



Biometry and paleoenvironment of *Retispora lepidophyta* (Kedo) Playford 1976 and associated miospores in the latest Famennian nearshore marine facies, eastern Ardenne (Belgium)

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Abstract

The size diameter of *Retispora lepidophyta*, a stratigraphically important miospore, is reexamined in greater detail than in previous studies using three sections of the latest Famennian nearshore marine facies of the eastern Ardenne. The evolutionary character of the size reduction with time is confirmed and is used for accurate correlations between the three sections. Cluster analyses (dendrograms) are performed on the percentages of a selection of miospore species from the two most complete sections and show a clear analogy in the lateral distribution of *R. lepidophyta* and *Vallatisporites hystricosus*, a species known elsewhere (West Virginia, USA) to belong to coastal 'downstream' near-swamp plant communities [Streeel and Scheckler, Rev. Palaeobot. Palynol. 64 (1990) 315–324]. By comparison also with the West Virginia data, three *Diducites* species are believed to represent the 'coal' swamp vegetation. A decrease in the proportion of the *Diducites* species from the lower to the upper portion of the studied sections is observed. Using biometric analysis, high resolution correlation between these sections reveals a lateral shift of facies with time during the latest Famennian in the eastern Ardenne. Local synsedimentary block-faulting processes were probably responsible. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: miospore; biometry; paleoenvironment; latest Famennian; eastern Ardenne; block-faulting; Belgium

1. Introduction

The palynostratigraphic correlation of late and latest Famennian sediments is well established (Fig. 1) because many miospore species are shared

by the respective miospore zonation schemes of the Euramerican and Gondwanan paleocontinents. *Retispora lepidophyta* is the most important and characteristic species of the latest Famennian due to its short stratigraphic range, abundance, and very distinctive morphology. Subdivision of the stratigraphic range of *R. lepidophyta* has been used to define three miospore Opper zones in the latest Famennian of western Europe. In ascending order, these are: the *Retispora lepidophyta*–*Knoxisporites literatus* (LL) Zone, the *Retispora lepidophyta*–*Indotriradites explanatus* (LE)

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Stage	Substage	BELGIUM Maziane et al. (1999)	USA Richardson & Ahmed (1988)	CANADA Braman & Hills (1992)	POLAND Turnau (1978)	RUSSIA Avkhimovitch et al. (1988)
FAMENNIAN	UPPERMOST	<i>Retispora lepidophyta</i> - <i>Indotriradites explanatus</i> LE	<i>Retispora lepidophyta</i> - <i>Indotriradites explanatus</i>			LE
		<i>Retispora lepidophyta</i> - <i>Knoxisporites illeceus</i> LL	<i>Retispora lepidophyta</i> - <i>Auroraspora prostata</i>	<i>lepidophyta</i> - <i>pustillites</i> LP <i>lepidophyta</i> <i>triangulatus</i> LT	<i>Tumulispora rarituberculata</i> Ra <i>Grandispora lupata</i> Lu	LMb LL LF
	UPPER	<i>Apiculiretusispora verrucosa</i> - <i>Vallatisporites hystricosus</i> VH	<i>Apiculiretusispora fructicosa</i> - <i>Vallatisporites pustillites</i>			VF
		<i>Diductes versabilis</i> - <i>Grandispora cornuta</i> VCo	<i>phillipsii</i> - cf. <i>V. grandis</i> <i>phillipsii</i> - <i>gradzinskii</i> <i>flexuosus</i> - <i>phillipsii</i> <i>cornuta</i> - <i>flexuosus</i>			

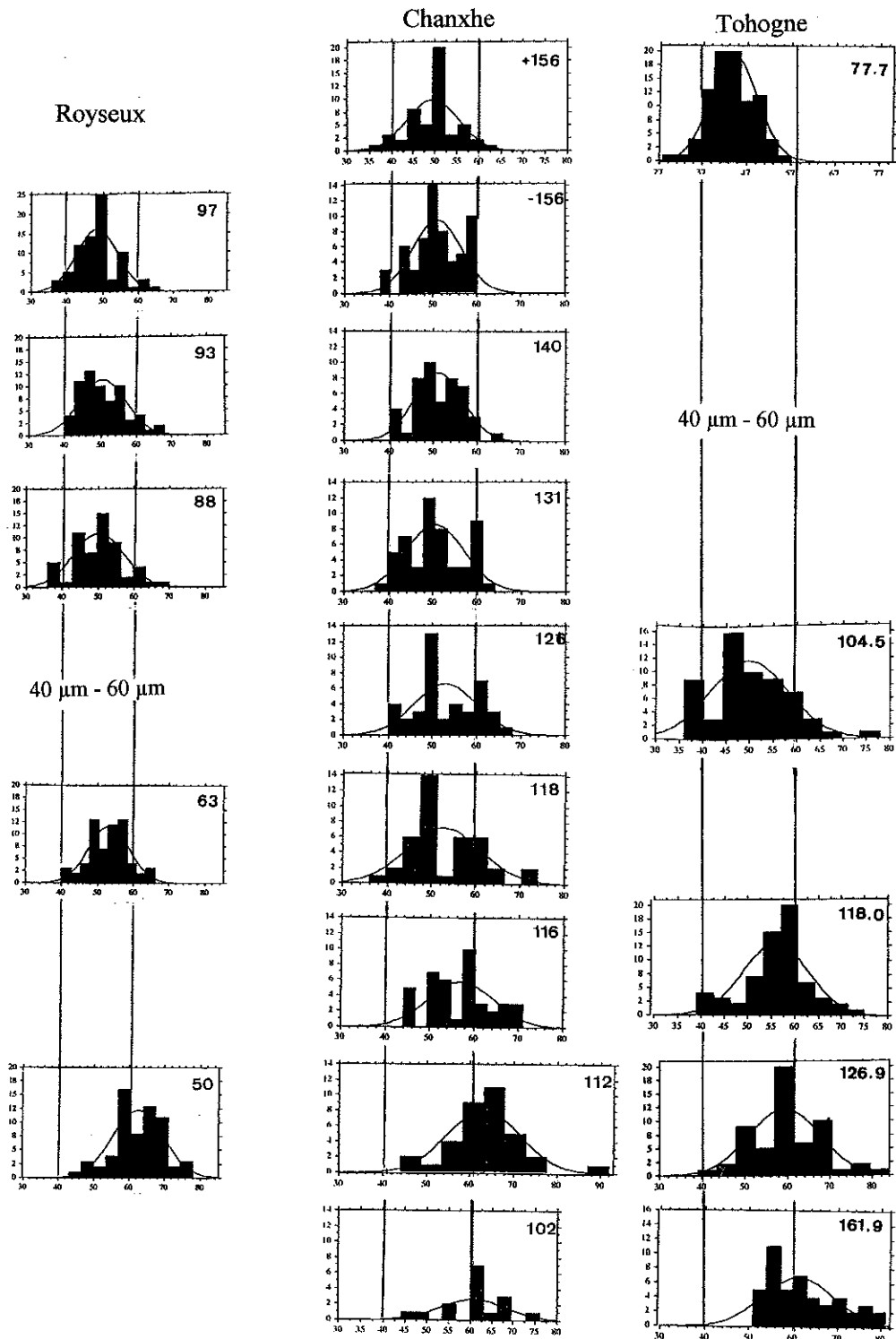
Fig. 1. Main zonation in use in the late and latest Famennian on the Euramerican paleocontinent. The uppermost Substage of the Famennian Stage is defined by the first occurrence of *Retispora lepidophyta* Zones (Turnau, 1978; Avkhimovitch et al., 1988; Richardson and Ahmed, 1988; Braman and Hills, 1992; Maziane et al., 1999).

