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Review of Palaeobotany and Palynology, 50 (1987): 211-229
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

SPORE STRATIGRAPHY AND CORRELATION WITH FAUNAS AND FLORAS IN THE TYPE MARINE DEVONIAN OF THE ARDENNE-RHENISH REGIONS

MAURICE STREEL[1], KENNETH HIGGS[2], STANISLAS LOBOZIAK[3], WALTER RIEGEL[4] AND PHILIPPE STEEMANS[1]

[1]*Department of Paleobotany and Paleopalynology, University of Liège (Belgium)*
[2]*Department of Geology, University College of Cork (Ireland)*
[3]*Department of Paleobotany and Stratigraphy, Greco 7 C.N.R.S., University of Lille (France)*
[4]*Department of Paleontology, University of Göttingen (Federal Republic of Germany)*

(Received October 8, 1986)

Abstract

Streel, M., Higgs, K., Loboziak, S., Riegel, W. and Steemans, P., 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. Rev. Palaeobot. Palynol., 50: 211–229.

A spore zonation scheme comprising fifty-one zones is proposed for the marine Devonian strata of the Ardenne-Rhenish regions of Western Europe. The zonation comprises a series of Oppel and interval-type zones and these are closely intercalibrated with the associated marine faunal zonations to give a seventy-five level scale of correlation for the Devonian succession. The spore zonation provides stratigraphical dating of the Devonian megafloras of the region, particularly those from the Lower and Middle Devonian. The proposed spore zonation is closely compared with that erected for the Devonian of the Old Red Sandstone Continent.

Introduction

It is more than twenty-five years since Leclercq (1960) described the first Devonian spore assemblage (of Givetian age) from Belgium. Since then about eighty papers have been published on Devonian spores from the Ardenne-Rhenish regions (see Streel, 1986b for citation and comments). The present paper offers a unified scheme for the diverse spore zonations described or initiated in these contributions. It also emphasizes the relationships with some of the typical reference sections of stages or substages as well as with various faunal zonations and megafloral assemblages in the Devonian stratigraphy of the Ardenne-Rhenish regions.

Zonal concept

The spore zonation scheme described in this paper is composed of a series of both Oppel and interval zones. We use these zones in the following sense: "The Oppel Zone may be defined as a zone characterized by an association or aggregation of selected taxons of restricted and largely concurrent range, chosen as indicative of approximate contemporaneity" ... "The Oppel Zone is difficult to define empirically because judgment may vary as to how many and which of the selected diagnostic taxons need be present to identify the zone" ... "Boundaries of adjacent Oppel Zones must often be placed within transition intervals, and different workers might well choose different

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positions" (Hedberg, 1976, p.58). "The interval-zone is an interval between two distinctive biostratigraphic horizons" ... "The base of such a zone might be marked by the horizon of first appearance of taxon-a or the last appearance of taxon-b, and the top might be marked by the horizon of first appearance of taxon-c or the last appearance of taxon-d" (Hedberg, 1976, p.60).

Although both types of zone are used in the proposed zonation scheme we have purposefully avoided mixing them, and they are always shown in separate columns in the accompanying figures. This zonal concept differs somewhat to that recently adopted by Richardson and McGregor (1986) in their spore zonation of Devonian Old Red Sandstone Continent. These authors described assemblage zones in which each zone was defined by a combination of different criteria. These are, the co-occurrence of characteristic taxa, first appearance of selected species and appearance of selected morphological features. This type of assemblage zone appears to mix true Oppel and interval zones. Nevertheless Richardson and McGregor (1986) considered that assemblage zones of this type provide the most comprehensive basis for correlation on a global scale. It maybe desirable for reference samples (Loboziak and Streel, 1981), where all the characteristic features of the assemblage zone are present, be designated as well as reference sections for the base of each zone.

We consider establishing a zonation is essentially a step by step process and it is important that the connotations of the zones erected at any given time should reflect these steps. Loboziak and Streel (1981) have used the "phase concept" of Van der Zwan (1980) as an assemblage zone not yet controlled by application in other localities and which therefore might just have a local significance. Loboziak and Streel (1980, 1981, 1986), Loboziak et al. (1983), present Roman ciphers to provisionally name zones where sampling is insufficient due to a strong sediment condensation or gaps. Steemans (1987) used greek letters for both the same reasons in subdividing his interval zones.

Spore zonation and correlation with faunal zones

Introduction

The following section describes the details of the spore zonation proposed for the relatively small area of marine Devonian in the Ardenne-Rhenish regions. The spore zones are discussed and compared with the inter-regional assemblage zones recently published by Richardson and McGregor (1986) for the Devonian Old Red Sandstone Continent. This section also attempts to accurately correlate the spore zones of the Ardenne-Rhenish regions with associated marine faunal and megafloral assemblages. In most cases these have all been recorded from the same section but where not, lateral correlation has been controlled by sedimentological and (Thorez et al., 1977) or (Steemans, 1986) biostratigraphical data. Controls of this type are essential when one attempts to evaluate the relationship between spore and faunal zones, both on a regional and inter-regional basis.

Comparison of biozones erected in different groups of fossils are often made by aligning biostratigraphical columns in a single chart. This however does not show where the correlations are proved and where they are only assumed. We prefer instead a system of intercalibration of zones (see also Streel, 1986a).

Such a system (see also the micropaleontological guide-marks in Bouckaert and Streel, 1974 and Streel, 1986a) has many obvious advantages. For instance, on Fig.10, the intercalibrated levels 63 and 64 between 62 and 65 mean that the bases of interval-zones *Fle.* and *Var.* are not to be correlated with the conodont *postera* zone only but anywhere between the lower *trachytera* and the lower *expansa* zones.

These intercalibrated level numbers are only used for regional correlation. For instance, the reader will note, comparing Figs.3 and 4, that these numbers have a different significance in Brittany and in the Ardenne regions. For practical reasons in this paper we have used a continuous series of numbers, from the base

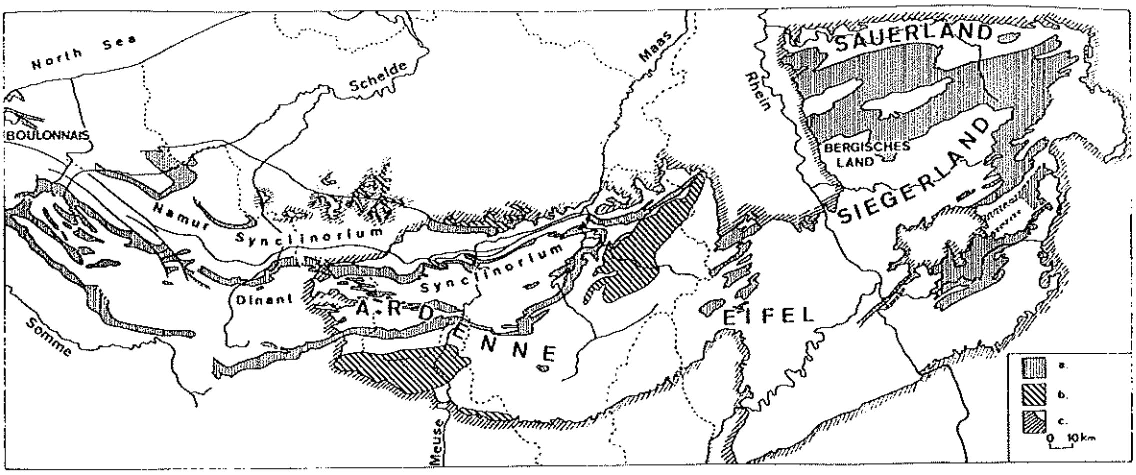

Fig.1. Map of the Ardenne-Rhenish Devonian, outcropping in Belgium and Germany and below the Mesozoic cover in northern France, after Lecompte (1967). *a* = Middle Devonian and Frasnian with limy, often reefal, facies. *b* = Cambrian to Silurian. *c* = post-Paleozoic cover.

to the top of the Devonian System in the Ardenne-Rhenish regions.

This system of intercalibration of the faunal data allows comprehensive control and correlation of the Devonian spore zones right across the Ardenne-Rhenish regions.

Zonation scheme

The spore zonation is described below and is illustrated and correlated with the faunal zones on Figs.2–12. Note that the assemblage zones referred to in the text are those published by Richardson and McGregor (1986).

