. [Imprinted 1970.]
- BRAMAN, D. R. & HILLS, L. V.
 1992 Upper Devonian and Lower Carboniferous miospores, western District of Mackenzie and Yukon Territory, Canada; *Palaeontographica Canada*, 8: 1-97, pl. 1-24.
- CLENDENING, J. A., EAMES, L. E. & WOOD, G. D.
 1980 *Retisporites philippsii* n. sp., a potential Upper Devonian guide palynomorph; *Palynology*, 4: 15-22, pl. 1.
- DRESEN, R. & DUSAR, M.
 1975 Description et interprétation géologique des coupes situées dans la région de Haverstin; *Service géologique de Belgique, Professionnel Paper*, 3, 1975: 1-69.
- DRESEN, R., POTY, E., STREEL, M. & THOREZ, J.
 1993 Late Famennian to Namurian in the Eastern Ardenne, Belgium; *IUGS Subcommittee on Carboniferous Stratigraphy, Guidebook*, Liège, 60 p.
- DUSAR, M. & DRESEN, R.
 1985 Stratigraphy of the Upper Frasnian and Famennian deposits in the region of Hamoir-sur-Ourthe (Dinant Synclinorium, Belgium); *Service géologique de Belgique, Professional Paper*, 209, 1984/85: 1-55.

REFERENCES

- ALLEN, P. A. & MARSHALL, J. E. A.
 1981 Depositional environments and palynology of the Devonian south-east Shetland Basin; *Scottish Journal of Geology*, 17: 257-273.

- HIGGS, K. & STREEL, M.
 1984 Spore stratigraphy at the Devonian-Carboniferous boundary in the northern "Rheinisches Schiefergebirge", Germany; *Courier Forschungsinstitut Senckenberg*, 67: 157-179, pl. 1-4.
 1994 Palynological age for the lower part of the Hangenberg Shales in Sauerland, Germany; *Annales de la Société géologique de Belgique*, 116.
- HIGGS, K. T., STREEL, L., KORN, D. & PAPROTH, E.
 1993 Palynological data from the Devonian-Carboniferous boundary beds in the new Stockum Trench II and the Hasselbachtal boreholes, northern Rhenish Massif, Germany; *Annales de la Société géologique de Belgique*, 115: 551-557.
- KLAPPER, G., SANDBERG, C. A., COLLINSON, C., HUDDLE, J. W., ORR, R. W., RICKARD, L. V., SCHUMACHER, D., SEDDON, G. & UYENO, T. T.
 1971 North American Devonian conodont biostratigraphy; in: SWEET, W. C. & BERGSTROM, S. M. (ed.), *Symposium on conodont biostratigraphy*; *Geological Society of America, Memoir*, 127: 285-316.
 1979 Devonian conodont biostratigraphy; in: HOUSE, M. R., SCRUTTON, C. T. & BASSETT, M. G. (ed.), *The Devonian System: Special Papers in Palaeontology*, 23: 199-224.
- LOBOZIAK, S., AVKHIMOVICH, V. & STREEL, M.
 1995 Miospores from the type locality of the Esneux Formation, Middle Famennian of the Ourthe valley, eastern Belgium; *Annales de la Société géologique de Belgique*, 117: 95-102, pl. 1, 2.
- LOBOZIAK, S. & STREEL, M.
 1980 Miospores in Givetian to lower Frasnian sediments dated by conodonts from the Boulonnais, France; *Revue of Palaeobotany and Palynology*, 29: 285-299, pl. 1-4.
 1981 Miospores in middle-upper Frasnian to Famennian sediments partly dated by conodonts (Boulonnais), France; *Revue of Palaeobotany and Palynology*, 34: 49-66, pl. 1-4.
 1988 Synthèse palynostratigraphique de l'intervalle Givétien-Famennien du Boulonnais (France); in: BRICE, D. (ed.), *Le Dévonien de Ferques, Bas-Boulonnais (N. France): Biostratigraphie du Paléozoïque, Université de Bretagne occidentale*, 7: 71-77, pl. 3-4.
 1989 Middle-Upper Devonian miospores from the Ghadamis Basin (Tunisia-Libya): systematics and stratigraphy; *Revue of Palaeobotany and Palynology*, 58: 173-196, pl. 1-9.