Zone and the *Retispora lepidophyta*-*Verrucosiporites nitidus* (LN) Zone (Higgs et al., 1988; Maziane et al., 1999). *Retispora lepidophyta* also exhibits some morphological changes with time, such as a progressive reduction in spore diameter size. This feature was first mentioned by Kedo (1957) and was later quantified in a biometric analysis by Strel (1966, 1969) which resulted in the further subdivision of its short stratigraphic range into even four smaller biostratigraphic units (biometric zones C–F). Subsequently, this biostratigraphic tool has been used by various authors: Bouckaert et al. (1971), Dolby (1971), Higgs (1975), Jarvis (1992), Kaiser (1971), Paproth and Strel (1971), Strel (1971), Turnau (1975). However, the number of samples investigated by Strel (1966) to develop his biometric zonation is low. Therefore, a more detailed biometric analysis has

been carried out on 110 samples from three reference sections in the classic latest Famennian of eastern Belgium (Maziane, 1999).

The three sections selected for the present study are from nearshore marine facies. These are: (1) the Chanxhe section (Conil et al., 1964; Strel, 1966); (2) the Royseux section (Strel 1966; Austin et al., 1970); and (3) the Tohogne borehole (Bouckaert and Dusar, 1976; Bouckaert et al., 1978). The Chanxhe section is the most important, because it is the reference section used by Strel (1966, hors-texte 1) in the original biometric study. It is also the most stratigraphically complete section and possesses abundant mudrock levels. The Tohogne borehole also displays a complete late Famennian succession, but cores provided less productive material. The Royseux section is the least satisfactory, in that it has yielded

Fig. 2. Histograms with comparable distribution of size values at the three sections. Royseux bed numbers after Austin et al. (1970); Chanxhe bed numbers after Conil et al. (1964); Tohogne sample depths after Bouckaert and Dusar (1976). Comparable histograms are aligned. See also Fig. 8 for correlation. They demonstrate a normal, generally unimodal distribution and a general trend for the respective populations to change into smaller sizes toward the top of the sections.



the smallest number of productive samples, due to the presence of more limestone beds, and secondly, it does not extend down to the base of the latest Famennian. Two of these eastern Belgian sections display a continuous succession of late to latest Famennian miospore zones ranging from the *Diducites versabilis*–*Grandispora cornuta* (VCo) and *Apiculiretusispora verrucosa*–*Vallatisporites hystricosus* (VH) in which *Retispora lepidophyta* is absent, up into the overlying *Retispora lepidophyta*–*Knoxisporites literatus* (LL) and *Retispora lepidophyta*–*Indotriradites explanatus* (LE) Zones (Maziane et al., 1999). Some of these miospore zones in the studied sections are independently dated by conodonts (Austin et al., 1970; Dreesen, 1993) and foraminifers (Conil et al., 1964; Bouckaert et al., 1978).

The second part of this paper discusses a statistical analysis of the composition of the miospore populations in two of the sections in an attempt to delineate groupings of spore taxa that may be associated with specific paleoenvironments. To achieve this objective, cluster analyses (dendrograms) is carried out on the percentages of 20 selected miospore taxa that frequently occur throughout the sections in order to identify any associations between these species.

Using biometric analysis, high resolution correlation between the sections will finally demonstrate lateral shifts of facies with time during the latest Famennian in the eastern Ardenne. Synsedimentary tectonics could explain these shifts of facies.

2. Biometry of *Retispora lepidophyta* in the eastern Belgian sections

The maximum diameter size of *Retispora lepidophyta* has been measured in all samples containing this species in each section. A few histograms resulting from these counts are shown in Fig. 2, those of Tohogne and Royselux being compared to those of the reference section of Chanxhe. The histograms show that the different populations have an overall normal, unimodal distribution. In addition, there is a general trend for the respective populations to decrease in size toward the top of the sections. This is the way comparison was made by Strel (1966) who selected two histograms in the Chanxhe section as limits C/D and D/E in the C–F biometric zones (Strel, 1969 used interquartile ranges rather than the complete histograms).

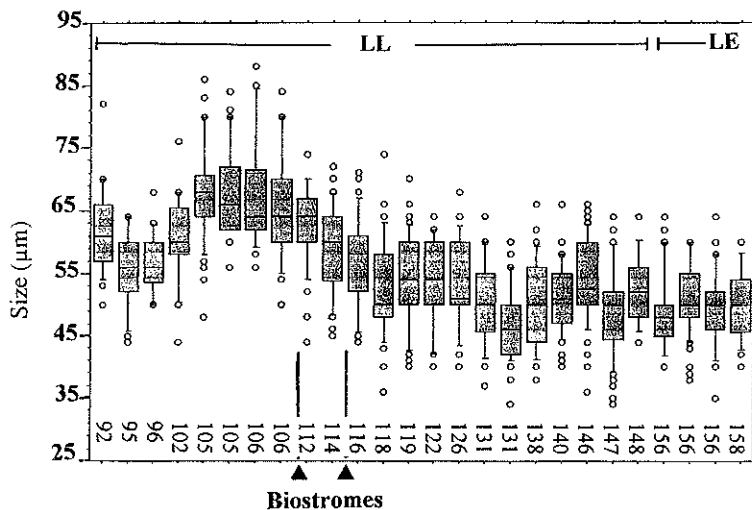


Fig. 3. Evolution of *Retispora lepidophyta* diameter size at Chanxhe section. The general trend for the respective populations to change to smaller sizes toward the top of the sections is studied in 26 samples, using box plots displaying the median, interquartiles, and extreme values.

2.1. Definition of a biometric zonation at Chanxhe

The diameter sizes of a total of 3752 specimens were measured in 68 shale samples. The sizes vary from 28 to 108 μm with a mean size of 54 μm . Most (49 of 68) of the measurements were based on a mean population of about 60 ± 6 specimens per sample. In the lowermost and uppermost parts of the section, the number of miospores available was in some cases low and the measurements of *Retispora lepidophyta* was made only on a few tens of specimens per sample. These levels are indicated in Fig. 4.