Lochkovian–early Emsian

Most of the detailed Lower Devonian spore zonation in the Ardenne (Fig.2) is described by Steemans (1987). The Oppel Zones MN and BZ are similar in name and characteristics to the *micrornatus–newportensis* and *breconensis–zavallatus* Assemblages Zones. The Oppel Zone PoW (*Verrucosisporites polygonalis–Dibolisporites wetteldorfensis*) has the same stratigraphic range as the *polygonalis–emsiensis* Assemblage Zone but a somewhat different character. The Oppel Zone AB (*Emphanisporites annulatus–Brochotriletes bellatulus*) corresponds only to the lowermost part of the *annulatus–sextantii* Assemblage Zone (See Fig.13). The associated interval zones are all defined by the first occurrence of one single taxon. Some might well be phylogenically related (Lineage zones, see Fig.2).

The base of the Ardennan Gedinnian Stage in the type region has been demonstrated by Steemans (1987) to be diachronous, ranging from the Interval Zone N_α (locality Willerzie) to the Interval Zone R (locality Lahonry) (Figs.3 and 4) and transgressing on Cambro-Ordovician rocks from southeast to northwest. He has also demonstrated that, in Brittany, the base of the Interval Zone R is higher than the base of the Chitinozoa Zone 27 (Paris, 1981) which in turn occurs in the Lochkovian Stage in Bohemia (Fig.3). Obviously, the basal layers of the Gedinnian at Lahonry (30 km west of Gedinne) do not reach the base of the Lochkovian which is also the base of the Devonian System. At Willerzie (6 km west of Gedinne), the Interval Zone N_α (occurring below the Interval Zone R and shown in Brittany to appear in the Lochkovian Chitinozoa Zone 26) was found in the Haybes beds. These beds are not the basal beds of the Gedinnian. Even though the spores demonstrate the diachronism of the Gedinnian base (the Fepin Conglomerate), it is not possible to tell whether it

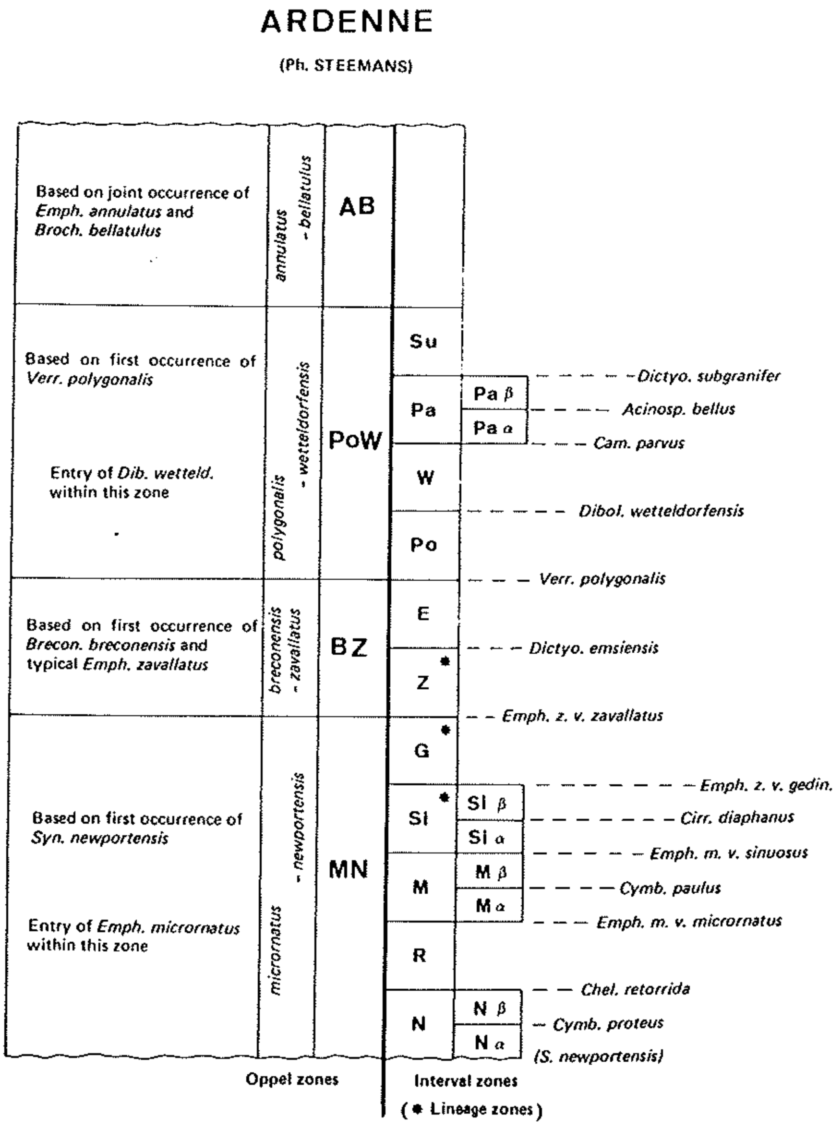

Fig.2. Zonation scheme of the Lochkovian–early Emsian in the Ardenne region after Steemans (1987).

reaches the base of the Devonian in the most southern part of the Ardenne, an uncertainty shared by the conodonts recorded in the same area by Bultynck (1982).

The Gedinnian in the type region is characterized by the succession of the placoderms *Rhinopteraspis crouchi* and *Althaspis leachi* but spore correlations have demonstrated (Steemans, 1987) that these species might well coexist from the Interval Zone Si_β to the succeeding Interval Zone G (lineage zones, Fig.2). The top of the Gedinnian in the type region is certainly within the *Althaspis leachi* Zone. It occurs in the Interval Zone E which can be correlated through Brittany (Fig.3) with the Chitinozoa Zones 31 to 34 (an interval of zones where also occurs the base of the Pragian Stage in Bohemia).

The lower part of the Rhenish Siegenian Stage in the Siegerland does not contain any

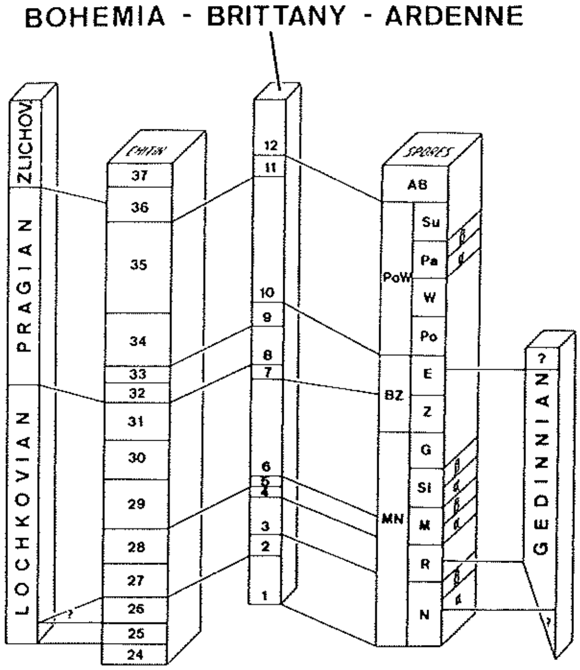

Fig.3. Intercalibration in Brittany of spore zones (Steemans, 1987) and chitinozoa zones (Paris, 1981) of the Lochkovian–early Emsian and correlations between the type Gedinnian Stage in the Ardenne and the type Lochkovian/Pragian/Zlichovian Stages in Bohemia.