- LOBOZIAK, S., STREEL, M. & BURJACK, M. I. A.
 1988 Miospores du Dévonien moyen et supérieur du bassin du Paraná, Brésil: systématique et stratigraphie; *Sciences Géologiques, Bulletin*, 41: 351-377, pl. 1-7.
 1989 Déductions paléoclimatiques d'une comparaison entre les assemblages de miospores du Dévonien moyen et supérieur de Libye et du Brésil; *Geobios*, 22: 247-251.
- LOBOZIAK, S., STREEL, M., CAPUTO, M. V. & DE MELO, J. H. G.
 1993 Middle Devonian to Lower Carboniferous miospores from selected boreholes in Amazonas and Paranaíba Basins (Brazil): additional data, synthesis, and correlation; *Documents du Laboratoire de Géologie de Lyon*, 125: 277-289.
- LOBOZIAK, S., STREEL, M. & VANGUESTAINE, M.
 1983 Miospores et acritarches de la Formation d'Hydrequant (Frasnien supérieur à Famennien inférieur, Boulonnais, France); *Annales de la Société géologique de Belgique*, 106: 173-183, pl. 1, 2.
- LOBOZIAK, S., STREEL, M. & WEDDIGE, K.
 1991 Miospores, the *lemurata* and *triangulatus* levels and their faunal indices near the Eifelian/Givetian boundary in the Eifel (F.R.G.); *Annales de la Société géologique de Belgique*, 113: 299-313, pl. 1, 2.
- MCGREGOR, D. C.
 1979a Spores in Devonian stratigraphical correlation; in: HOUSE, M. R., SCRUTTON, C. T. & BASSETT, M. G. (ed.), *The Devonian System; Special Papers in Palaeontology*, 23: 163-184.
- 1979b Devonian miospores of North America; *Palynology*, 3: 31-52, pl. 1-4.
 1981 Spores and the Middle-Upper Devonian boundary; *Revue of Palaeobotany and Palynology*, 34: 25-47.
 MCGREGOR, D. C. & PLAYFORD, G.
 1990 Morphology and distribution of the miospore *Tetrahloporon torquata* comb. nov. in the Upper Devonian of Euramerica and Australia; *Palynology*, 14: 7-18, pl. 1, 2.
 1992 Canadian and Australian Devonian spores: zonation and correlation; *Geological Survey of Canada, Bulletin*, 438: 1-125, pl. 1-20.
 NAUMOVA, S. N.
 1953 Spore-pollen assemblages of the Russian platform and their stratigraphic significance; *Trudy Instituta Geologicheskikh Nauk, Akademiia Nauk SSSR*, 143, *Geologicheskikh Seriya*, 60, 204 p., 25 pl. (In Russian.)
 OLIVER, W. A., JR. & CHLUPAC, I.
 1991 Defining the Devonian: 1979-89; *Lethaia*, 24: 119-122.
 PAPROTH, E. & STREEL, M. (ed.)
 1982 Devonian-Carboniferous transitional beds of the Northern "Rheinisches Schiefergebirge"; *IUGS Working Group on the Devonian-Carboniferous boundary, Guidebook*, Liège, 63 p.
 PARIS, F., RICHARDSON, J. B., RIEGEL, W., STREEL, M., VANGUESTAINE, M.
 1985 Devonian (Emilian-Famennian) palynomorphs; *Journal of Micropalaeontology*, 4(1): 49-81, pl. 17-32.
 PARIS, F. & ROBARDET, M.
 1990 Early Palaeozoic palaeobiogeography of the Variscan regions; *Tectonophysics*, 177: 193-213.
 RICHARDSON, J. B.
 1962 Spores with bifurcate processes from the Middle Old Red Sandstone of Scotland; *Palaeontology*, 5: 171-194, pl. 25-27.
 1965 Middle Old Red Sandstone spore assemblages from the Orcadian basin north-east Scotland; *Palaeontology*, 7: 559-605, pl. 88-93.
 RICHARDSON, J. B. & AHMED, S.