The general trend for the respective populations to decrease in size toward the top of the sections is illustrated in more detail using box plots in Fig. 3. Box plots display the median, interquartiles and extreme values for 26 samples, distributed through the section. Two main size groups are recognized: one with a median of 65 μm

(mostly below the biostrome levels), and the other with a median of 50 μm (well above the biostrome levels). The first group corresponds to the typical variety of *Retispora lepidophyta* (*R. lepidophyta* var. *lepidophyta*); the second group corresponds to the variety *minor* (*Retispora lepidophyta* var. *minor* Kedo 1971 in Kedo and Golubcov (1971): diameter size 42–54 μm). Immediately below and above the first group, transitional groups seem to show sharply increasing and decreasing phases of size respectively.

Means and standard deviations of the diameters of *Retispora lepidophyta* populations are shown against the lithological log of the Chanxhe section (Fig. 4). Five biometric zones are arbitrarily delimited from the size data. In ascending stratigraphic order these are:

Zone V: one sample with a mean size of 60 μm ;

Zone W: 13 samples ranging between 50 and 60 μm ;

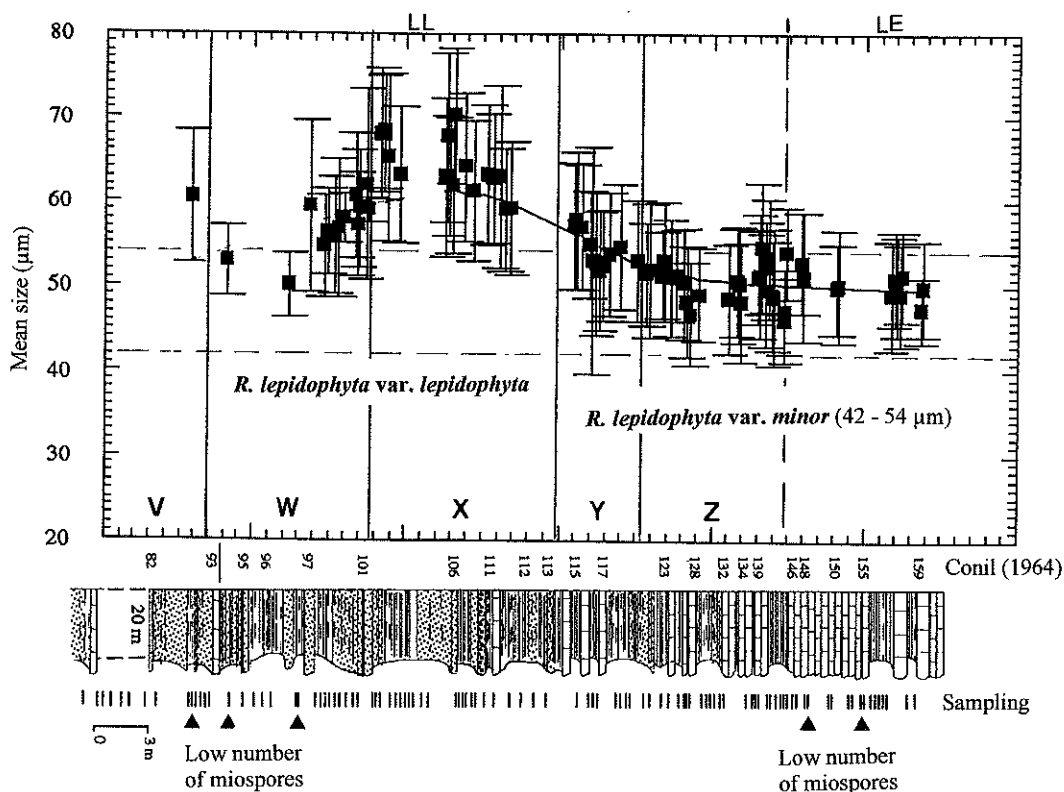


Fig. 4. Mean size and standard deviation of the population of *Retispora lepidophyta* at Chanxhe section. Bed numbers after Conil et al. (1964). Five biometric zones are arbitrarily delimited from the size data.

Zone X: 16 samples slowly decreasing up section from 70 to 59 μm ;

Zone Y: 11 samples sharply decreasing up section from 58 to 52 μm ;

Zone Z: 33 samples slowly decreasing up section and mostly ranging between 52 and 47 μm .

These results can be compared with the original biometric study of Strel (1966, 1969). However, zone V was not recorded and zone W corresponded to a particularly shaly part of the section (containing small *Girvanella* as shown by Conil et al., 1964), from which Strel (1966) had poor sample coverage and therefore obtained only a few specimens of *Retispora lepidophyta*. It appears that zones X and Y would more or less correspond to biometric zones C and D of Strel (1966, hors-texte 2, from Conil's samples 100–129) because they show the largest changes in size range of *R. lepidophyta* (compare the mean size curve in Strel, 1969, fig. 1). Zone Z, with a rather constant or slowly decreasing mean size curve, would more or less correspond to biometric zone E (Strel, 1969, fig. 1). The old and new biometric zonation boundaries do not exactly coincide because those of the new study have been determined using a higher number of samples.

Furthermore, Strel (1966, 1969) also used other morphological criteria in his analysis.

The maximum diameter size of all miospores other than *Retispora lepidophyta* has been measured in most Chanxhe samples (1227 specimens from 41 samples). This procedure was carried out in order to check if the size trends seen in the *R. lepidophyta* populations were also present in the other miospores and could possibly be caused by some sedimentological sorting effects. Fig. 5 illustrates and compares the mean sizes of *R. lepidophyta* with the other miospore populations. In zones V and W, the percentage of *R. lepidophyta* in the total miospore population is rather low (less than 20%) but it is much higher (20–75%) in zones X–Z. In zones V and W, the mean sizes of *R. lepidophyta* fluctuate in parallel with the mean sizes of the other miospores. In these zones, the smaller diameter of all miospores other than *R. lepidophyta* suggests some control, such as a sedimentary sorting (Strel, 1969), on the size distribution of the whole assemblage of miospores from which the biggest specimens of *R. lepidophyta* are eliminated. In contrast, in the overlying biometric zones X–Z, where *R. lepidophyta* is more abundant, the size populations do not fol-

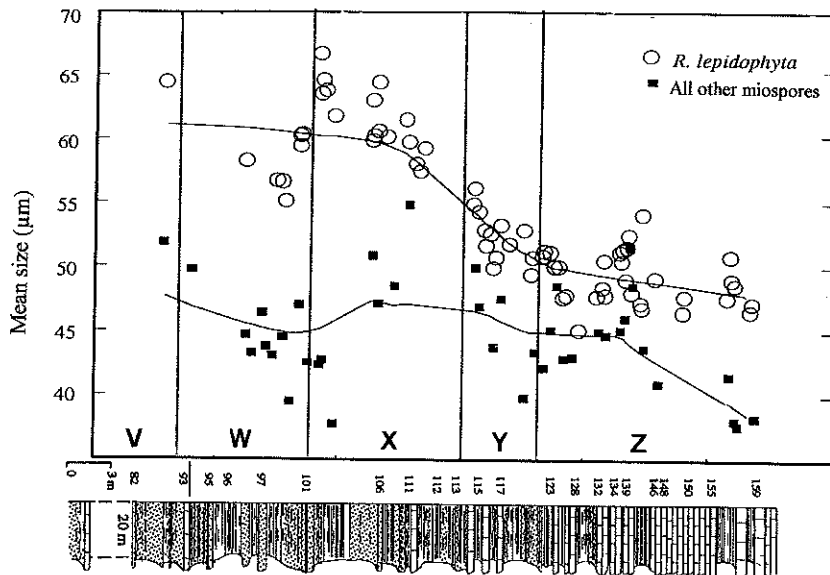


Fig. 5. Comparison between the mean sizes of *Retispora lepidophyta* and of all other miospores at Chanxhe section. In zones V and W, the low size value of all miospores other than *R. lepidophyta* suggests some control, such as a sedimentary sorting effect.