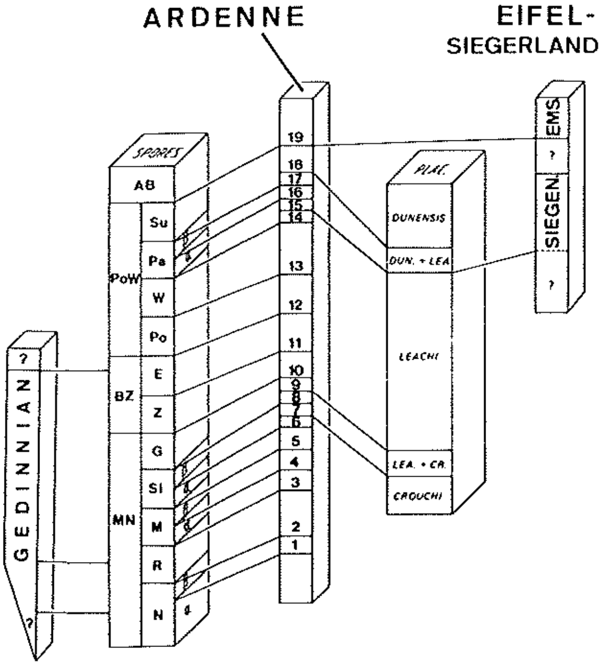

Fig.4. Intercalibration in the Ardennes of spore zones (Steemans, 1987) and placoderms zones (Blieck, 1982) of the Lochkovian–early Emsian and correlations between the type Gedinnian Stage in the Ardenne and the type Siegenian and Emsian Stages in the Siegerland and Eifel.

characteristic fossils. The lowest fossiliferous level occurs there more than 240 m above the base of the lithologically defined Siegenian. It contains the joint occurrence of *Rhinopteraspis dunensis* and the Interval Zone Pa_α (Steemans, 1987)[1]. Thus the biostratigraphic data allows a more precise correlation of the top of the Gedinnian in Belgium with the base of the Pragian in Bohemia than with the base of the Siegenian in the Siegerland. It is therefore recommended to follow without any delay the Subcommission on Devonian Stratigraphy in its use of Lochkovian, Pragian and Emsian as the international standard stage nomenclature for the Lower Devonian. There is as yet no agreement on the position of the base of the Emsian in the Eifel region (F.R.G.). According to Solle (1950), the limit is at the base of the Beinhausen Formation. Brachiopod evidence allows correlation of this base within the Pesche Formation in the Belgian Ardenne (Godefroid and Stainier, 1982). According to Mittmeyer (1973), the limit is at the base of the underlying Ulmen Group, and brachiopod evidence in Godefroid and Stainier (1982), place it somewhere near the contact of the Ville and Laroche Formations in the Ardenne. There is no spore record between these two limits either in Germany or in Belgium (Fig.4). The base of the Oppel Zone AB occurs at the higher limit in both regions (Riegel and Karathanasopoulos, 1982; Steemans, 1987), and it occurs within the Odenspiel Formation in the Siegerland (Steemans, 1987).

Late Emsian–early Givetian

A late Emsian, Eifelian and basal Givetian detailed spore zonation (Fig.5) has been pro-

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[1] *Althaspis leachi* is known (Steemans, 1987) in two localities of Belgium (Fraipont and Wihéries) as high in the "Siegenian" as the Interval Zone Su.

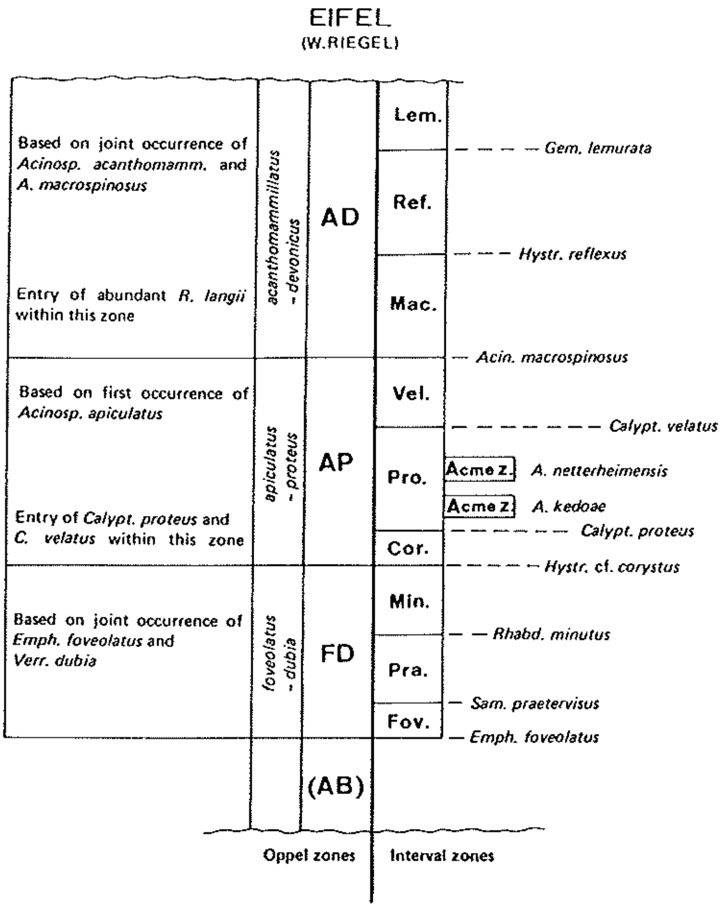

Fig.5. Modified zonation scheme of the late Emsian–early Givetian in the Eifel region after Riegel (1975, table 2).

posed, in the Eifel region, in an unpublished thesis by Riegel (1975) and a modified version is used here (Fig.5). The range of selected species was published by Riegel (1982).

The Oppel Zone FD (*Emphanisporites foveolatus–Verruciretusispora dubia*) is characterized by the joint first occurrence of *Emphanisporites foveolatus* and *Verruciretusispora dubia* together with the persistance of *Emphanisporites annulatus* and *Calyptosporites biornatus*. It corresponds to most of the *annulatus–sextantii* Assemblage Zone (Fig.13).

The Oppel Zone AP (*Acinosporites apiculatus–Calyptosporites proteus*) is characterized by the first occurrence of *Acinosporites apiculatus* and several species of *Hystricosporites, Ancyrospora, Calyptosporites, Spinozonotriletes, Samarisporites and Perotrilites.* It corresponds to the *douglastownense–eurypterota* Assemblage Zone and to the lower part of the *velatus–langii* Assemblage Zone (Fig.13).

The Oppel Zone AD (*Acinosporites acanthomammillatus–Densosporites devonicus*) is characterized by the first occurrence of *Acinosporites acanthomammillatus, A. macrospinosus, Rhabdosporites langii* and *Densosporites devonicus.* It corresponds to the upper part of the *velatus–langii* Assemblage Zone, the *devonicus–naumovii* Assemblage Zone and the lower part of the *lemurata–magnificus* Assemblage Zone (Fig.13).

The nine associated interval zones are

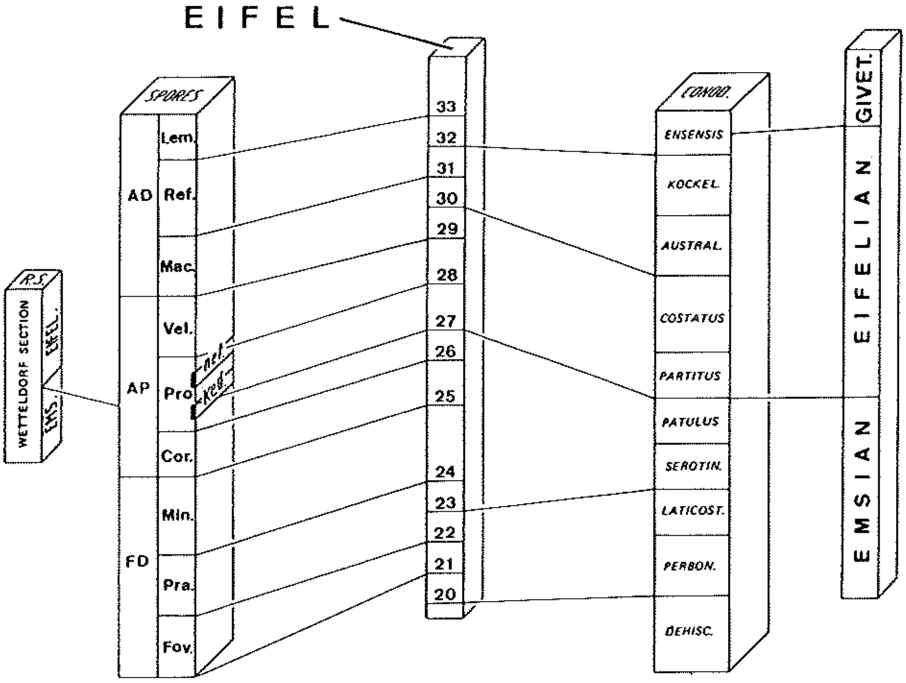

Fig.6. Intercalibration in the Eifel of spore zones (Riegel, 1975) and conodont zones (Weddige, 1977) of the late Emsian–early Givetian and correlations with the type Eifelian Stage. *R.S.* = reference section.

defined by the successive entries of *Emphanisporites foveolatus, Samarisporites praetervisus, Rhabdosporites minutus* (small *Rhabdosporites* species in Riegel, 1982), *Hystricosporites* cf. *corystus, Calyptosporites proteus, Calyptosporites velatus, Acinosporites macrospinosus, Hystricosporites reflexus* (*Hystricosporites* with proximal radial ribs) and *Geminospora lemurata.* Two Acme Zones (*Ancyrospora kedoae* and *A. nettersheimensis*) are recorded within the Interval Zone *Pro.* (*Calyptosporites proteus*).