 1989 Miospores, zonation and correlation of Upper Devonian sequences from western New York State and Pennsylvania; in: McMILLAN, N. J., EMBRY, A. F. & GLASS, D. J. (ed.), *Devonian of the World*, 3, *Palaeontology, paleoecology and biostratigraphy*; *Canadian Society of Petroleum Geologists, Memoir*, 14: 541-558, pl. 1-5. [Unprinted 1988.]
 RICHARDSON, J. B. & MCGREGOR, D. C.
 1986 Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions; *Geological Survey of Canada, Bulletin*, 364: 1-79, pl. 1-21.
 RIEGEL, W.
 1982 Palynological aspects of the Lower/Middle Devonian transition in the Eifel region; in: ZIEGLER, W. & WERNER, R. (ed.), *On Devonian stratigraphy and palaeontology of the Ardennes-Rhenish Mountains and related Devonian matters*; *Courier Forschungsinstitut Senckenberg*, 55: 279-292, pl. 1.
 SCHECKLER, S. E.
 1986 Geology, floristics and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (USA); in: BLESS, M. J. M. & STREEL, M. (ed.), *Late Devonian events around the Old Red Continent, Annales de la Société géologique de Belgique*, 109: 209-222.
 SCOTSE, C. R. & MCKERROW, W. S.
 1990 Revised world maps and introduction; in: MCKERROW, W. S. & SCOTSE, C. R. (ed.), *Palaeozoic palaeogeography and biogeography*; *Geological Society of London, Memoir*, 12: 1-21.
 STREEL, M.
 1964 Une association de spores du Givétien inférieur de la Vesdre, à Goé (Belgique); *Annales de la Société géologique de Belgique*, 87: 1-30, pl. 1, 2.
 1966 Critères palynologiques pour une stratigraphie détaillée du Trias dans les bassins ardennes-rhénaux; *Annales de la Société géologique de Belgique*, 89: 65-96, pl. 1, 2.

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- 1967 Association de spores du Dévonien inférieur belge et leur signification stratigraphique. *Annales de la Société géologique de Belgique*, 90: 11-54, pl. 1-5.
- 1980 Evidences palynologiques sur les relations entre le climat et la distribution géographique des flores dévoniennes et dinantiennes. *Mémoire du Muséum national d'Histoire naturelle, série B*, 27: 261-267.
- 1986 Miospore contribution to the upper Famennian-Strunian event stratigraphy. *in*: BLESS, M. J. M. & STREEL, M. (ed.), Late Devonian events around the Old Red Continent. *Annales de la Société géologique de Belgique*, 109: 75-92.
- STREEL, M., BLESS, M. J. M., BOUCKAERT, J., COEN, M., COEN-AUBERT, M., CONIL, R., DREESSEN, R., DUSAR, M., MOURAVIEFF, N. & THOREZ, J.
- 1974 Chief micropaleontological limits in the Belgian Upper Devonian. *in*: BOUCKAERT, J. & STREEL, M. (ed.), International Symposium on Belgian Micropaleontological Limits, Namur 1974. *Geological Survey of Belgium, Publication*, 19: 1-29, 4 pl.
- STREEL, M., FAIRON-DEMARET, M. & LOBOZIAK, S.
- 1990 Givetian-Frasnian phytogeography of Euramerica and western Gondwana based on miospore distribution. *in*: MCKERROW, W. S. & SCOTSE, C. R. (ed.), Palaeozoic palaeogeography and biogeography. *Geological Society of London, Memoir*, 12: 291-296.
- STREEL, M., HIGGS, K., LOBOZIAK, S., RIEGEL, W. & STEEMANS, P.
- 1987 Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardene-Rhenish regions. *Review of Palaeobotany and Palynology*, 50: 211-229.
- STREEL, M. & LOBOZIAK, S.
- 1994 Observations on the establishment of a Devonian and Lower Carboniferous high-resolution miospore biostratigraphy. *Review of Palaeobotany and Palynology*, 83: 261-273.
- STREEL, M., PARIS, F., RIEGEL, W. & VANGUESTAINE, M.
- 1988 Aetnach, chitinozoan and spore stratigraphy from the Middle and Late Devonian of northeast Libya. *in*: EL-ARNAUTI, A., OWENS, B. & THUSU, B. (ed.), *Subsurface palynostratigraphy of northeast Libya*. Garyouns University Publications, Benghazi, Libya (SPLA), p. 111-128, pl. 21.