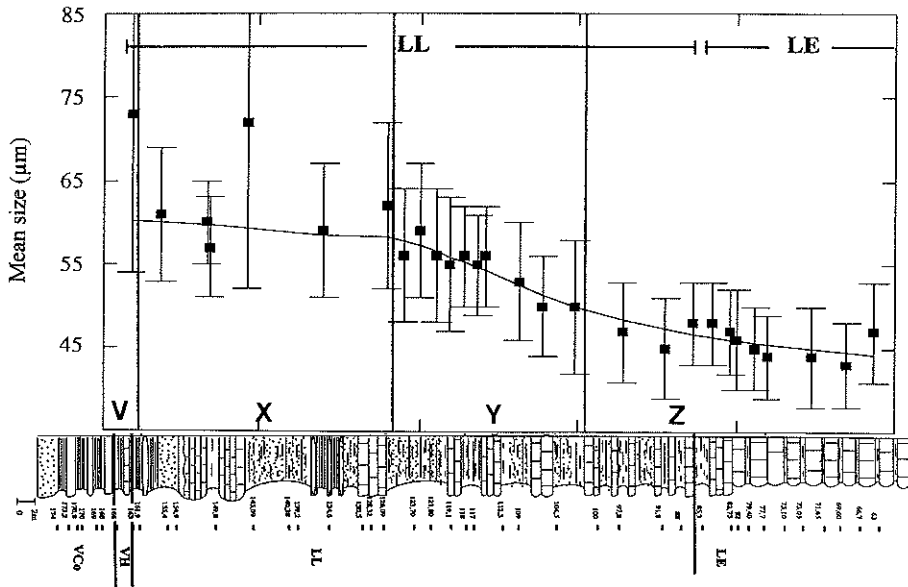


Fig. 6. Mean size and standard deviation of the population of *Retispora lepidophyta* and biometric zones at Tohogne section. Sample depths after Bouckaert and Dusar (1976).

low the associated total miospore size curve. This implies that the sharp size decrease of *R. lepidophyta* in this part of the section is less dependent on sedimentary sorting, a feature also shown by Strel (1969, fig. 1).

2.2. Tohogne

The diameter sizes of a total of 1359 specimens have been measured in 29 samples.

The mean size and their standard deviation of

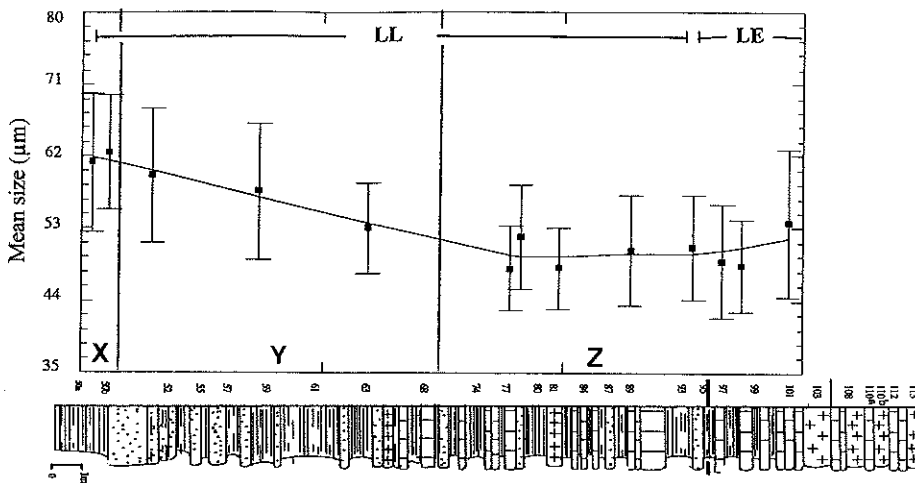
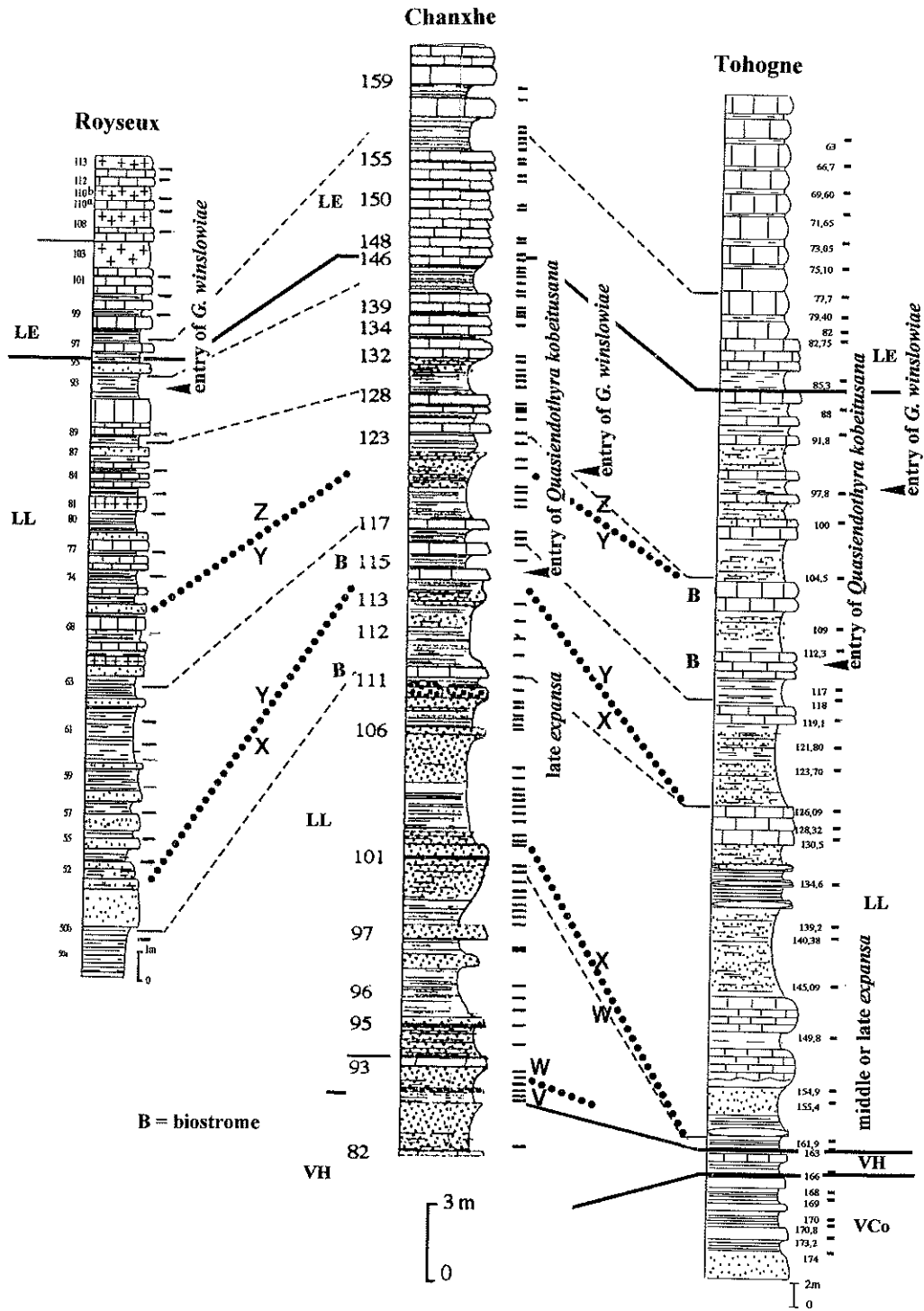