The base of the Eifelian Stage (Heisdorf/Lauch Formation limit in the type Wetteldorf section) (Fig.6) is also within this Interval Zone *Pro*, at the top of the *Ancyrospora kedoae* Acme Zone.

The faunal data (mostly brachiopods and conodonts) are rather abundant in the Eifel Region but they have not been documented in all of the spore bearing sections and lateral lithostratigraphical correlations are needed. Therefore, intercalibration of data (Fig.6) are kept to a minimum. So far, there is no internationally accepted position for the base of the Givetian. The base of the Givet Limestone in the type area of the Ardenne is probably within the higher part of the conodont *ensensis* Zone and may be close to the base of the *varcus* Zone (Bultynck, 1985). This does not quite correspond to the modern German authors' base of this stage, which is drawn between the Ahbach beds and the Loogh beds in the middle part of the *ensensis* Zone (Ziegler, 1979).

Spores are not known in the type Givetian of the Ardenne due to adverse sedimentary conditions. They are well known in the Boulonnais area (Northern France) from the middle–upper *varcus* Zone upwards (Loboziak and Streel, 1987). *Geminospora lemurata*[1] (and *Verrucosi-*

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[1] *Geminospora antaxios* (Chibrikova) Owens in Riegel (1982) is believed now to belong to the enlarge concept of *Geminospora lemurata* Balme emend. Playford 1983.

sporites cf. *uncatus*) first occurs in the Eifel region within the *ensensis* Zone but it is not yet known for certain on which side of the Eifelian/Givetian boundary. However, in the Boulonnais area *Geminospora lemurata* first appears in the overlying Oppel Zone TA which is within the upper *varcus* Zone (Loboziak and Streel, 1987).

Middle Givetian–early Famennian

A Givetian, Frasnian and basal Famennian detailed spore zonation (Fig.7) has been proposed by Loboziak and Streel (1980, 1981, 1987), and Loboziak et al. (1983) in the Boulonnais area of Northern France.

As all the Oppel zones described below have

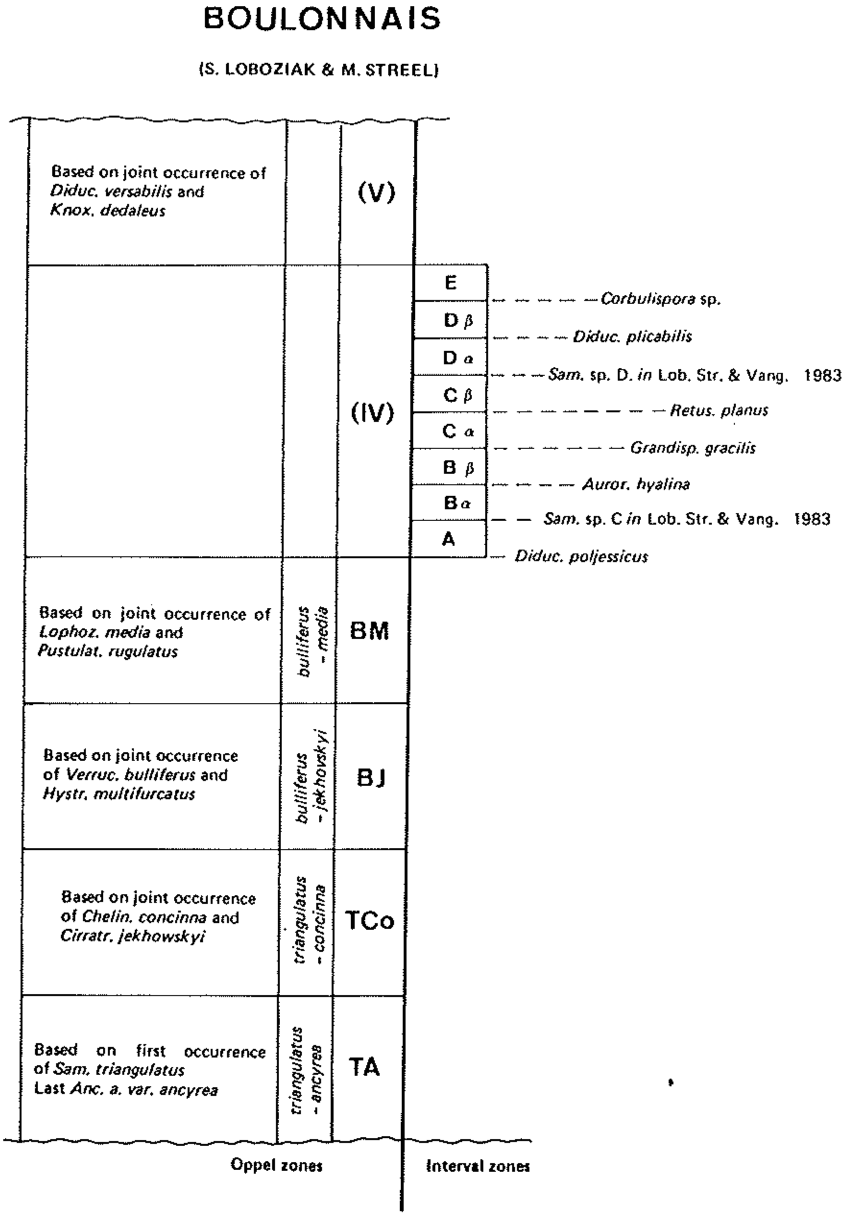

Fig.7. Zonation scheme of the middle Givetian–early Famennian in the Boulonnais region after Loboziak and Streel (1980, 1981) and Loboziak et al. (1983).

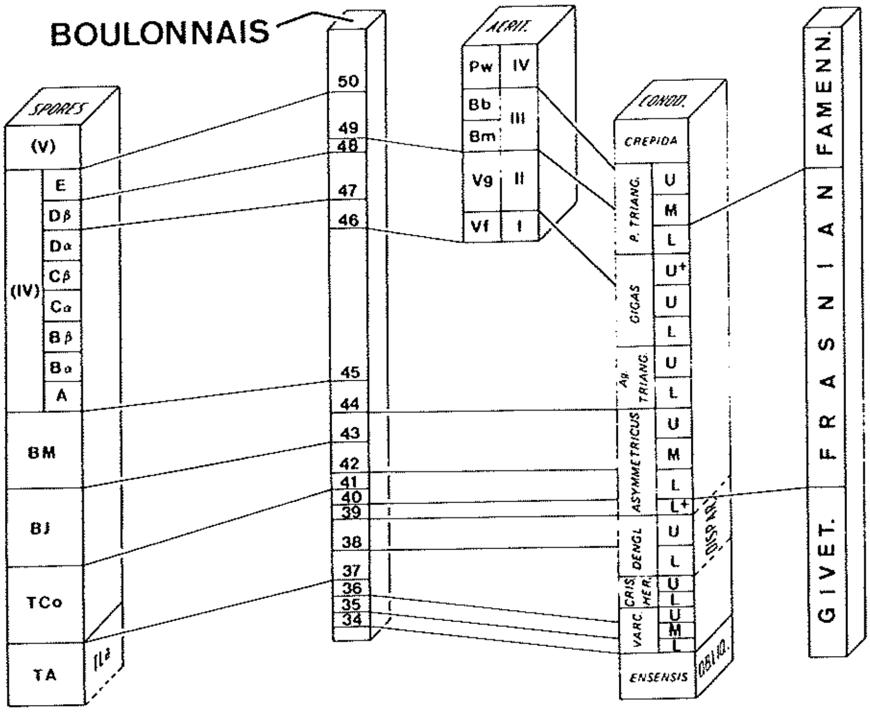

Fig.8. Intercalibration in the Boulonnais of spore zones (see legend of Fig.7), conodont zones (Brice et al., 1979, 1981) and acritarch zones (Loboziak et al., 1983; Martin, 1985; and Vanguestaine, 1986) of the middle Givetian–early Famennian and correlations with the type Frasnian and Famennian Stages in the Ardenne.

not yet been used for regional correlation, they all have the status of "Phase" (see zonal concept).

The lowermost part of the TLa *phase* (with *Grandispora douglastownense* and *Rhabdosporites langii*) reflected by the sample G.02 and "dated" by the *ensensis* Zone at the base of the Blacourt Formation is now better attributed to the preceeding Oppel Zone AD. We now consider the single specimen of *Samarisporites triangulatus* found in this level and illustrated by Loboziak and Streel (1980, pl.II. fig.11)[1] as an atypical specimen without really prominent development of the zona in the radial regions. Consequently this specimen is here transferred to *Samarisporites* sp.