- STREEL, M. & RICHELLOT, C.
- 1994 Wind and water transport and sedimentation of miospores along two rivers subject to major floods and entering the Mediterranean Sea at Calvi (Corsica, France). *in*: TRAVERSE, A. (ed.), *Sedimentation of organic particles*. Cambridge University Press, p. 59-67.
- STREEL, M. & SCHECKLER, S. E.
- 1990 Miospore lateral distribution in upper Famennian alluvial lagoonal to tidal facies from eastern United States and Belgium. *Review of Palaeobotany and Palynology*, 64: 315-324.
- STREEL, M. & TRAVERSE, A.
- 1978 Spores from the Devonian/Mississippian transition near the Horseshoe Curve section, Altoona, Pennsylvania, U.S.A.; *Review of Palaeobotany and Palynology*, 26: 21-39, pl. 1, 2.
- STREEL, M. & VANGUESTAINE, M.
- 1989 Palynomorph distribution in a siliciclastic layer near the Frasnian/Famennian boundary at two shelf facies localities in Belgium. *Bulletin de la Société belge de Géologie*, 98: 109-114.
- STRUVE, W.
- 1982 The great gap in the record of marine Middle Devonian. *Courier Forschungsinstitut Senckenberg*, 55: 433-448.
- THOREZ, J., STREEL, M., BOUCKAERT, J. & BLESS, M. J. M.
- 1977 Stratigraphie et paléogéographie de la partie orientale du Synclinorium de Dinant (Belgique) au Famennien supérieur: un modèle de bassin sédimentaire reconstruit par analyse pluridisciplinaire sédimentologique et micropaléontologique. *Mémoires du Rijks Geologische Dienst, n. série*, 28(2): 17-32.
- VAN DER ZWAN, C. J.
- 1979 Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. I. The *Cyrtospora cristifera* morphon. *Review of Palaeobotany and Palynology*, 28: 1-20, pl. 1-5.
- 1980 Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. III. Palynology of Devonian-Carboniferous transition sequences with special reference to the Bantry Bay area, Co. Cork. *Review of Palaeobotany and Palynology*, 30: 165-286, pl. 1-30.
- VAN DER ZWAN, C. J. & VAN VEEN, P. M.
- 1978 The Devonian-Carboniferous transition sequence in southern Ireland: integration of paleogeography and palynology. *Palinologia, numero extraordinario*, 1: 469-479, pl. 1, 2.
- VAN VEEN, P. M.
- 1981 Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. IV. Morphological variation within *Diducites*, a new formgenus to accommodate canerate spores with two-layered outer wall. *Review of Palaeobotany and Palynology*, 31: 261-287, pl. 1-5.
- WEDDIGE, K.
- 1984 Zur Stratigraphie und Paläogeographie des Devons und Karbons von NE-Iran. *Senckenbergiana lethaea*, 65: 179-223.
- 1988 Eifel conodonts. *in*: ZIEGLER, W. (ed.), 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V). Part I: Guide to field trip, trip A: Eifel Hills. *Courier Forschungsinstitut Senckenberg*, 102: 103-110, 116-118, 132-133, 140-142, 150.
- WITZKE, B. J.
- 1990 Palaeoclimatic constraints for Palaeozoic palaeolatitudes of Laurentia and Euramerica. *in*: MCKERROW, W. S. & SCOTSE, C. R. (ed.), Palaeozoic palaeogeography and biostratigraphy. *Geological Society of London, Memoir*, 12: 57-73.
- ZIEGLER, W. & SANDBERG, C. A.
- 1990 The Late Devonian standard conodont zonation. *Courier Forschungsinstitut Senckenberg*, 121: 1-115, pl. 1-17.

Authors' addresses

- Maurice Streeel
Paléontologie
Université de Liège
7 place du Vingt-Août
B-4000 Liège
Belgium
- Stanislas Loboziak
Paléobotanique
Université des Sciences
et Techniques de Lille
URA 1365 CNRS
F-59655 Villeneuve d'Ascq
France