Fig. 7. Mean size and standard deviation of the population of *Retispora lepidophyta* and biometric zones at Royseux section. Bed numbers after Austin et al. (1970).



the *Retispora lepidophyta* populations are shown against the lithological log in Fig. 6.

Zone V: one sample with a high size of 73 μm ;

Zone W is not present;

Zone X: six samples mostly ranging between 72 and 60 μm ;

Zone Y: 10 samples sharply decreasing up section from 60 to 50 μm ;

Zone Z: 11 samples slowly decreasing up section and mostly ranging between 50 and 44 μm .

2.3. Royseux

The diameter sizes of a total of 636 specimens have been measured in 13 samples.

The mean size and their standard deviation of the *Retispora lepidophyta* populations are shown against the lithologic log in Fig. 7.

Zones V and W are not present;

Zone X may be present in part (the two lowest samples, size about 62 μm);

Zone Y: three samples decreasing up section from 60 to 53 μm ;

Zone Z: eight samples mostly ranging between 52 and 48 μm .

2.4. Correlation between the Chanxhe, Tohogne and Royseux sections

Biostratigraphic and biometric zonal correlations between the three sections are shown in Fig. 8. The continuous lines mark the limits between the VCo, VH, LL, and LE Opperl miospore zones (see Section 1). The dotted lines correspond more or less to the limits discussed above for the five biometric zones (V–Z). The almost parallel interrupted lines correlate the histograms with comparable distribution of *Retispora lepidophyta* size values (as shown in Fig. 2). Characteristic acritarchs, conodonts and foraminifers are also given in Fig. 8, thus establishing the best documented biostratigraphic correlation scheme of lat-

est Famennian sections in the Franco–Belgian regions. Of particular significance for international correlation is the near-coincidence of the first occurrence of the foraminifer *Quasiendothyra kobeitusana* (*Q. kobeitusana kobeitusana*) and the change in the population of *R. lepidophyta* from *R. lepidophyta* var. *lepidophyta* to *R. lepidophyta* var. *minor* in the early Y zone (see Fig. 4).

3. Cluster analyses (dendrograms)

Cluster analyses were performed on the percentages of 20 selected miospore taxa (see ‘List of taxa’) that occurred frequently to abundantly in the two most complete sections at Chanxhe and Tohogne. In order to identify any associations between these taxa, the similarity between the percentages of taxa in all samples has been evaluated using parametric statistical methods. According to the central limits theorem, parametric statistical methods are applicable to the database as the sample size is large and the population does not differ greatly from normality (Davis, 1986). The agglomerative method which has been applied to the matrix is the complete linkage or method of the furthest neighbour.

In the hierarchy which resulted from the cluster analysis, the three first levels of division (Fig. 9) discriminate four main groups of taxa, consisting of 11 characteristic taxa which are common to both sections.

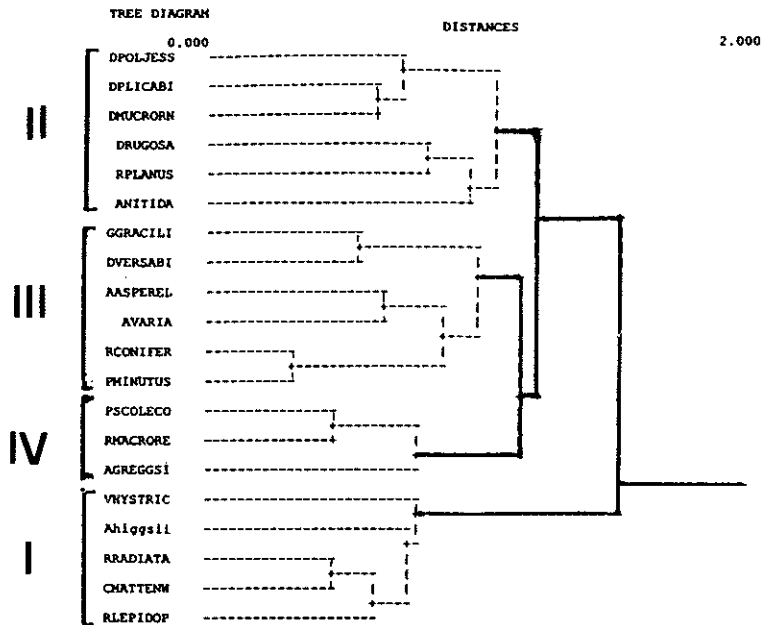
Group I is the most distinctive and compositionally consistent group and is composed in both sections of *Retispora lepidophyta*, *Vallatisporites hystricosus*, *Cristatisporites matthewsii*, *Apiculiretusispora* sp. and *Rugospora radiata*.

The three other groups have fewer taxa in common.

Group II has *Diducites poljessicus*, *Diducites mucronatus* and *Diducites plicabilis* common to both sections;

Fig. 8. Correlation between the sections of Royseux, Chanxhe and Tohogne. Continuous lines: limits between the four Opperl zones (see Section 1). Dotted lines: limits between the five biometric zones. Interrupted lines: correlation between histograms with comparable distribution of size values (see Fig. 2). Conodonts and foraminifers after Streef et al. (1999). Acritarch *Gorgonisphaeridium winslowiae* after Maziane and Vanguetaine (1997) and Maziane (1999).