The upper part of the previous TLa phase does not contain *Rhabdosporites langii* and is therefore here renamed Oppel Zone TA (*Samarisporites triangulatus–Ancyrospora ancyrea* var. *ancyrea*). The age of the base of this new zone is unknown but probably occurs in or below the middle *varcus* Zone (new interpretation of fauna IV in Loboziak and Streel, 1980, fig.1; P. Bultynck, pers. comm., 1986). The Oppel Zone TCo (*Samarisporites triangulatus–Chelinospora concinna*) which also contains *Samarisporites triangulatus* is based on the joint occurrence of *Chelinospora concinna* and *Cirratriradites jekhowskyi*. It ranges from the upper *varcus* Zone (new interpretation of fauna V in Loboziak and Streel, 1980, fig.1; P. Bultynck, pers. comm., 1986) to the lower *asymmetricus* Zone (Fig.8). It spans the base of the Frasnian Stage as defined at the base of the lower *asymmetricus* Zone (Ziegler and Klapper, 1983). Whether it corresponds to all

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[1] In Loboziak and Streel (1980, legend of pl.II, fig.11) should read : "level A" instead of "level H".

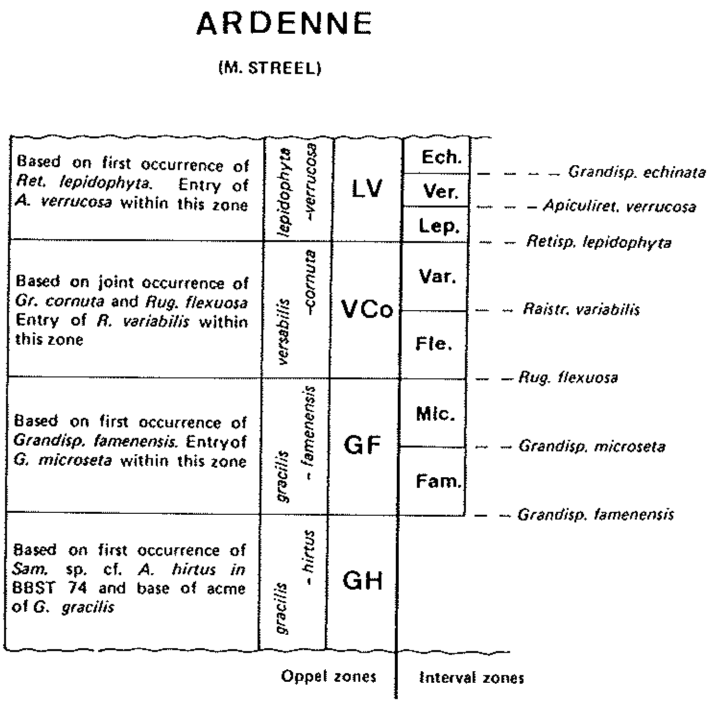
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Fig.9. Zonation scheme of the middle to late Famennian in the Ardenne region after Bouckaert et al., 1968; Becker et al., 1974; Paproth and Streel, 1971; and Paproth et al., 1983.

or only to the upper part of the *optivus–triangulatus* Assemblage Zone is not yet clear. The Oppel Zones BJ (*Verrucosisporites bulliferus*[1]*–Cirratriradites jekhowskyi*) and BM (*Verrucosisporites bulliferus–Lophozonotriletes media*) range (Fig.8) from the lower *asymmetricus* Zone to at least the *Ancyrognathus triangularis* Zone (See Brice et al., 1981).

Succeeding zones IV and V are not yet named (see zonal concept). The Interval Zones IV B, C and D are here subdivided (α, β) to mark the succession of important "Famennian" species in the upper part of the Hydrequent Formation.

The Oppel Zones BJ, BM and zones IV and V correspond to the *ovalis–bulliferus* and part of the *torquata–gracilis* Assemblage Zones. The limit between these assemblage zones is poorly defined. Among the characteristics of the *torquata–gracilis* Assemblage Zone given by Richardson and McGregor (1986, pp.20–21), we have noted the following sequence of occurrences in the Boulonnais[2]: *Diducites poljessicus* (base of IV A), *Auroraspora macra* (base of IV B_α), *A. hyalina* (base of IV B_β), *Grandispora gracilis* (base of IV C_α), *Diducites versabilis* and *Knoxisporites dedaleus* (base of V). Conodonts are not available at these levels in the Boulonnais but we have attempted to provide stratigraphic control by comparing (Fig.8) the acritarchs with those "dated" by conodonts in the type region of the Ardenne (Loboziak et al., 1983; Vanguestaine, 1986). The conclusions are that Zones IV D_β and IV E range from the upper *gigas* to the upper *Palmatolepis triangularis* Zone and contain the base of the Famennian Stage as defined at the base of the middle

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[1] *V. bulliferus* is a new name for *V. bullatus* (Richardson and McGregor, 1986, p.18).

[2] *Hystricosporites multifurcatus*, we accept the same concept as stated by Richardson and McGregor (1986, p.21), occurs at the base of the Oppel Zone BJ in the Boulonnais.

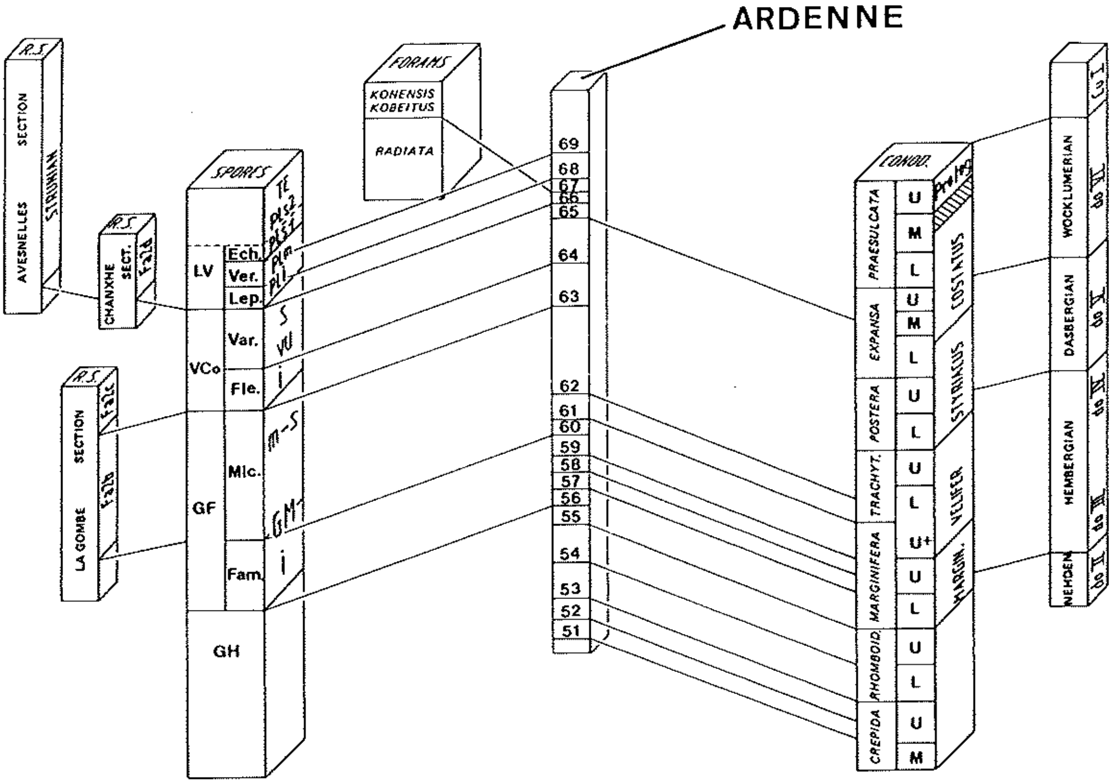


Fig.10. Intercalibration (Streel, 1986a) in the Ardennes of spore zones (see legend of Fig.9), conodont zones (Dreesen et al., 1986) and foraminifer zones (Paproth et al., 1983) of the middle to late Famennian and correlations between the type Belgian Famennian chronozones (Fa2b, Fa2c, Fa2d) in their reference sections (*R.S.*) and the type German Substages.

P. triangularis Zone (Ziegler and Klapper, 1983). Zone IV should cover a rather long timespan, corresponding for instance, with six spore-zones on the Russian Platform (Raskatova, 1974; Loboziak and Streel, 1987, fig.2). Notably the Lower Famennian spore zonation is also poorly defined in the Ardenne-Rhine regions.

Middle to latest Famennian

In the type area of the Ardenne, due to adverse sedimentary conditions, spores do not provide lateral correlations until the base of the middle Famennian (Becker et al., 1974, p.23).

The base of the Oppel Zones GH in the Lower Famennian is not known.

The former Zone GM is here renamed Oppel Zone GF (*Grandispora gracilis–G. famenensis*). The succeeding zones (Fig.9) have been renamed in Paproth et al. (1983).

Grandispora famenensis, with distinct coarse mamillate ornament, occurring in the conodont *marginifera* Zone, initiates a succession of typical spinose cavate forms (*G. microseta*, *G. cornuta*, *G. echinata*, see Becker et al., 1974, fig.12). With other species (Fig.9) they allow definition of seven interval zones which are proposed here to replace the old subdivisions of lower (i), middle (m) and upper (s) subzones (Fig.10).

The base of the Oppel Zone VCo (*Rugospora versabilis–Grandispora cornuta*) is characterized by the joint first occurrence of *Grandispora cornuta*, *Rugospora flexuosa* and *Retusotriletes phillipsii*, it also marks the base of the chrono-

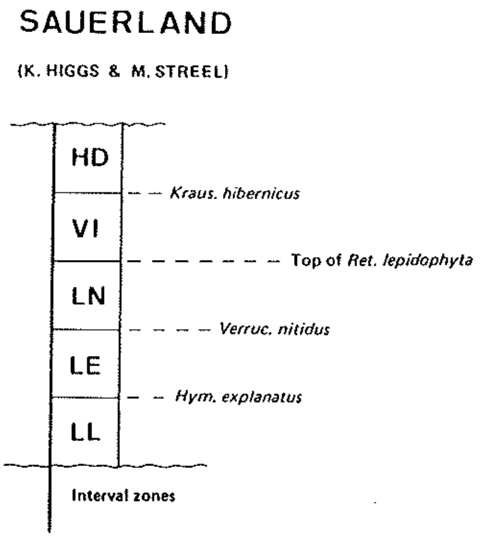


Fig.11. Zonation scheme of the latest Famennian and early Tournaisian in the Sauerland region after Higgs and Streel (1984).

zone Fa2c "dated" by the conodont *trachytera* to *ex-pansa* Zones (see Introduction). The *flexuosa–cornuta* Assemblage Zone is a new name for the Oppel Zone VCo, however it possesses the same characteristics and the same stratigraphical range.

The base of the Oppel Zone LV (*Retispora lepidophyta–Apiculiretusispora verrucosa*) marks the base of the chronozone Fa2d and occurs near the limit between the conodont middle and upper *expansa* Zones. *Protognathodus meischneri* which is found near the base of the Oppel Zone LV in the Yves-Gomezée road section in Belgium (Dreesen et al., 1976) is considered by Sandberg (1979) as an indicator for the base of the "old" conodont middle *costatus* Zone. The base of the Fa2d (which is also the base of the "Strunian stage" sensu Conil and Lys, 1980) is thus a lateral equivalent of the base of the Wocklumerian Substage of the German nomenclature (Fig.10).

A major lithological change occurs at the boundary between the Etroeungt Formation and the Hastière Formation in the Dinant Synclinorium (Fig.1) and also between the Wocklumer Limestone and the Hangenberg Shales in the Sauerland (the Devonian/Carboniferous event of Walliser, 1984). Clastic terrigeneous miospore-bearing facies only occur below the contact in the Ardennes and practically only above the contact in the Sauerland. Nowhere in Western Europe, the two zonal schemes which have resulted of their study, have been identified in a single rock sequence.

The spore zonation, displayed near the

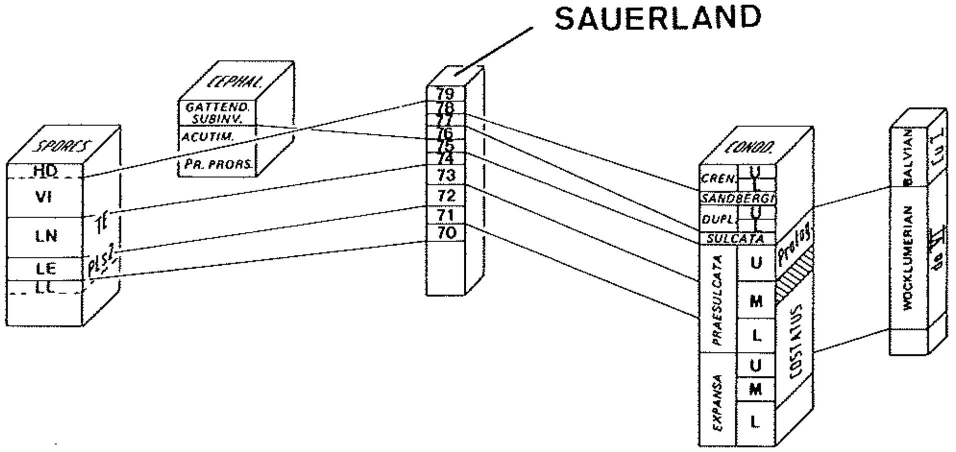


Fig.12. Intercalibration (Higgs and Streel, 1984; Streel, 1986a) in the Sauerland of spore zones, conodont zones and cephalopod zones of the latest Famennian and early Tournaisian and correlations with the type German Substages.