Chanxhe



Tohogne

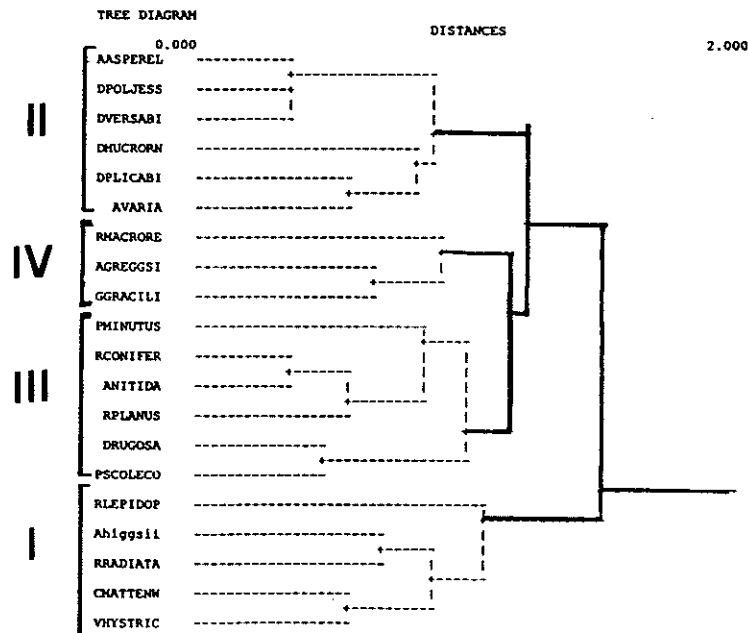


Fig. 9. Hierarchical group resulting from the cluster analyses. Only the three first levels of division are taken into account for delimiting the group. For abbreviations of taxa, see List of taxa.

Group III has *Punctatisporites minutus* and *Apiculiretusispora coniferus* common to both sections;

Group IV has *Retispora macroreticulata* and *Aneurospora greggsii* common to both sections.

In a paleoecological study of late Famennian (pre-*Retispora lepidophyta*) alluvial to nearshore marine facies in the eastern USA and eastern Belgium, Strel and Scheckler (1990) have shown that certain associations of spore taxa can be related to specific environments of production. These are: the *Diducites plicabilis*–*Auroraspora varia* Complex (the *Rhacophyton* isospores) characteristic of downstream or upstream 'coal' swamps; *Vallatisporites hystricosus* and *Auroraspora asperella* (parent plants unknown) characteristic of downstream swamp margins; *Grandispora gracilis* and *Apiculiretusispora coniferus* (parent plants unknown) characteristic of upstream swamp margins, and *Aneurospora greggsii* (probably *Archaeopteris* microspores) characteristic of well drained alluvial plains.

Some species analyzed in the present study are common to, or have close affinity with, the spore associations of Strel and Scheckler (1990). Therefore, we suggest that: (1) group I could correspond to downstream swamp margin environments; (2) group II could be associated with 'coal' swamp environments; (3) group III could be associated with upstream swamp margin environments; and (4) group IV could be associated with well-drained alluvial plain environment.

4. Paleoenvironment of parent plants of miospores from groups I and II and the characteristics of the 'Strunian' transgression in the eastern Dinant Synclinorium

Most of the miospore species belonging to groups I and II (*Retispora lepidophyta*, *Vallatisporites hystricosus*, *Cristatisporites matthewsii* and *Rugospora radiata*; *Diducites poljessicus*, *Diducites mucronatus* and *Diducites plicabilis*) are typical Famennian species which disappear close to the Devonian/Carboniferous limit. This is well illustrated (Higgs et al., 1993) in the Sauerland area in Germany where Strel (1999) noted the coinci-

dence between their extinction and the peak of a global marine regression followed by the onset of a colder climate. Downstream swamps and swamp margins were indirectly but strongly affected by the very rapid sea level drop which lowered the onshore fresh water table and, temporarily, prevented the existence of coastal marshes.

Due to palynologically unfavorable lithofacies, the outcrops of the Ourthe Valley have not revealed the Famennian miospore extinction and the global marine regression. However, the preceding 'Strunian' marine transgression is well documented and provides a good opportunity to test the relation between sea level and coastal swamp development in a highstand context.

A paleogeographic reconstruction of the late Famennian of the eastern Dinant Synclinorium immediately before the 'Strunian' marine transgression (VCo–VH zones time equivalent) has been proposed by Thorez and Dreesen (1986). These authors (1986, p. 314 and fig. 30) have shown that the late Famennian in this area (Fig. 10), which includes the present Hoyoux and Ourthe Valleys, displays the following sedimentary environments: alluvial deposits with red beds (locality of Modave, near Royseux); alluvial deposits (Eviewux, La Gombe, and Chanxhe localities) bordered, in the east, by sublagoonal environments; and tidal environments in the south (Beverire locality and Tohogne borehole).

In the Chanxhe locality (Fig. 11), detailed quantitative data show that *Retispora lepidophyta* and associated miospores (group I) increase in proportion from the lower part to the upper part of the section. At the onset of the latest Famennian or 'Strunian' marine transgression (at the lowermost LL time equivalent or V–W biometric zones), the miospores of group I are poorly represented compared to the other miospores. The miospores of group II, already quite abundant at the end of the late Famennian, are often more abundant than those of group I. From biometric zone X upwards, this latter trend is reversed, group I and proportionally *R. lepidophyta* being more and more abundant, suggesting that the swamp margin vegetation is progressively taking over the 'coal' swamp vegetation. The phenomenon starts when biostromes appear to build

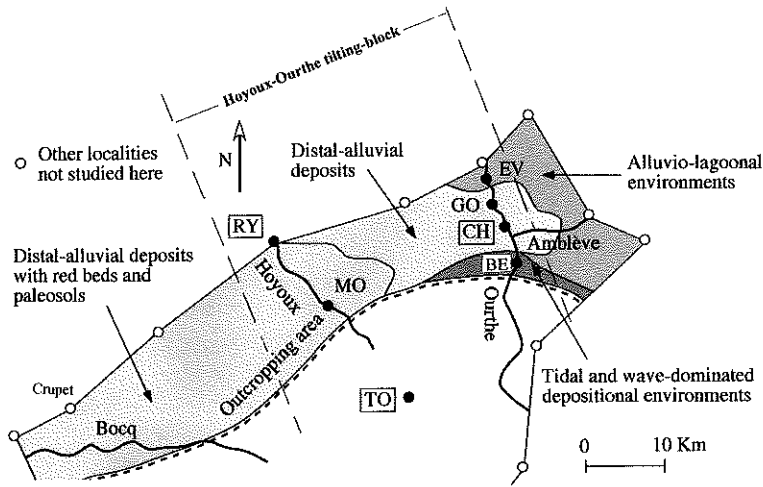


Fig. 10. Late Famennian maximum progradation of the 'Psammites du Condroz' on the north-eastern flank of the Dinant Synclorium, after Thorez and Dreesen (1986). Location of outcrops and borehole after tectonic defolding (palinspastic reconstruction). BE = Beverire, CH = Chanxhe, EV = Evieux, GO = La Gombe, MO = Modave, RY = Royseux, TO = Tohogne.