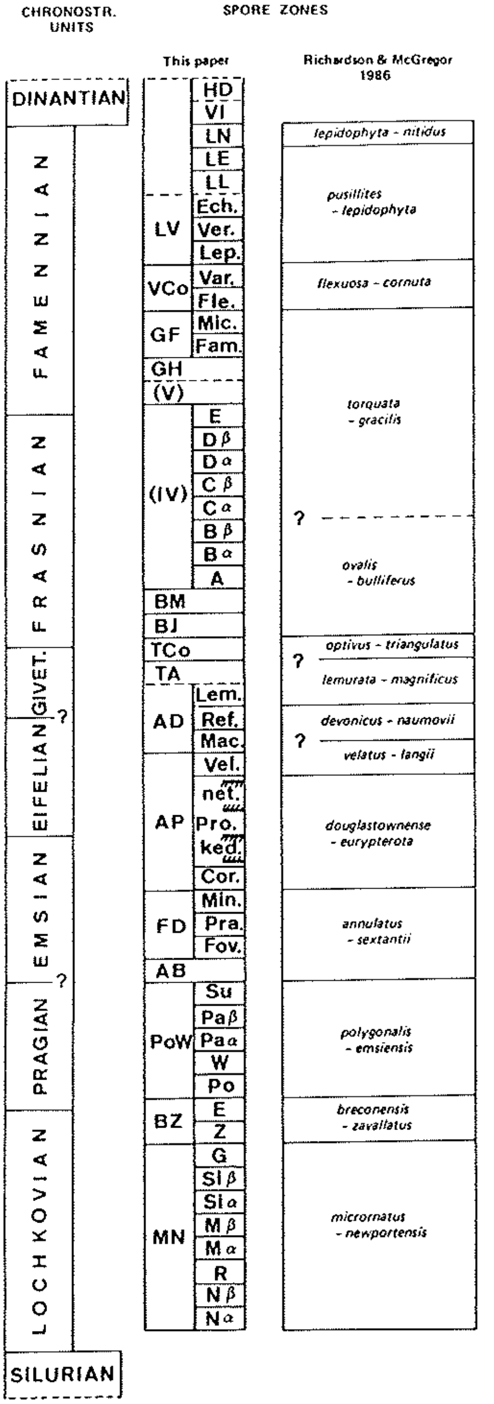
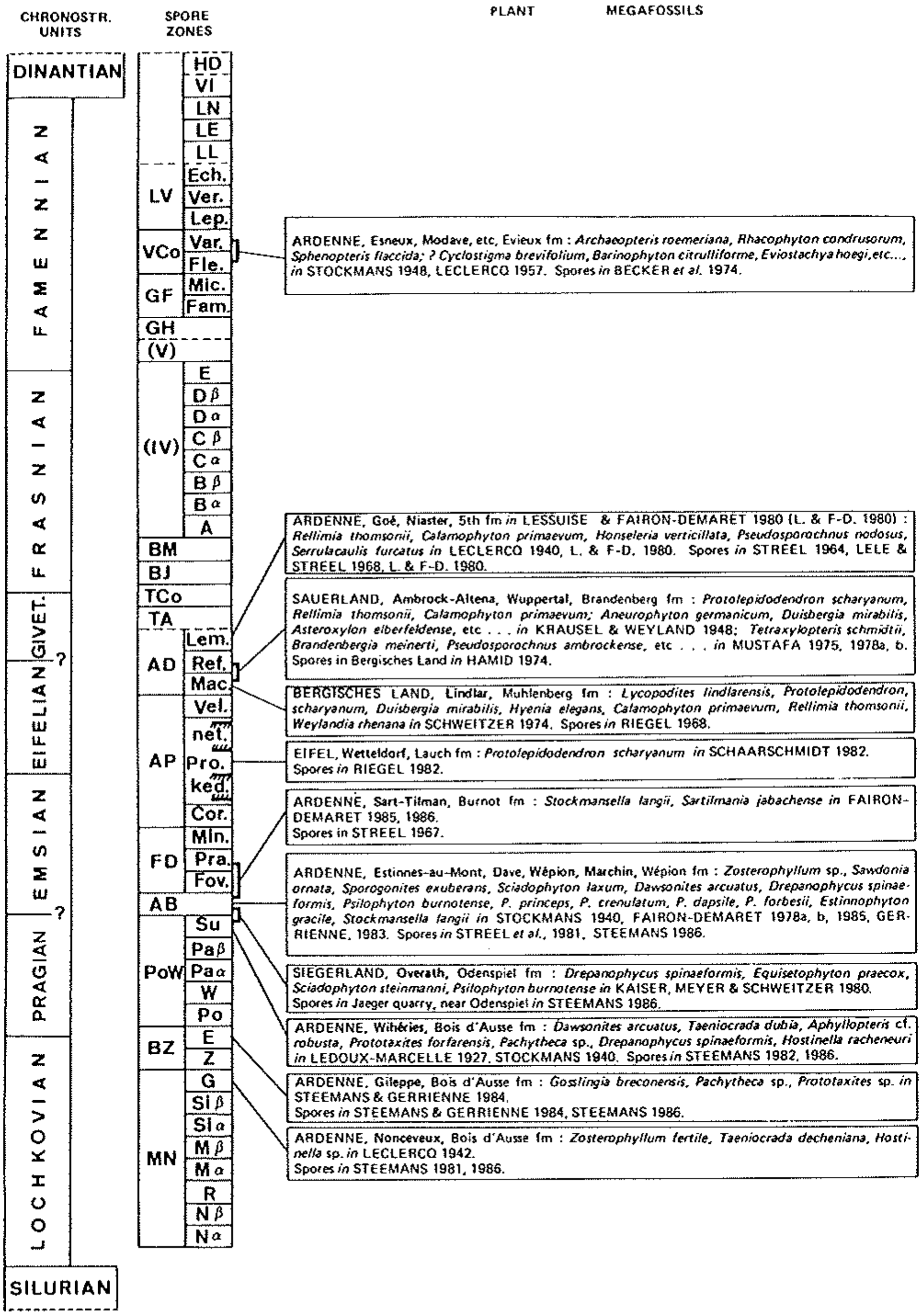


Fig.13. Comparison of spore zones in Richardson and McGregor (1986) and the present paper.

Devonian/Carboniferous boundary has been established in Ireland and Britain and recently up-dated by Higgs et al. (1986). The zonation is composed of several interval zones defined by the successive first occurrence of *Hymenozonotriletes explanatus*, *Verrucosisporites nitidus* and *Krauselisporites hibernicus* and by the last occurrence of *Retispora lepidophyta*. Higgs and Streel (1984) have applied this zonation in the Sauerland where the faunal control is much better that in the British Isles (Figs.11 and 12). The base of the Interval Zone LL (*lepidophyta–literatus*) is not known and might be (partly?) equivalent to the last Interval Zone *Ech* of the Ardenne. The Interval Zones LE and LN range from the conodont lower to upper *praesulcata* zones. The Devonian/Carboniferous boundary is characterized by the first entry of *Siphonodella sulcata* and is located at or near the base of the Interval Zone VI.

Relation of plant megafossils with the spore zonation

Devonian plant megafossils are known from many localities in the Ardenne-Rhenish region and it is beyond the scope of this paper to make a survey of these contributions. Only a few of these have also been studied by palynological methods. The most important ones are listed on Fig.14 where their ages are also given through the spore zones. Lower and Middle Devonian megafloras are rather well documented. However, Frasnian and Lower Famennian megafloras are poorly known in these regions. New palynological studies of these plant localities (many known since a century ago) may prove very fruitful, particularly in the Lower Devonian where the megaflora is richer than expected, reflecting an explosive development of land plants. An accurate dating of these megaflora by palynology will certainly help to improve biostratigraphy as well as our evolutionary concepts on early vascular plant development.



ARDENNE, Esneux, Modave, etc, Evieux fm : *Archaeopteris roemeriana, Rhacophyton condrusorum, Sphenopteris flaccida; ? Cyclostigma brevifolium, Barinophyton citrulliforme, Eviostachya hoegi*, etc..., *in* STOCKMANS 1948, LECLERCQ 1957. Spores *in* BECKER *et al.* 1974.

ARDENNE, Goé, Niaster, 5th fm *in* LESSUISE & FAIRON-DEMARET 1980 (L. & F-D. 1980) : *Rellimia thomsonii, Calamophyton primaevum, Honseleria verticillata, Pseudosporochnus nodosus, Serrulacaulis furcatus in* LECLERCQ 1940, L. & F-D. 1980. Spores *in* STREEL 1964, LELE & STREEL 1968, L. & F-D. 1980.

SAUERLAND, Ambrock-Altena, Wuppertal, Brandenberg fm : *Protolepidodendron scharyanum, Rellimia thomsonii, Calamophyton primaevum; Aneurophyton germanicum, Duisbergia mirabilis, Asteroxylon elberfeldense*, etc . . . *in* KRAUSEL & WEYLAND 1948; *Tetraxylopteris schmidtii, Brandenbergia meinerti, Pseudosporochnus ambrockense*, etc . . . *in* MUSTAFA 1975, 1978a, b. Spores in Bergisches Land *in* HAMID 1974.

BERGISCHES LAND, Lindlar, Muhlenberg fm : *Lycopodites lindlarensis, Protolepidodendron, scharyanum, Duisbergia mirabilis, Hyenia elegans, Calamophyton primaevum, Rellimia thomsonii, Weylandia rhenana in* SCHWEITZER 1974. Spores *in* RIEGEL 1968.

EIFEL, Wetteldorf, Lauch fm : *Protolepidodendron scharyanum in* SCHAARSCHMIDT 1982. Spores *in* RIEGEL 1982.

ARDENNE, Sart-Tilman, Burnot fm : *Stockmansella langii, Sartilmania jabachense in* FAIRON-DEMARET 1985, 1986.
Spores in STREEL 1967.

ARDENNE, Estinnes-au-Mont, Dave, Wépion, Marchin, Wépion fm : *Zosterophyllum* sp., *Sawdonia ornata, Sporogonites exuberans, Sciadophyton laxum, Dawsonites arcuatus, Drepanophycus spinaeformis, Psilophyton burnotense, P. princeps, P. crenulatum, P. dapsile, P. forbesii, Estinnophyton gracile, Stockmansella langii in* STOCKMANS 1940, FAIRON-DEMARET 1978a, b, 1985, GERRIENNE, 1983. Spores *in* STREEL *et al.*, 1981, STEEMANS 1986.

SIEGERLAND, Overath, Odenspiel fm : *Drepanophycus spinaeformis, Equisetophyton praecox, Sciadophyton steinmanni, Psilophyton burnotense in* KAISER, MEYER & SCHWEITZER 1980.
Spores *in* Jaeger quarry, near Odenspiel *in* STEEMANS 1986.

ARDENNE, Wihéries, Bois d'Ausse fm : *Dawsonites arcuatus, Taeniocrada dubia, Aphyllopteris* cf. *robusta, Prototaxites forfarensis, Pachytheca* sp., *Drepanophycus spinaeformis, Hostinella racheneuri in* LEDOUX-MARCELLE 1927, STOCKMANS 1940. Spores *in* STEEMANS 1982, 1986.

ARDENNE, Gileppe, Bois d'Ausse fm : *Gosslingia breconensis, Pachytheca* sp., *Prototaxites* sp. *in* STEEMANS & GERRIENNE 1984.
Spores *in* STEEMANS & GERRIENNE 1984, STEEMANS 1986.

ARDENNE, Nonceveux, Bois d'Ausse fm : *Zosterophyllum fertile, Taeniocrada decheniana, Hostinella* sp. *in* LECLERCQ 1942.
Spores *in* STEEMANS 1981, 1986.

Fig.14. Plant megafossil assemblages dated by spores in the Ardenne-Rhenish regions.

Acknowledgements

We are grateful to Colin McGregor, Geological Survey of Canada for stimulating discussions although he has not seen the manuscript of the present paper. M. Fairon-Demaret, Liège, Belgium, is especially thanked for her contribution on the megaflora list on Fig.14. F. Paris, Rennes, France (Chitinozoa), A. Blieck, Lille, France (placoderms), M. Vanguestaine, Liège, Belgium (acritarchs), P. Bultynck, Brussels, Belgium and R. Dreesen, Liège, Belgium (conodonts) are thanked for their significant help in discussing marine floras and faunas.

Appendix — List of given species

Acinosporites acanthomammillatus Richardson, 1965	Fig.5
Acinosporites apiculatus (Streel) Streel, 1967	Fig.5
Acinosporites bellus (Arkhangelskaya) Steemans, 1987	Fig.2, Fig.4: level *16*
Acinosporites macrospinosus Richardson, 1965	Fig.5, Fig.6: level *29*
Ancyrospora ancyrea (Eisenack) Richardson var. *ancyrea* Richardson, 1962	Fig.7
Ancyrospora eurypterota Riegel, 1973	
Ancyrospora kedoae (Riegel) Turnau, 1974	Fig.5, Fig.6: level *27*
Ancyrospora nettersheimensis Riegel, 1973	Fig.5
Apiculiretusispora verrucosa (Caro-Moniez) Streel, 1977	Fig.9, Fig.10: level *68*
Auroraspora hyalina (Naumova) Streel in Becker et al., 1974	Fig.7
Auroraspora macra Sullivan, 1968	
Auroraspora torquata Higgs, 1975	
Breconisporites breconensis Richardson, Streel, Hassan and Steemans, 1982	Fig.2
Brochotriletes bellatulus Steemans, 1987	Fig.2, Fig.4: level *19*
Calyptosporites biornatus (Lanninger) Richardson, 1974	
Calyptosporites proteus (Naumova) Allen, 1965	Fig.5, Fig.6: level *26*
Calyptosporites velatus (Eisenack) Richardson, 1962	Fig.5, Fig.6: level *28*
Camarozonotriletes parvus Owens, 1971	Fig.2, Fig.4: level *14*
Camarozonotriletes sextantii McGregor and Camfield, 1976	
Chelinospora concinna Allen, 1965	Fig.7, Fig.8: level *37*
Chelinospora retorrida Turnau, 1986	Fig.2, Fig.4: level *2*
Cirratriradites diaphanus Steemans, 1987	Fig.2, Fig.4: level *6*
Cirratriradites jekhowskyi Taugourdeau-Lantz, 1967	Fig.7, Fig.8: level *37*
Contagisporites optivus (Chibrikova) Owens var. *optivus* Owens, 1971	
Cymbosporites paulus McGregor and Camfield, 1976	Fig.2, Fig.4: level *4*
Cymbosporites proteus McGregor and Camfield, 1976	Fig.2, Fig.4: level *1*
Densosporites devonicus Richardson, 1960	
Dibolisporites wetteldorfensis Lanninger, 1968	Fig.2, Fig.4: level *13*
Dictyotriletes emsiensis (Allen) McGregor, 1973	Fig.2, Fig.4: level *11*
Dictyotriletes subgranifer McGregor, 1973	Fig.2, Fig.4: level *17*
Diducites plicabilis Van Veen, 1981	Fig.7, Fig.8: level *47*
Diducites poljessicus (Kedo) Van Veen, 1981	Fig.7, Fig.8: level *45*
Diducites versabilis (Kedo) Van Veen, 1981	Fig.7, Fig.8: level *50*
Emphanisporites annulatus McGregor, 1961	Fig.2, Fig.4: level *19*
Emphanisporites foveolatus Schultz, 1968	Fig.5, Fig.6: level *21*
Emphanisporites micrornatus Richardson and Lister, 1969	
Emphanisporites micrornatus Richardson and Lister var. *micrornatus* Steemans and Gerrienne, 1984	Fig.2, Fig.4: level *3*
Emphanisporites micrornatus Richardson and Lister var. *sinuosus* Steemans and Gerrienne, 1984	Fig.2, Fig.4: level *5*
Emphanisporites zavallatus Richardson, Streel, Hassan and Steemans, 1982	
Emphanisporites zavallatus Richardson, Streel, Hassan and Steemans var. *gedinniensis* Steemans and Gerrienne, 1984	Fig.2, Fig.4: level *8*
Emphanisporites zavallatus Richardson, Streel, Hassan and Steemans var. *zavallatus* Steemans and Gerrienne, 1984	Fig.2, Fig.4: level *10*
Geminospora lemurata Balme, emend. Playford, 1983	Fig.5, Fig.6: level *33*

Appendix (*continued*)

Grandispora cornuta Higgs, 1975	Fig.9
Grandispora douglastownense McGregor, 1973	
Grandispora echinata Hacquebard, 1957	Fig.9, Fig.10: level *69*
Grandispora famenensis (Naumova) Streel in Becker et al., 1974	Fig.9, Fig.10: level *56*
Grandispora gracilis (Kedo) Streel in Becker et al., 1974	Fig.7, Fig.9
Grandispora microseta (Kedo) Streel in Becker et al., 1974	Fig.9, Fig.10: level *60*
Grandispora naumovii (Kedo) McGregor, 1973	
Hymenozonotriletes explanatus (Luber) Kedo, 1963	Fig.11, Fig.12: level *70*
Hystricosporites cf. *corystus* Richardson, 1965	Fig.5, Fig.6: level *25*
Hystricosporites multifurcatus (Winslow) Mortimer and Chaloner, 1967	Fig.7, Fig.8: level *41*
Hystricosporites reflexus Owens, 1971	Fig.5, Fig.6: level *31*
Knoxisporites dedaleus (Naumova) Streel, 1977	Fig.7, Fig.8: level *50*
Knoxisporites literatus (Waltz) Playford, 1963	
Krauselisporites hibernicus Higgs, 1975	Fig.11, Fig.12: level *79*
Lophozonotriletes media Taugourdeau-Lantz, 1967	Fig.7, Fig.8: level *43*
Pustulatisporites rugulatus (Taugourdeau-Lantz) Loboziak and Streel, 1981	Fig.7, Fig.8: level *43*
Raistrickia variabilis Dolby and Neves, 1970	Fig.9, Fig.10: level *64*
Retispora lepidophyta (Kedo) Playford, 1976	Fig.9, Fig.10: level *66*, Fig.11, Fig. 12: level *74*
Retusotriletes phillipsii Clendening, Eames and Wood, 1980	
Retusotriletes planus Dolby and Neves, 1970	Fig.7
Rhabdosporites langii (Eisenack) Richardson, 1960	Fig.5
Rhabdosporites minutus Tiwari and Schaarschmidt, 1975	Fig.5, Fig.6: level *24*
Rugospora flexuosa (Jushko) Streel in Becker et al., 1974	Fig.9, Fig.10: level *63*
Samarisporites praetervisus (Naumova) Allen, 1965	Fig.5, Fig.6: level *22*
Samarisporites triangulatus Allen, 1965	Fig.7
Samarisporites sp. cf. *Acanthotriletes hirtus* Naumova 1953 in Becker et al., 1974	Fig.9
Streelispora newportensis (Chaloner and Streel) Richardson and Lister, 1969	Fig.2
Verruciretusispora dubia (Eisenack) Richardson and Rasul, 1978	Fig.5
Verrucosisporites bulliferus Richardson and McGregor, 1986	Fig.7, Fig.8: level *41*
Verrucosisporites nitidus (Naumova) Playford, 1964	Fig.11, Fig.12: level *72*
Verrucosisporites polygonalis Lanninger, 1968	Fig.2, Fig.4: level *12*
Verrucosisporites cf. *uncatus* (Naumova) Richardson, 1965	

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ERRATA

p. 214 : fig. 4 and p. 225 : read Pteraspids instead of Placoderms.

p. 227 : read Gerrienne, P., 1983, instead of Fairon-Demaret, M. and Gerrienne, P., 1983.