(slightly earlier in the north than in the south), suggesting that the transgression has reached its maximum level (Maximum Flooding Surface underlining a Highstand Systems Tract after Van Steenwinkel, 1993). Moreover, the phenomenon is not really linear and some cyclicity is ob-

vious, for instance in biometric zone X (two cycles marked 1 and 2 in Fig. 11). These cycles are even more apparent when only *R. lepidophyta* and miospores of group II are compared (Fig. 12).

A comparison of the proportion of *Retispora lepidophyta* versus miospores of group II in the

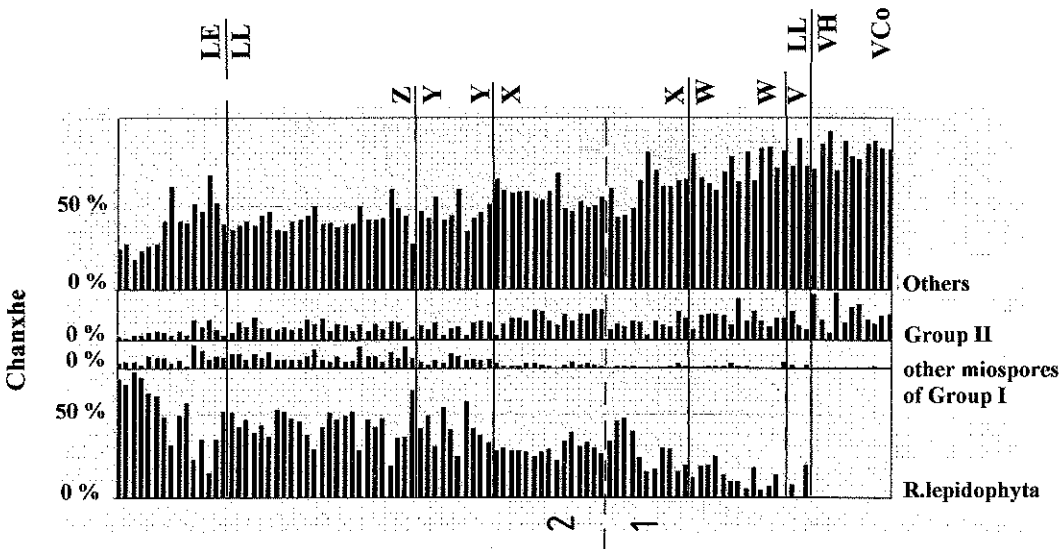


Fig. 11. Relative values of selected miospores at Chanxhe section. *R.lepidophyta*: *Retispora lepidophyta*; other miospores of Group I: other taxa of group I; Group II: taxa of group II; Others: all other taxa.

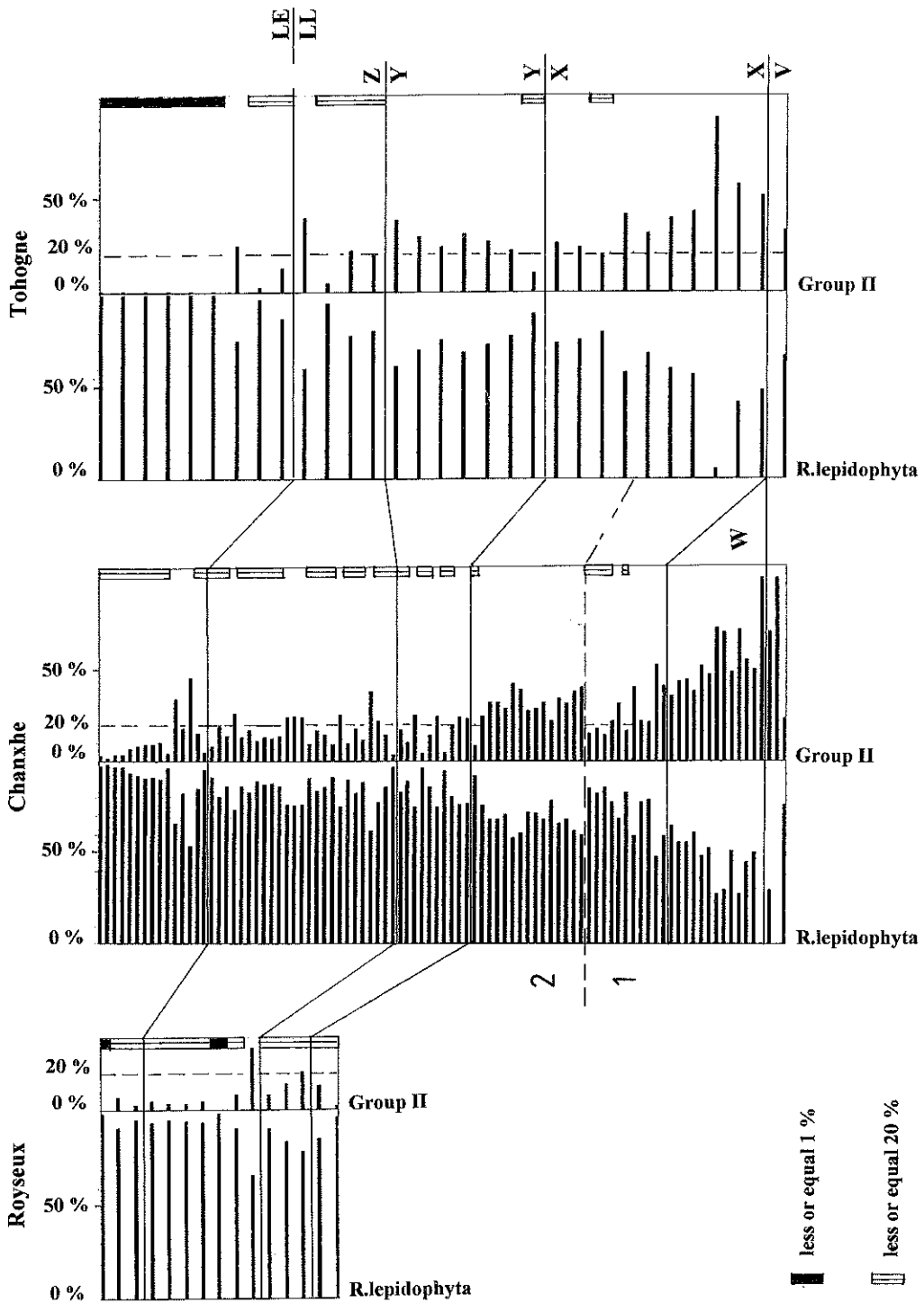


Fig. 12. Relative values of *Retispora lepidophyta* versus taxa of group II at the three sections investigated in the eastern Dinant Synclinorium. Vertical bars indicate intervals with 20% or less miospores belonging to group II.

three sections investigated (Fig. 12) is very instructive, even if the data are less dense in Tohogne and Royseux than in Chanxhe. Taking the 20% miospores of group II versus 80% *R. lepidophyta* as an arbitrary reference limit allows some interesting considerations. Within the biometric zone X limits, 'coal' swamp miospores are more abundant in Tohogne than in Chanxhe during cycle 1 and more abundant in Chanxhe than in Tohogne during cycle 2, suggesting that these cycles are not governed by uniform climatic changes but rather by changing edaphic conditions. This is corroborated by the observation that, in biometric zone Y, the proportion of 'coal' swamp miospores is obviously decreasing from Tohogne to Chanxhe and from Chanxhe to Royseux. In biometric zone Z (the late LL and early LE zones), the 'coal' swamp proportions are almost similar everywhere, suggesting that the edaphic conditions have reached some stability.

Thorez and Dreesen (1986, p. 314) report on "...the influence of an important mechanism which has largely controlled the evolution of the depositional environments. This mechanism is related to synsedimentary tectonic movements, episodically occurring along deep-seated block-faults, which are intermittently and locally reactivated during certain sedimentary phases, in particular in the Dinant Synclinorium.' The area investigated (Fig. 10) belongs to two of these blocks, the 'Crupe Block' in the west and the 'Hoyoux-Ourthe' Block in the east (Thorez and Dreesen (1986, fig. 33). These blocks are delimited by parallel faults with NNW–SSE orientation and the three studied sections belong to the latter. It is tempting to relate the changes in the edaphic conditions described above with tilting movements of this block: a N–S tilt during the biometric zone X, a more E–W-oriented tilt during biometric zone Y and a stability phase during biometric zone Z. The 'Strunian' transgression, in this area, was rather active during its initial phase (eroding sediments at Tohogne in the south, whilst depositing the *Girvanella* shales at Chanxhe in the north, see Section 2.1) and would have soon reached a maximum and then been modulated by local synsedimentary tectonic processes.

5. Conclusion

The biometric study of the size diameter of the stratigraphically important miospore *Retispora lepidophyta* suggests an evolutionary trend of the reduction of size with time, which allows accurate correlations between three late to latest Famennian sections in the eastern Dinant Synclinorium. In addition, cluster analyses (dendrograms), performed on the percentages of a selection of miospore species throughout the same sections, conclude that four distinct groups (I–IV) can be discriminated which are related to specific paleoenvironments by comparison with data from a previous study (Streel and Scheckler, 1990). Amongst these groups, *R. lepidophyta* and a complex of *Diducites* species would respectively represent downstream swamp margin and 'coal' swamp environments. Comparison of the proportion of these latter taxa indicates a significant change in the investigated sections from the abundance of miospores originating from the 'coal' swamp environment in the lower part to the dominance of miospores linked to the downstream swamp margin environment in the upper part of these sections. This change is most likely linked to the onset of the 'Strunian' marine transgression (which allows the development of coastal swamp by rising of the freshwater table). Accurate correlation between the sections using biometric analysis permits detailed characterization of the steps of this transgression in the marine nearshore as well as in the coastal environments. It is also proposed that local synsedimentary tectonic movements are responsible for small changes in edaphic conditions between the investigated localities.

6. List of taxa and code names in Fig. 9

- Apiculiretusispora coniferus* (Kedo) Higgs 1996 (RCONIFER)
- Apiculiretusispora nitida* Owens 1971 (ANITIDA)
- Apiculiretusispora* sp. (Ahiggsii)
- Aneurospora greggsii* (McGregor) Streel, in Becker et al. (1974) (AGREGGSI)

- Auroraspora asperella* (Kedo) Van der Zwan 1980 (AASPEREL)
Auroraspora varia (Naumova) Ahmed 1980 (AVARIA)
Cristatisporites matthewsi Higgs, Clayton and Keegan 1988 (CMATHENW)
Diaphanospora rugosa (Naumova) Byvsheva 1985 (DRUGOSA)
Diducites mucronatus (Kedo) Van Veen 1981 (DMUCRORN)
Diducites plicabilis Van Veen 1981 (DPLICABI)
Diducites poljessicus (Kedo) Van Veen 1981 (DPOLJESS)
Diducites versabilis (Kedo) Van Veen 1981 (DVERSABI)
Grandispora gracilis (Kedo) Streel, in Becker et al. (1974) (GGRACILI)
Plicatispora scolecophora (Neves and Ioannides) Higgs, Clayton and Keegan 1988 (PSCOLECO)
Punctatisporites minutus Kosanke 1950 (PMINUTUS)
Retispora lepidophyta (Kedo) Playford 1976 (RLEPIDOP)
Retispora macroreticulata (Kedo) Byvsheva 1985 (RMACRORE)
Retusotriletes planus Dolby and Neves 1970 (RPLANUS)
Rugospora radiata (Juschko) Byvsheva 1985 (RRADIATA)
Vallatisporites hystricosus Winslow emend Byvsheva 1985 (VHYSTRIC)

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Archaeopteris from the Upper Famennian of Belgium: heterospory, nomenclature, and palaeobiogeography

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Abstract

New fertile specimens of *Archaeopteris roemeriana* from Upper (but not uppermost) Famennian strata of Belgium have been studied. Crowded sporangia are borne on non-laminate, three times bifurcate fertile leaves helically arranged around the fertile ultimate axes. Vegetative leaves occur both proximal and distal to the fertile leaves. Heterospory is demonstrated with miospores belonging to the *Geminospora*–*Aneurospora* complex and macrospores most probably to *Contagisporites* genus. The established morphological traits allow us to substantiate a synonymy between *A. roemeriana* and *A. halliana*. The apparent dominance of *A. halliana* on the eastern side of the Acadian mountains during Late Famennian times is discussed. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Famennian; *Archaeopteris*; spores; synonymy; palaeobiogeography; progymnosperms

1. Introduction

Remains of large leafy branching systems, the so-called penultimate and ultimate branches of *Archaeopteris*, are the predominant element in several Upper (but not uppermost) Famennian plant assemblages in Belgium. These specimens are usually referred to *A. roemeriana* (Goepfert) Lesquereux 1880 despite the fact there is some doubt over the delimitation of this species (Stockmans, 1948; Kenrick and Fairon-Demaret, 1991). In 1941, Kräusel and Weyland put *A. roemeriana* from Europe in synonymy with *A. halliana* from North America on the basis of leaf size, nature of leaf margin, and density and degree

of leaf overlap. Both species share similarities in leaf form and arrangement, as well as degree of leaf overlap and insertion on the penultimate or ultimate axes. Kenrick and Fairon-Demaret (1991), and Fairon-Demaret and Leponce (2001) retained them as separate because the known morphological details are not equivalent for both. The anatomy of *A. halliana* has not yet been described but the morphology of its fertile leaves, arrangement of sporangia, and details of mega- and microspores are known; a reconstruction of a fertile ultimate axis of *A. halliana* has been proposed (Phillips et al., 1972). No comparable morphological information on the fertile parts was available for *A. roemeriana* before this work, but the anatomy of its penultimate and ultimate axes, both vegetative and fertile, had been described (Kenrick and Fairon-Demaret, 1991). Anisophylly on the ultimate vegetative branches has more recently been demonstrated (Fairon-Demaret and Leponce, 2001).

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